INTRODUCTION OF NON-NATIVE OYSTERS:
Ecosystem Effects and Restoration Implications

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■ **Abstract** Oysters have been introduced worldwide to 73 countries, but the eco-
logical consequences of the introductions are not fully understood. Economically,
introduced oysters compose a majority of oyster harvests in many areas. Oysters are
ecosystem engineers that influence many ecological processes, such as maintenance of
biodiversity, population and food web dynamics, and nutrient cycling. Consequently,
both their loss, through interaction of overharvest, habitat degradation, disease, poor
water quality, and detrimental species interactions, and their gain, through introduc-
tions, can cause complex changes in coastal ecosystems. Introductions can greatly
enhance oyster population abundance and production, as well as populations of as-
sociated native species. However, introduced oysters are also vectors for non-native
species, including disease-causing organisms. Thus, substantial population, commu-
nity, and habitat changes have accompanied new oysters. In contrast, ecosystem-level
consequences of oyster introductions, such as impacts on flow patterns, sediment and
nutrient dynamics, and native bioengineering species, are not well understood. Eco-
logical risk assessments for future introductions must emphasize probabilities of es-
tablishment, spread, and impacts on vulnerable species, communities, and ecosystem
properties. Many characteristics of oysters lead to predictions that they would be suc-
cessful, high-impact members of recipient ecosystems. This conclusion leaves open
the discussion of whether such impacts are desirable in terms of restoration of coastal
ecosystems, especially where restoration of native oysters is possible.

INTRODUCTION

Oysters (Family Ostreidae) occupy nearshore marine and estuarine habitats at
temperate to tropical latitudes worldwide. The hundred or so living Ostreidae
species include at least 18 species consumed by humans (Carriker & Gaffney 1996).

Their good flavor and relative accessibility have contributed to the overexploitation of many native populations (Menzel 1991). By the mid-1800s, *Ostrea edulis* in Germany, England, and France had experienced 10- to 30-year boom-and-bust cycles of yield (Mobius 1877). By the late 1800s, reefs of *Crassostrea virginica* in Chesapeake Bay contained low densities of adult oysters and evidence of poor recruitment (Brooks 1891). In western North America, *Ostreola conchaphila* declined severely in yield by two orders of magnitude between 1880 and 1915 (Ruesink et al. 2005). We do not know if oyster populations were overexploited in China, Japan, or Korea because aquaculture began in those countries at least 500 years ago without record of whether it replaced a failed wild-stock fishery (Kusuki 1991).

Oyster fisheries, in which fishers exploit a common resource that is repopulated by natural recruitment, have poor records of sustainability (Kirby 2004). Most native populations of oysters have not been successfully restored after overexploitation, but instead remain at low population abundance for extended periods of time (Grizel & Heral 1991, Utting & Spencer 1992, Rothschild et al. 1994, Drinkwaard 1998, Ruesink et al. 2005). Explanations for failure to recover are myriad and include continued exploitation, habitat degradation through destructive fishing practices, disease, reduced water quality, and detrimental species interactions (Lenihan & Peterson 1998, Lenihan et al. 1999, Jackson et al. 2001). Aquaculture, on the other hand, can provide long-term productivity by allowing growers to "reap what they sow" with seed (newly settled) oysters from hatcheries or wild populations. Sometimes aquaculture is focused on native species, for instance, in East Asia (Kusuki 1991, Nie 1991), New Zealand (Dinamani 1991a), India (Nagabhushanam & Mane 1991), the Caribbean (Baqueiro 1991), and Central (Nascimento 1991) and South America (Velez 1991), and thereby provides a form of conservation. This review documents the worldwide changes in oyster populations during recent history. It focuses primarily on the consequences of introductions intended to replace and augment native species that have declined through overexploitation or other causes.

Decline of these conspicuous members of the nearshore community has been accompanied by economic losses and ecological change. Oysters are ecosystem engineers that provide many ecosystem goods and services. As such, they can have strong ecosystem-level impacts that must be adequately considered prior to their introduction into estuarine, lagoon, and rocky shore coastal ecosystems. Major questions concerning future introductions include the following: Do introduced oyster species provide the same ecological goods and services provided by native species? Can the loss of natural populations be compensated through introductions of new oyster species? What are the potential ecological impacts associated with both purposeful and unintentional introductions?

Oyster Introductions

Oysters have proved highly amenable to aquaculture, and today, exploitation of wild populations contributes little to worldwide oyster production (FAO 2002).

Ecological impacts of aquaculture techniques may be substantial in terms of biodeposits, altered flow regimes, and disturbance of the substrate (Everett et al. 1995); other reports indicate low environmental effects (Buschmann et al. 1996, Crawford et al. 2003). An assessment of aquaculture impacts is beyond the scope of this review. Our focus is on the ecological roles of oysters themselves. Many oyster species have been introduced to new ecosystems through aquaculture. One of the first ecologists to sound an alarm about species introductions, Charles Elton, paid particular attention to oysters among marine species (Elton 1958): "The greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture." Introductions of oysters for aquaculture were already widespread by the 1950s, when Elton's book was published, often to replace ailing populations of native oyster species and sometimes in attempts to develop new exportable commodities.

Rising concern about harmful impacts of non-native species has prompted a substantial literature that evaluates risks of oyster introductions. Of course, ecological concerns must be balanced against human need. Introductions of oysters, and advances in oyster aquaculture, could provide an important source of protein and revenue, particularly in developing countries.

The volume edited by Mann (1979) covers successful introductions in western North America, the United Kingdom, and France, in addition to legislation and risk assessment for eastern North America. Mann et al. (1991) and Gottlieb & Schweighofer (1996) argued strongly for the introduction of new oysters to the eastern United States to replace lost ecosystem functions of *C. virginica* [now at less than 1% of historic densities (NRC 2004)]. Chew (1982) compiled overviews of North American oyster practices, and Menzel (1991) provided a more global perspective. Shatkin et al. (1997) reviewed the consequences of oyster introductions in the western United States, France, Australia, and New Zealand in their risk assessment for the introduction of *Crassostrea gigas* to Maine, and the Maryland Sea Grant (MDSG 1991) and the National Research Council (NRC 2004) presented similar assessments relevant to the possible introduction of *C. gigas* or *Crassostrea ariakensis* to Chesapeake Bay. Finally, 73 oyster introductions are on record in a database maintained by the Food and Agriculture Organization (FAO/FIGIS) and based on published literature and questionnaires (http://www.fao.org/figis/servlet/static?dom=collection&xml=dias.xml).

These reviews provided a launching point for our analyses, but we have pursued a substantially different strategy. Most importantly, we expanded our scope to include all oyster introductions, rather than the four or five examples that have received most attention. Rather than present information as a series of case studies organized by country, we have instead organized by impact and applied data from several different areas to each possible introduction outcome.

In our view, the ecological consequences of oyster introductions have not received sufficient critical scrutiny. This conclusion is the only way we can reconcile the following disparate statements: "Examples of serious alterations of biotic communities by importations of exotic oysters with their associated faunas are found on the maritime coasts of western Europe and western North America" (Andrews

1980) and "With regard to deliberate introduction of mollusks, none has led to significant ecological disruption" (Grizel 1996). Our objectives are to provide a detailed examination of the potential ecosystem impacts of oyster introductions, thereby extending incomplete ecological assessments made by prior reviews (e.g., NRC 2004), and to identify key research priorities. Oyster introductions may, in fact, be highly desirable in terms of the ecological goods and services they can provide. However, as ecosystem engineers, oysters can have disproportionately high impacts, many of which are potentially undesirable (Davis et al. 2000, Shea & Chesson 2002, Cuddington & Hastings 2004). This review addresses the general ecological role of oysters, then focuses on the ecological impacts of introduced oysters, with respect to novel ecosystem impacts. In the final section, we consider implications for restoration of nearshore systems where formerly abundant oysters have declined.

OYSTERS AS ECOSYSTEM ENGINEERS

Understanding the broader ecosystem impacts of oysters and how they vary among species is crucial for assessing the realized and potential ecological impacts of non-native oyster introductions. As ecosystem engineers (Margalef 1968), oysters have major impacts in coastal ecosystems: They create habitat used by other species and modify the physical and chemical environment with major consequences on estuarine populations, communities, and food webs. A critical service provided by oysters is the creation of hard-substrate biogenic reefs that form conspicuous habitat in otherwise large expanses of soft-sediment estuarine and lagoonal seascapes. *Crassostrea virginica* forms more extensive reefs than do other oyster species (e.g., Rothschild et al. 1994). Available evidence suggests that reefs created by *C. gigas* (mostly in the intertidal) and *C. ariakensis* (mostly subtidal) are much smaller in size, occupy less area in estuaries, and are a more heterogenous mix of shell and sediment compared with *C. virginica* reefs (Ruesink et al. 2003; M. Luckenbach, personal communication). Most descriptions of *O. edulis*, *O. conchaphila*, and *Tiostrea chilensis* assemblages emphasize mainly loose accumulations of shell in the subtidal and intertidal (Mobius 1877, Hopkins 1937, Yonge 1960, Miller & Morrison 1988, Chanley & Chanley 1991, Baker 1995).

Large *C. virginica* reefs occupy water depths from the high intertidal to deep subtidal (>5 m depth) in estuaries on the Atlantic Coast of the United States. Before being degraded and reduced in size by destructive harvesting practices, single reefs covered areas more than 1 ha and stood over 3 m tall in many subtidal areas (Rothschild et al. 1994, Lenihan & Peterson 1998). These reefs are habitat for sessile, mobile, and even infaunal invertebrates, such as sponges, bryozoans, hydroids, corals, anemones, tunicates, crabs, shrimp, amphipods, isopods, cumaceans, polychaete, oligochaete, and flat worms (Wells 1961, Bahr & Lanier 1981, Coen et al. 1999b, Meyer & Townsend 2000). On the West Coast of the United States, reefs created by the native *O. conchaphila* and introduced *C. gigas* also harbor many

invertebrate species (Armstrong & Gunderson 1985, Miller & Morrison 1988), as do subtidal reefs in New Zealand created by *T. chilensis*, tunicates, bryozoans, and mussels (Cranfield et al. 1998, 2004). *Crassostrea* spp. and *O. conchaphila* reefs also support other bivalves, including mussels such as *Geukensia* spp. and clams such as *Macoma* spp., *Ensis* spp., *Mya arenaria*, and *Mercenaria mercenaria* (Miller & Morrison 1988, Micheli & Peterson 1999). Invertebrates occupy reefs because they provide refuge from predators and environmental stress, attachment surfaces, and populations of prey (Fernandez et al. 1993, Bartol & Mann 1999, Posey et al. 1999, Dumbauld et al. 2000). Many fishes utilize reefs as recruitment substrate (e.g., gobies, blennies, clingerfish, and oyster toadfish) (Hardy 1978a,b, Breitburg 1999, Lenihan et al. 2001, Grabowski 2004), nursery habitat (e.g., red drum, silver perch, pinfish, pigfish, and flounder) (Lenihan et al. 2001), and foraging ground (weakfish, bluefish, Atlantic croaker, pinfish, striped bass, mummichog, flounder, pigfish, toadfish, silver perch, and pompano) (Harding & Mann 2001a,b, 2003, Lenihan et al. 2001, Carbines et al. 2004).

The contribution of oysters as food for fish and invertebrates varies among species and locations. Bishop & Peterson (2005) found that blue crabs (*Callinectes sapidus*) in North Carolina had higher predation rates on non-native *C. ariakensis* than on native *C. virginica* because the shells of *C. ariakensis* are thinner than the native species, which makes them easier for crabs to crush. Relatively thin shells allow *C. ariakensis* faster growth rates than *C. virginica* (Grabowski et al. 2004). In addition, the physical structure of reef habitat is an important determinant of the foraging efficiency of consumers and other associated bivalves. Predation rates by the mud crab *Panopeus herbstii* are greatest in dense, structurally complex oyster beds because physical complexity likely decreases competitive interference among predators (Grabowski & Powers 2004). Similarly, blue crab predation on *C. virginica* is density-dependent, and foraging efficiency increases linearly with prey density (Eggleston 1990). Thus, variation in the shell morphologies, densities, and reef structural characteristics among different oyster species are important factors in the value of oysters as food resources for estuarine species.

Oyster populations and reef habitat also serve important ecosystem functions that extend beyond reef structures. Reefs influence the flow of water within estuaries and, in doing so, modify patterns of sediment deposition, consolidation, and stabilization (Dame & Patten 1981). Reefs disrupt flow on open bottoms or within tidal channels, and thereby create depositional zones, usually downstream of the reef structure, that accumulate sediment and organic material (Lenihan 1999). The alteration of flow and the physical barrier imposed by reefs influences the distribution and abundance of other biogenic habitats, such as seagrass beds, salt marshes, and algal beds, by preventing the erosion of channel banks, stabilizing and protecting the edges of salt marshes (Coen et al. 1999a), and providing attachment substrate for algae (Everett et al. 1995). Alteration of flow by reefs also influences biotic processes. Deposition of particles is enhanced downstream of reefs because of eddy formation, which thereby enhances settlement of fish (Breitburg et al. 1995) and invertebrate (Lenihan 1999) larvae. Acceleration of flow over reefs and

the associated increase in the delivery rate of suspended food particles increases oyster growth, condition, and survivorship (Lenihan et al. 1995, Lenihan 1999) and influences in complex ways oyster disease dynamics (Lenihan et al. 1999). Enhanced flow probably has similar positive effects on other suspension feeders that inhabit reefs, such as tunicates, sponges, and bivalves.

Oyster populations influence energy flow and geochemical and ecological processes at the spatial scale of estuaries because they can filter large volumes of water through active suspension feeding. Oysters remove particles from the water column during suspension feeding and convert them to benthic sediments (feces and pseudofeces) and production (growth). Filtration rates are generally size related (Powell et al. 1992), and the relatively large size and high densities reached by oysters allow them to influence water properties and nutrient cycling. Research on *C. virginica* indicates that suspension feeding by oysters can reduce local concentrations of suspended solids, carbon, and chlorophyll a but increase ammonia and local deposition of fine-grained sediment and detritus (Dame 1976; Dame et al. 1984, 1986, 1992; Nelson et al. 2004). The removal of particulate matter through suspension feeding increases water clarity, which probably has a positive influence on the growth and abundance of seagrass and other benthic primary producers (Peterson & Heck 1999, Newell 2004, Newell & Koch 2004). Newell (1988) calculated that oyster abundance in Chesapeake Bay before 1870 was high enough that oysters could filter the entire volume of the bay in about 3 days, but after nearly a century of exploitation and habitat destruction, the reduced populations require 325 days to perform the same activity (see also Coen & Luckenbach 2000). Along with increased nutrient loading, loss of massive suspension-feeding capacity in Chesapeake Bay and other systems is thought to have caused shifts from primarily benthic to pelagic primary production, increased blooms of nuisance algae, and shifts in community dominance from macrophytes and nekton to bacteria and jellyfish (Jackson et al. 2001). Different oyster species exhibit significant variation in filtration rates. Filtration rates increase with size and result, for example, in higher filtration rates for larger (frequently cultivated) *Crassostrea* species as compared with the small-sized *Ostreola* species (Powell et al. 1992).

The influences of oyster habitat on associated populations, assemblages, and ecological processes can extend beyond the oyster reefs into adjacent habitats. Spatial configuration of estuarine habitats, such as salt marshes, seagrass beds, and oyster reefs, affects their use by fish and crustaceans, predator-prey interactions within each habitat type, and resulting diversity and structure of resident assemblages (Irlandi & Crawford 1997, Micheli & Peterson 1999). The specific locations, sizes, and relative proximity of introduced oyster reefs to native habitat patches is expected to influence their function as habitat and food for invertebrates and fish and possibly their influences on water quality, sediment erosion rates, and hydrodynamic patterns within estuaries. Thus, the ecological role and the effects of introduced oysters in estuaries and bays are likely to depend on context.

CONSEQUENCES OF OYSTER INTRODUCTIONS

We compiled published records of both introductions and transplantations of oysters on a country-by-country basis (Table 1). In total, we collected 182 records (168 introductions and 14 transplants) of 18 oyster species moved to 73 countries (or smaller regions). Almost all oyster introductions have occurred through oyster aquaculture; however, the introduction of the mangrove oyster (*C. rhizophorae*) from Brazil to the United Kingdom for research purposes and its subsequent eradication provides a notable exception (Spencer 2002).

Oyster introductions probably occurred as early as the seventeeth century, when the so-called Portuguese oyster (*Crassostrea angulata*) arrived in Europe from Asia (Carlton 1999). Overall, oysters have been introduced and established permanently in at least 24 countries outside their native ranges and have been introduced without successful establishment in 55 countries. Status of the remaining introductions is undocumented (Table 1). Most introductions (66) were of *C. gigas*, of which 17 established and 23 did not. *C. gigas* has been imported to most of the temperate zone (and some tropical areas) worldwide (Figure 1). It is one of the most cosmopolitan macroscropic marine invertebrates. Other widely introduced species include *C. virginica* (14 cases), *O. edulis* (11 cases), and *Saccostrea commercialis* (6 cases); these species had slightly lower rates of establishment. France has been the recipient of the most introduced species; eight species were brought in for aquaculture or research in the past 150 years. The United Kingdom, Fiji, Tonga, and the US (West Coast), each received six introductions (Table 1). Only a few instances exist of an oyster arriving in a new location without deliberate introduction. *C. gigas* appeared on the northwest coast of New Zealand through an unknown pathway, potentially hull fouling from Asian boats or larval transport from Australia (Dinamani 1991a), and this species has also spread through the Mediterranean Sea after deliberate introduction to France and Italy (Galil 2000).

Failed introductions of *C. gigas* were the result mostly of transport to locations that are too warm and oligotrophic for survival of the species [Pacific Oceania (Eldredge 1994)] or too cold for successful reproduction (Alaska). For example, on Madeira Island in the subtropical Atlantic, *C. gigas* introduced at about half market size grew in shell dimensions but lost glycogen, and more than 70% died within 5 months (Kaufmann et al. 1994). However, even in "successful" introductions, particularly on western continental shores, spatfall occurs only in restricted locations that retain larvae and exceed critical temperatures (e.g., $18°C$ to $20°C$ for spawning and higher than $16°C$ for larval development in *C. gigas*) for several weeks. So, for instance, natural recruitment in western North America occurs regularly in perhaps only three locations in British Columbia, Canada, and in Hood Canal and Willapa Bay in Washington state (Kincaid 1951, Quayle 1969). The crash in summer 2004 of *C. gigas* populations introduced to France are causing concern that another case of a failed introduction is developing (P. Garcia Meunier, personal communication).

TABLE 1 Oyster introductions from one country (or smaller region) to another country (or smaller region) outside and inside the native range of the species

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
Algeria	*Crassostrea gigas*		<1984		Yes	FAO 2002a, Zibrowius 1992
Argentina	*Crassostrea gigas*	Chile	1982	1987	Yes	Orensanz et al. 2002
Australia (New South Wales)	*Crassostrea gigas*	Australia (Victoria, Tasmania)	1967[a]	1985	Yes	Chew 1990, Pollard & Hutchings 1990, Ayres 1991
Australia (Tasmania)	*Tiostrea chilensis*	New Zealand	1969			Pollard & Hutchings 1990
Australia (Victoria)	*Crassostrea gigas*	Australia (Tasmania)	1955	Yes	Yes	Thomson 1959
Australia (Western Australia, Tasmania)	*Crassostrea gigas*	Japan	1947–1970	Yes	Yes	Thomson 1952, 1959, Chew 1990, Pollard & Hutchings 1990, FAO/FIGIS
Bahamas	*Crassostrea virginica*			No		Glude 1981, Mann 1983
Belgium	*Crassostrea gigas*		1990[a]	Yes		Coutteau et al. 1997, FAO/FIGIS
Belize	*Crassostrea gigas*	United States (USA) (west)	1980			Chew 1990, FAO/FIGIS
Brazil	*Crassostrea gigas*	Chile	<1989	Unlikely	Yes	Nascimento 1991, Tavares 2003

Location	Species	From	Date			References
Canada (east)	*Ostrea edulis*	UK	1957–1959	No		Mann 1983, Chew 1990, Hidu & Lavoie 1991, FAO/FIGIS
Canada (west)	*Crassostrea gigas*	Japan, USA (west)	1912–1977	1925	Yes	Bourne 1979, Chew 1990, FAO/FIGIS
	Crassostrea virginica	USA (east), Canada (east)	1883–1940	1917		Stafford 1913, Bourne 1979, Carlton & Mann 1996
Channel Islands [United Kingdom (UK)]	*Crassostrea gigas*		<1986		Yes	FAO 2002a
Chile	*Crassostrea gigas*	USA (west)	1983		Yes	Chew 1990, Buschmann et al. 1996, FAO/FIGIS
China	*Crassostrea gigas*[c]	Japan	1979			Tan & Tong 1989, FAO/FIGIS
Costa Rica	*Crassostrea gigas*	USA (west)	1979			Mann 1983, Chew 1990, FAO/FIGIS
Croatia	*Crassostrea gigas*		1980[a]		Unlikely	Zibrowius 1992, Galil 2000
Denmark	*Crassostrea gigas*	USA (west), Germany	1980	Yes	Unlikely	Mann 1983, Chew 1990, FAO/FIGIS
	Crassostrea virginica	Canada (east)	1880–1930	No	Unlikely	Carlton & Mann 1996
Ecuador	*Crassostrea gigas*	USA (west), Chile	1980	No	Yes	Chew 1990, FAO/FIGIS

(*Continued*)

TABLE 1 (*Continued*)

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
Fiji	*Crassostrea echinata*	Australia, Tahiti	1910, 1981	No	No	Eldredge 1994
	Crassostrea gigas	Japan, USA (west), Australia, Philippines	1968–1977	Unlikely		Bourne 1979, Eldredge 1994, FAO/FIGIS
	Crassostrea iredalei	Philippines	1975–1976	Unlikely		Eldredge 1994, FAO/FIGIS
	Crassostrea virginica	Hawaii	1970			Eldredge 1994, FAO/FIGIS
	Ostrea edulis	Japan	1977	Unlikely		Eldredge 1994, FAO/FIGIS
	Saccostrea commercialis	USA (west), Australia	1880, 1970–1973	No		Bourne 1979, Eldredge 1994
France	*Crassostrea angulata*	Portugal	1868	Unlikely	No longer	Andrews 1980
	Crassostrea ariakensis	USA (west)		No	No	NRC 2004
	Crassostrea densalamellosa	Korea	1982		Unlikely	Mann 1983
	Crassostrea gigas	Japan, Canada (west)	1966–1977	1975	Yes	Andrews 1980, Mann 1983, Chew 1990, Grizel & Heral 1991, Heral & Deslous-Paoli 1991, FAO/FIGIS

	Crassostrea rhizophorae	French Guyana	1976–1978	Unlikely	Unlikely	Maurin & Gras 1979
	Crassostrea virginica	USA (east)	1861–1875	No	No	Carlton & Mann 1996
	Ostrea puelchana	Argentina	1990			Pascual et al. 1991
	Tiostrea chilensis	Chile	1981			Mann 1983
	Ostrea edulis[c]	USA (west)	1970	No	Unlikely	Chew 1990, FAO/FIGIS
French Polynesia	*Crassostrea echinata*	New Caledonia	1972–1983	Unlikely	Unlikely	Eldredge 1994
	Crassostrea gigas	USA (west)	1972–1976	Unlikely	Unlikely	Eldredge 1994, FAO/FIGIS
Germany	*Crassostrea angulata*		1961	Unlikely		Drinkwaard 1999
	Crassostrea gigas	Scotland	1971	1991	Yes	Gollasch & Rosenthal 1994, Drinkwaard 1999
	Crassostrea virginica	UK	1913	No		Carlton & Mann 1996, Drinkwaard 1999, Wolff & Reise 2002
	Ostrea edulis[c]					Drinkwaard 1999
Greece	*Crassostrea gigas*				Unlikely	Zibrowius 1992
Guam	*Crassostrea echinata*	Palau	1979		Unlikely	Eldredge 1994
	Crassostrea gigas	Taiwan	1975	No	Unlikely	Eldredge 1994, FAO/FIGIS
	Saccostrea cucullata	Solomon Islands	1978		Unlikely	Eldredge 1994

(*Continued*)

TABLE 1   (*Continued*)

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
Ireland	*Crassostrea gigas*	France, UK	<1993		Yes	FAO/FIGIS
	Crassostrea virginica			No	Unlikely	Went 1962, Carlton & Mann 1996
Israel	*Crassostrea gigas*	UK	1976	Unlikely	Yes	Hughes-Games 1977, Chew 1990
	Ostrea edulis	UK	1976			Shpigel 1989
Italy	*Crassostrea angulata*	Portugal	1850		Unlikely	Zibrowius 1992, Galil 2000
	Crassostrea gigas	France	1972	Likely		Galil 2000, FAO/FIGIS
	Saccostrea commercialis	Australia	1985	Likely		Zibrowius 1992, Galil 2000, 2003
Japan	*Crassostrea virginica*	USA	1968			Chiba et al. 1989, FAO/FIGIS
	Ostrea edulis	France	1952			FAO/FIGIS
	Ostreola conchaphila	USA (west)	1948			FAO/FIGIS
	Crassostrea gigas[c]	USA (west)	1980			Chew 1990, FAO/FIGIS
Korea Republic	*Crassostrea gigas*[c]	USA (west)	1980			Chew 1990, FAO/FIGIS
Madeira Island (subtropical Atlantic)	*Crassostrea gigas*	UK	1991	No		Kaufmann et al. 1994
Malaysia	*Crassostrea gigas*	USA (west)	1980			Chew 1990, FAO/FIGIS

Location	Species	Origin	Date			References
Mauritius (Indian Ocean)	*Crassostrea gigas*	USA (west)	1971	Unlikely	Likely	Bourne 1979, Macdonald et al. 2003
	Crassostrea virginica	USA (west)	1972		Likely	Macdonald et al. 2003
	Ostrea edulis	USA (west)	1972		Likely	Macdonald et al. 2003
	Saccostrea commercialis	Australia	1967		Likely	Macdonald et al. 2003
Mexico (east)	*Crassostrea gigas*					FAO 2002a
Mexico (west)	*Crassostrea gigas*	USA (west)	1973	Yes	Yes	Islas 1975, Chew 1990, FAO/FIGIS
	Crassostrea virginica					Carlton & Mann 1996
Morocco	*Crassostrea gigas*	France	<1966		Yes	Shafee & Sabatie 1986, Chew 1990
Myanmar	*Crassostrea gigas*				Unlikely	www.fao.org/documents/show_cdr.asp?url_file=/docrep/004/ad497e/ad497e05.htm
Namibia	*Crassostrea gigas*	Chile	1990	No	Yes	FAO/FIGIS; P. Schneider, personal communication
	Ostrea edulis		1990			FAO/FIGIS
Netherlands	*Crassostrea angulata*	Portugal	1800s			Wolff & Reise 2002
	Crassostrea gigas	Canada (west), Belgium, France, USA (west)	1964–1981	1976	Yes	Chew 1990, Drinkwaard 1999, FAO/FIGIS

(*Continued*)

TABLE 1 (*Continued*)

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
	Crassostrea virginica	USA (east), UK	1939–1940	No	Unlikely	Carlton & Mann 1996, Wolff & Reise 2002
	Crassostrea sikamea		1964			Drinkwaard 1999
	Ostrea edulis[c]	France, Greece, Ireland, Italy, UK, Norway	1963–1977			Drinkwaard 1999
New Caledonia	*Crassostrea echinata*	Tahiti	1979–1980	Unlikely	Unlikely	Eldredge 1994
	Crassostrea gigas	Japan, USA (west), Australia, Tahiti	1967–1977	Unlikely	Yes	Bourne 1979, Eldredge 1994, FAO/FIGIS
	Saccostrea commercialis	Australia	1971	Unlikely	Unlikely	Eldredge 1994
New Hebrides	*Crassostrea gigas*	USA (west)	1972–1973	No		Bourne 1979
New Zealand	*Crassostrea gigas*	Japan or Australia (Victoria, Tasmania)	1958[a]	Yes	Yes	Chew 1990, Pollard & Hutchings 1990, FAO/FIGIS
	Ostrea edulis		1869	No		Cranfield et al. 1998
Norway	*Crassostrea gigas*	USA (west)	1985		Yes	Chew 1990, FAO/FIGIS
Palau	*Crassostrea gigas*	USA (west)	1972–1973	Unlikely		Bourne 1979, Eldredge 1994, FAO/FIGIS

Location	Species	Source	Date			References
Peru	*Crassostrea gigas*		<1997			FAO 2002a
Philippines	*Crassostrea gigas*	Japan			Likely	Juliano et al. 1989, FAO/FIGIS
Portugal	*Crassostrea angulata*			Yes		Andrews 1980
	Crassostrea gigas	France, USA (west)	1977	Likely		Chew 1990, FAO/FIGIS
Puerto Rico	*Crassostrea gigas*	USA (west)	1980	No		Chew 1990, FAO/FIGIS
	Crassostrea virginica[d]			No		Walters & Prinslow 1975, Mann 1983
Russia (Black Sea)	*Crassostrea gigas*		1976	Unlikely		FAO/FIGIS
Samoa	*Crassostrea gigas*	USA (west)	1980			Chew 1990, FAO/FIGIS
Senegal	*Crassostrea gigas*		<2001			FAO 2002a
Serbia and Montenegro	*Crassostrea gigas*				Unlikely	Zibrowius 1992
Seychelles	*Crassostrea gigas*	Japan	1974	Unlikely		FAO/FIGIS
Singapore	*Crassostrea gigas*		2003	Unlikely	Yes	Quek 2004
Slovenia	*Crassostrea gigas*				Unlikely	Zibrowius 1992
South Africa	*Crassostrea gigas*	USA (west), Chile, France, UK	1950	2001	Yes	Chew 1990, Robinson et al. 2005, FAO/FIGIS
	Ostrea edulis		<1992		Yes	FAO 2002a
Spain	*Crassostrea angulata*	France	1980	Yes	Likely	Andrews 1980
	Crassostrea gigas				Yes	FAO/FIGIS

(Continued)

TABLE 1 (*Continued*)

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
Sweden	*Crassostrea gigas*		1980	No	Unlikely	Mann 1983
Tahiti	*Crassostrea gigas*	USA (west)	1972–1976	No		Bourne 1979
	Saccostrea echinata	New Caledonia	1978			Mann 1983
Tanzania	*Saccostrea cucullata*[d]					Macdonald et al. 2003
Tonga	*Crassostrea belcheri*	Malaysia (Sabah)	1977–1978	No	No	Bourne 1979, Eldredge 1994, FAO/FIGIS
	Crassostrea gigas	Japan, Australia (Tasmania)	1975	Unlikely		Bourne 1979, Eldredge 1994, FAO/FIGIS
	Crassostrea iredalei		1976			Eldredge 1994, FAO/FIGIS
	Crassostrea virginica	USA (west)	1973			Eldredge 1994, FAO/FIGIS
	Ostrea edulis	Japan, USA	1975	Unlikely		Eldredge 1994, FAO/FIGIS
	Saccostrea commercialis	New Zealand, USA (west)	1973	Unlikely		Eldredge 1994
Tunisia	*Crassostrea gigas*	France	<1984		Yes	Galil 2000, FAO 2002a
Turkey	*Crassostrea gigas*				Unlikely	Zibrowius 1992
	Saccostrea commercialis		2000[a]			Galil 2003
UK	*Crassostrea angulata*	Portugal		No		Andrews 1980

Location	Species		Date			References
	Crassostrea gigas	Canada (west), USA (west), Hong Kong, Israel	1926, 1965–1979	Dis-agreement	Yes	Walne & Helm 1979, Mann 1983, Chew 1990, Drinkwaard 1999, FAO/FIGIS
	Crassostrea rhizophorae	Brazil	1980	No	No	Utting & Spencer 1992, Mann 1983, FAO/FIGIS
	Crassostrea virginica	Canada (east), USA (east)	1870–1939, 1984	Unlikely		Utting & Spencer 1992, Carlton & Mann 1996, FAO/FIGIS
	Saccostrea cucullata	Israel	1979	No	No	Mann 1983
	Tiostrea chilensis	Chile, New Zealand	1962–1963	Yes		Utting & Spencer 1992, Richardson et al. 1993, FAO/FIGIS
	Ostrea edulis[c]	Norway	1972			Askew 1972
Ukraine (Black Sea)	*Crassostrea gigas*		1976	Unlikely		FAO/FIGIS
U.S. Virgin Islands	*Crassostrea gigas*	USA (west)	1980	Unlikely		Chew 1990, FAO/FIGIS
USA (Alaska)	*Crassostrea gigas*	USA (west)	1980	Unlikely	Yes	Chew 1990, FAO/FIGIS
USA (east)	*Crassostrea ariakensis*	China, USA (west)	<2001	Unlikely		NRC 2004
USA (west)	*Crassostrea gigas*	USA (west)	1930–1990	Unlikely	No	Hickey 1979, Chew 1990, NRC 2004

(*Continued*)

TABLE 1 (*Continued*)

Introduced to	Species	Introduced from	Date	Established (yes/no, date if known)	Current aquaculture?	References
	Ostrea edulis	Netherlands	1949–1961	Likely	Yes	Mann 1983, Chew 1990, Hidu & Lavoie 1991, FAO/FIGIS
	Crassostrea virginica[c]	USA (east), USA (Gulf)	1808–1960			Carlton & Mann 1996
USA (Gulf)	*Crassostrea cortezensis*		1980		No	Mann 1983
	Crassostrea gigas		1930	No	No	NRC 2004
	Crassostrea rhizophorae		1980		No	Mann 1983
USA (Hawaii)	*Crassostrea gigas*	Japan, USA (west)	1926, 1980	1960? (Pearl Harbor)	Yes	Chew 1990, Eldredge 1994, FAO/FIGIS
	Crassostrea sikamea	Japan	1947	No		Woelke 1955
	Crassostrea virginica		1866–1949	1895	Likely	Carlton & Mann 1996

Location	Species	Origin	Date			References
USA (west)	Crassostrea ariakensis	Japan	1977[b]	No	Likely	Perdue & Erickson 1984, Langdon & Robinson 1996
	Crassostrea gigas	Japan, Korea	1902	Likely	Yes	Kincaid 1968, Andrews 1980, Chew 1990, FAO/FIGIS
	Crassostrea sikamea	Japan	1947	No	Yes	Woelke 1955
	Crassostrea virginica	USA (east)	1867–1935	Unlikely	Yes	Andrews 1980, Chew 1990, Carlton & Mann 1996
	Ostrea edulis	USA (east)			Yes	Chew 1990
Vanuatu	Crassostrea gigas	USA (west)	1972	Unlikely		Eldredge 1994, FAO/FIGIS
Yugoslavia	Crassostrea gigas			Unlikely		Zibrowius 1992

[a]Range expansion.

[b]Hitchhiker with other oysters.

[c]Transplantation in native range.

[d]Possible transplantation within native range, but taxonomy uncertain.

Oyster Production

One major consequence of introductions has been a shift in production from native to non-native oysters, largely in places where oysters have successfully established (e.g., *C. gigas* in the western United States, Europe, Australia, New Zealand, and South Africa) but also in places where they have not established and artificial reproduction is practiced (*C. gigas* in Namibia and *C. sikamea* in the western United States). The FAO compiles fishery statistics by species and country worldwide (FAO 2002). We used their recent data (1993–2002) to assess the contributions of non-native and native species to global oyster production (Table 2). These values differ substantially by region. In Asia, most production is based on native *Crassostrea* species [China: *C. plicatula* = *Saccostrea cucullata* (Nie 1991); Japan and Korea: *C. gigas* (Kusuki 1991)]; no records of cultured non-native species have emerged. *C. gigas* also contributes substantially to oyster production outside of Asia where it is not native. *C. gigas* constitutes 95% of European oyster production and 37% of African oyster production. On the western coast of North America, 99.8% of oyster production comes from non-native species, primarily *C. gigas*. However, only 20% of total U.S. production derives from introduced oysters, as much of the production still relies on the native *C. virginica* in Atlantic and Gulf Coast states. In the 26 countries where the FAO reports production from introduced oysters, 48% of production comes from introduced species (Table 2).

In most cases, historical yields of oysters are poorly known, so we cannot compare former productivity, on the basis of native species, with current productivity in which non-native species have replaced native species. However, isolated records do exist. In Willapa Bay, Washington, *C. gigas* yields about four times more shucked meat weight annually than at the peak of native oyster production in the late 1800s (Ruesink et al. 2005). The shift does not reflect an increase in area occupied by oysters (Townsend 1896, Hedgpeth & Obrebski 1981). In France, production of more recently introduced *C. gigas* outpaces the peak in *C. angulata* production by 30% (Goulletquer & Heral 1991, Heral & Deslous-Paoli 1991). Peak yields of the native *O. edulis* occurred more than 150 years ago, and data are not available for comparison. In New Zealand, aquaculture of the native *S. commercialis* yielded 500 metric tons a year until the 1970s (Dinamani 1991a), and its replacement by *C. gigas*, which reportedly grows twice as fast locally (Dinamani 1991a,b, Honkoop et al. 2003), has yielded 5,000 metric tons a year over the past decade (FAO 2002). Intrinsic differences between native and introduced oysters are difficult to distinguish from advances in hatchery techniques, more intensive aquaculture, and increased consumer demand. For comparison, China's oyster production, based exclusively on native species, is reported to have increased by a factor of 180 over the past 20 years (FAO 2002).

Habitat Impacts

Oysters have potentially high impact when introduced into ecosystems because of their influence on habitat quantity and quality (Crooks 2002). Their role as

TABLE 2 Production of native and non-native species of oysters by country

Country and region	Introduced*	Native*	Uncertain*	Introduced/ Total
Africa				
Algeria	5			1.00
Kenya		108		0.00
Mauritius		68		0.00
Morocco	1741	18		0.99
Namibia	310			1.00
Senegal	13	1381		0.01
South Africa	4513	1		1.00
Tunisia	13	9642		0.00
Regional total	6595	11218		0.37
Americas				
Argentina	82			1.00
Brazil	15313			1.00
Canada	55038	55553		0.50
Chile	33822	3355		0.91
Columbia		28		0.00
Cuba		16735		0.00
Dominican Republic		275		0.00
Ecuador	46			1.00
Mexico	16243	374194		0.04
Peru	90			1.00
USA	408831	1679965		0.20
Venezuela		24559		0.00
Regional total	514152	2154664	15313	0.19
Asia				
Australia	43478.5	53595	319	0.45
China		26067607		0.00
China, Hong Kong		4805		0.00
India		82		0.00
Indonesia		14717		0.00
Japan		2206168		0.00
Korea Republic		2049443		0.00
Malaysia			1335	0.00
New Caledonia	554			1.00
New Zealand	54638.5	11044		0.83
Philippines		143244		0.00
Taiwan		224856		0.00
Thailand		196024		0.00
Regional total	98671	30971585	1654	0.00
Europe				
Bosnia and Herzogovina		15		0.00

(*Continued*)

TABLE 2 (*Continued*)

Country and Region	Introduced*	Native*	Uncertain*	Introduced/ Total
Croatia		539		0.00
Channel Islands	2217	4		1.00
Denmark		698		0.00
France	1353313	20793.5		0.98
Germany	806			1.00
Greece		5842		0.00
Ireland	41306	7947		0.84
Italy	302			1.00
Netherlands	21486	1154		0.95
Norway	10.5	54		0.16
Portugal	6390	10.5	457	0.93
Russian Federation		38		0.00
Serbia andMontenegro		6		0.00
Slovenia		9		0.00
Spain	8312.5	30057		0.22
Sweden		27		0.00
United Kingdom	9425.5	7098		0.57
Regional total	1443568.5	74292	457	0.95
World total	2062986.5	33211759	17424	0.06
World total without China, Hong Kong, Japan, Korea and Taiwan	2062986.5	2658880	17424	0.44
Countries (n = 26) that report introduced oysters	2062986.5	2255866	776	0.48

*Numbers reported are shucked weights in metric tons/10 yr.

ecosystem engineers is particularly pronounced in soft-sediment environments, where hard substrate is rare except for shell deposits of oysters. Introduced ecosystem engineers are expected to improve conditions for some species and exclude others. Ideally, experiments would be conducted in which oyster reefs are created or removed, and associated communities are compared with those in unmanipulated areas. Lenihan et al. (2001) used the native oyster *C. virginica* to compare fish and epibenthic invertebrate (blue crab, mud crabs, grass shrimp, and amphipods) assemblages on experimentally constructed reefs with assemblages on soft-sediment bottom in Pamlico Sound, North Carolina. Fish abundance was 325% greater, and epibenthic invertebrate abundance was 213% greater per trap placed on reefs than on the unstructured sand/mud bottom, a finding consistent with observational studies (Kennedy 1996). However, few such manipulative experiments exist for introduced oysters (but see Escapa et al. 2004). Instead, most

studies involve mensurative experiments that compare assemblages on existing habitat types.

Two soft-sediment systems have been examined in detail by use of this mensurative experimental approach. In Willapa Bay, infaunal, epifaunal, and nekton communities have been compared across habitats, including cultured oyster (introduced *C. gigas*) habitats and unstructured tideflat. Consistently, oysters harbor a higher diversity of epifauna (Hosack 2003) and higher densities of mussels, scaleworms, and tube-building amphipods (Dumbauld et al. 2001). Infaunal assemblages were unaffected (Dumbauld et al. 2001), as were small fish and year-old Dungeness crab (*Cancer magister*) (Hosack 2003). Nekton communities differed among regions of the bay, however, which suggests that small fish and crabs species may respond to habitat on scales larger than individual parcels of several hectares (Hosack 2003). Nevertheless, shells of *C. gigas* placed at high density in the intertidal zone provided excellent habitat for newly recruited crab (*C. magister*) in nearby Grays Harbor, Washington: crabs recruited preferentially to shell, and survival of tethered crabs was 70% higher on shell than over open bottom (Fernandez et al. 1993).

In Arcachon Bay, France, both seagrass (*Zostera noltii*) and oyster (*C. gigas*) culture contained higher densities of meiofauna (<0.5 mm) than did nearby sandflats; macrofauna reached highest densities in seagrass (Castel et al. 1989). The authors speculated that biodeposits of oysters provided a food resource for meiofauna, whereas macrofauna associated with oysters were negatively affected by hypoxic conditions. Alternatively, macrofauna could be depressed by effective predators foraging on oysters, in which case oyster habitats might support higher trophic levels (Lenihan et al. 2001, Leguerrier et al. 2004).

Clearly, the provision of hard surface in soft sediments influences many associated species, but few data exist on the rate of conversion of native habitats, such as unvegetated tideflat or eelgrass, into introduced oyster reefs. In many cases, these transitions are mediated by aquaculture practices (Simenstad & Fresh 1995). However, some evidence exists that oyster reefs can reduce eelgrass cover directly. In western Canada, eelgrass (*Zostera marina*) was relatively rare downslope from dense *C. gigas*, and transplanted shoots survived poorly relative to transplants within natural eelgrass beds located away from reefs (J. Kelly, unpublished data).

We found little published evidence of major impacts of introduced oysters on communities located on hard substrate. Natural recruitment of introduced *C. gigas* in British Columbia, Canada, occurs primarily in the rocky intertidal zone (Bourne 1979; J. Ruesink, unpublished data), which entails much less modification of substrate than in cases of reefs forming on soft sediment. In the Strait of Georgia, *C. gigas* are dominant in high (1.3 to 2.4 m) intertidal areas. This area is partially in the barnacle zone, and oysters may actually provide greater surface area for barnacles (Bourne 1979, p. 22). Introduced oysters inhabit a niche that was largely vacant and not dominated by any organism at the time of introduction. A more quantitative analysis has recently been published for Argentina, where *C. gigas*

was introduced in 1982 and now occurs exclusively on rock outcrops (Escapa et al. 2004). Among eight epifaunal species, three occurred at higher densities inside oyster beds, and three occurred at higher densities outside. Shorebirds also spent a disproportionate amount of time associated with oysters, where foraging rate was often higher (Escapa et al. 2004).

Impacts on Species Interactions

Introduced oysters provide a new resource for native predators. Rocky intertidal predators such as seastars and crabs reduced monthly survival rates of *C. gigas*, introduced in western Canada, by 25% relative to caged oysters (J. Ruesink, unpublished data). Indeed, predator control is widely practiced to achieve higher aquaculture yields (see Menzel 1991). Some introduced oysters appear to be an easier resource than native species to handle or consume (Yamada 1993, Richardson et al. 1993), whereas other introduced oysters tend to be avoided (Richardson et al. 1993). In theory, then, introduced oysters may enhance the resource base for higher trophic levels of bivalve predators. Species interactions may also be modified by the shell habitat provided by oysters. In Grays Harbor, higher densities of crabs (*C. magister*) in oyster-shell habitats led to enhanced predation on and lower densities of native clams in these habitats, even though clam recruitment was not directly affected by shell (Iribarne et al. 1995). Grabowski (2004) demonstrated that the structural complexity of native-oyster reef habitat strongly controlled the strength of predation by oyster toadfish (*Opsanus tau*) on resident mud-crab populations (*P. herbstii*).

Competition between native and introduced oysters is expected to be most intense if they share similar habitat. Temperature, salinity, and desiccation are three primary physical factors that determine each species' fundamental niche. In many cases, native and introduced oysters differ in their environmental tolerances, which suggests the potential for few competitive interactions. On the western coast of North America, the native *O. conchaphila* tends to occur at lower depths with less temperature stress than does the introduced *C. gigas* (Stafford 1913). In contrast, in Australia, the native Sydney rock oyster *S. commercialis* actually survives longer out of water than does *C. gigas* (Pollard & Hutchings 1990). This difference in desiccation tolerance has been exploited to control *C. gigas* in places where it has been classified as noxious (e.g., in New South Wales, Australia). When both species settle on common substrate, *C. gigas* can be killed by holding the substrate out of water for sufficiently long time. Several examples exist in which native and introduced species do not overlap in their spatial distributions (Walne & Helm 1979, Andrews 1980).

Despite different habitats of many native and introduced oysters, they often overlap in some part of their range. When overlap occurs, introduced oysters consistently outgrow natives, presumably because higher-yielding species were specifically introduced for that characteristic. *C. gigas* grows five times faster than *O. conchaphila* in western North America (Baker 1995), possibly because of its

higher per-area filtration rate (Galtsoff 1932). In the United Kingdom, *T. chilensis* (introduced from New Zealand) outgrows *C. gigas* (also introduced), which outgrows the native *O. edulis*, at least under some conditions (Askew 1972, Richardson et al. 1993). Ironically, in Chile, where *T. chilensis* is native, the relative growth rates are reversed; introduced *C. gigas* reaches market size "much more rapidly" than the 4 to 5 years required for the native species (Chanley & Chanley 1991). On the East Coast of the United States, *C. gigas* (introduced but not established) outgrows *O. edulis*, which outgrows the native *C. virginica* (Dean 1979). Indeed, *C. gigas* has been selected for worldwide introduction in part because of its rapid growth rate, which yields high biomass for growers.

Direct tests of competition between native and non-native oysters require comparisons of growth and survival in monocultures and mixed cultures, but few examples exist in the literature. In North Carolina, introduced *Crassostrea ariakensis* outgrows native *C. virginica* and introduced *C. gigas*, probably because *C. ariakensis* is better at assimilating food and has lower energy requirements to produce a relatively thin shell (Grabowski et al. 2004). Anecdotally, the arrival of *C. gigas* in New Zealand rapidly reduced native *S. commercialis*. On spat collectors, the ratio of *S. commercialis* to *C. gigas* in 1972 strongly favored the native (1000:1); they were evenly represented in 1977, and by 1978, the non-native outrecruited the native 4:1 (Dinamani 1991c). Whether this recruitment differential emerged from higher fecundity of *C. gigas*, better larval survival, or simply the introduced species' higher individual growth rate (Dinamani 1991c) is not clear.

A historical example in which an introduced species likely outcompeted a native oyster occurred in France after the introduction of *Crassostrea angulata* around 1868. Afterwards, native *O. edulis* began a steady decline until, by 1870, it was completely gone from certain sections of the French coast and fully replaced by *C. angulata*. French government figures on oyster production document this inverse relationship of the species' abundances. By 1925, 300 million *C. angulata* were produced; the figure climbed to 914 million by 1929. In sharp contrast, only 2.4 million *O. edulis* were harvested in 1925 and declined to 668,000 by 1929 (Galtsoff 1932). Mechanistic studies of these oysters' filtration rates by Viallanes (1892) demonstrated that *C. angulata* filtered water 5.5 times faster than did *O. edulis* and, thus, would be a superior competitor for seston resources. Furthermore, Danton (1914) observed that because *C. angulata* grows more quickly, it is superior at pre-empting settlement space. The possibility certainly exists that a disease helped mediate the rapid replacement by *C. angulata* because oyster diseases were not well known at the time. Nonetheless, the competitive advantages of *C. angulata* were pronounced, well documented, and certainly played some if not the central role in its dominance (Ranson 1926).

Competition between oyster species also occurs indirectly through habitat modification. The introduced *C. gigas* in Willapa Bay inhabits both feral oyster reefs and planted aquaculture beds, mostly in the intertidal zone (Kincaid 1951, Feldman et al. 2000). Neither of these habitat types likely provides a functional replacement for the largely subtidal accumulations of shell where the native *O. conchaphila*

previously occurred (Townsend 1896). The native oyster has remained rare, although many observations over the past century suggest it is not recruitment limited (Kincaid 1968). Recent evidence suggests that native-oyster larvae disproportionately settle in areas with large accumulations of shell. Because intertidal *C. gigas* comprises most shell habitat in the bay, the native oysters only have the option of recruiting to zones where immersion times are too short for survival (A. Trimble, unpublished data). Thus, the introduced oyster has developed into a recruitment sink for natives, particularly in the absence of remnant subtidal native-oyster reefs.

Competition may also occur with species other than oysters. *C. gigas* introduced to Argentina recruits on native mussels that normally dominate intertidal rocky shores (Orensanz et al. 2002), and it similarly recruits to mussel beds that occupy tideflats of the Wadden Sea (Reise 1998). Oyster densities in these locations appear to be too low to achieve population-level impacts on mussels, but oysters can kill individual mussels (Reise 1998). In other locations, mussels are probably less vulnerable to novel oysters. On wave-exposed western North American shores, mussels are known to be dominant competitors (Paine 1966), and they reduce growth rates of *C. gigas* by more than 30% (J. Ruesink, unpublished data).

Many prior evaluations of oyster introductions suggest that introduced species had little impact on native populations in part because the native species was already at such low densities (Goulletquer & Heral 1991, NRC 2004). This suggestion begs the question of whether the new species has any impact on the ability of the native species to recover—certainly, competition can occur even when one species is rare. Native oysters have failed to recover in places where new species have been introduced (western North America and Europe), but they have also failed to recover where non-native species are not abundant (eastern North America). These comparisons are confounded by disease—the introduction of an oyster may not in itself prevent recovery, but rather the introduction of a disease carried by that oyster (reviewed by NRC 2004). The role of disease is explored more fully below (see Impacts of Hitchhiking Species).

Ecosystem Impacts

Oysters in high-density aquaculture experience reduced growth rates as their production increases and populations presumably approach carrying capacity (Kincaid 1968, Heral & Deslous-Paoli 1991, Kusuki 1991, Crawford 2003, Robinson et al. 2005). Such density dependence suggests that oysters can reach sufficiently high density, particularly via aquaculture, to reduce food availability to conspecifics as well as other species dependent on suspended particulate food. Filtration by large populations of introduced species (or restored native populations), therefore, has the potential to influence trophic dynamics and water quality (Newell 1988, Ulanowicz & Tuttle 1992, Coen & Luckenbach 2000, NRC 2004). For example, many investigators have hypothesized that overproduction of phytoplankton in Chesapeake Bay, generated by anthropogenic nutrient loading, could be

reduced by increase of biofiltration rates through restoration of native populations of *C. virginica* or the introduction of *C. gigas* and *C. ariakensis* (Tuttle et al. 1987, Newell 1988, NRC 2004). Recent experimental results indicate that transplants of native oysters can significantly increase water quality in small bodies of water, such as tidal creeks (Nelson et al. 2004). Therefore, the probability is high that introductions of oysters that survive at high densities could improve water quality.

Oyster introductions may also enhance estuarine-wide production of other economically valuable species, such as finfish and crabs. Peterson et al. (2003) calculated that over a 20-year to 30-year period, a restored oyster reef could enhance the cumulative amount of fish and large decapod biomass by 38 to 50 kg per 10 m^{-2} of bottom area, discounted for present-day value. This positive effect would occur only where the introduction involved a reef builder and local species of fishes responded positively to that habitat through enhanced recruitment anduse of the substrate as refuge and as foraging ground.

Fecal pellets of suspension feeders on tidal flats tend to be organically rich relative to sediment and to provide sites for nutrient exchange, including nitrification and especially denitrification (Reise 1985). For introduced oysters, in particular, few data on biogeochemical impacts are available, and most come from aquaculture and should be applied tentatively to impacts of naturalized populations. At high densities, *C. gigas* generates biodeposits, which leads to reduced particle size and increased organic content in sediment (Castel et al. 1989), impacts that are avoided at lower oyster densities or higher flow rates (Crawford et al. 2003). The ability of suspension feeders, particularly oysters, to couple pelagic production to the benthos is well accepted (Dame et al. 1984), and researchers also hypothesized that release of inorganic nutrients into the water column by oysters may accelerate phytoplankton productivity (Leguerrier et al. 2004).

Impacts of Hitchhiking Species

The oyster industry has been one of the largest vectors of introduced marine invaders, despite early recognition that movement of oysters could also transport pests of aquaculture (Carlton 1992a,b). Early screening of imported oysters was driven entirely by the desire to prevent incidental importation of oyster pests such as drilling snails (*Urosalpinx cinerea* and *Ocinebrellus inornatus*) (Galtsoff 1932, McMillin & Bonnot 1932). For example, entire contents of infected shipments were often sacrificed to prevent the importation of oyster pest species; however, nonpest exotic species were not considered (Bonnot 1935). Nevertheless, few of the hitchhiker species of concern were ultimately prevented from introduction (Garcia-Meunier et al. 2002, Martel et al. 2004).

To explore the contribution of oyster culture to species invasions, we compiled data from the literature on the number of marine species introduced to nine regions of the world, where expert opinions had been expressed about the vectors of species introductions (Figure 2). A total of 78 established invasive marine algae,
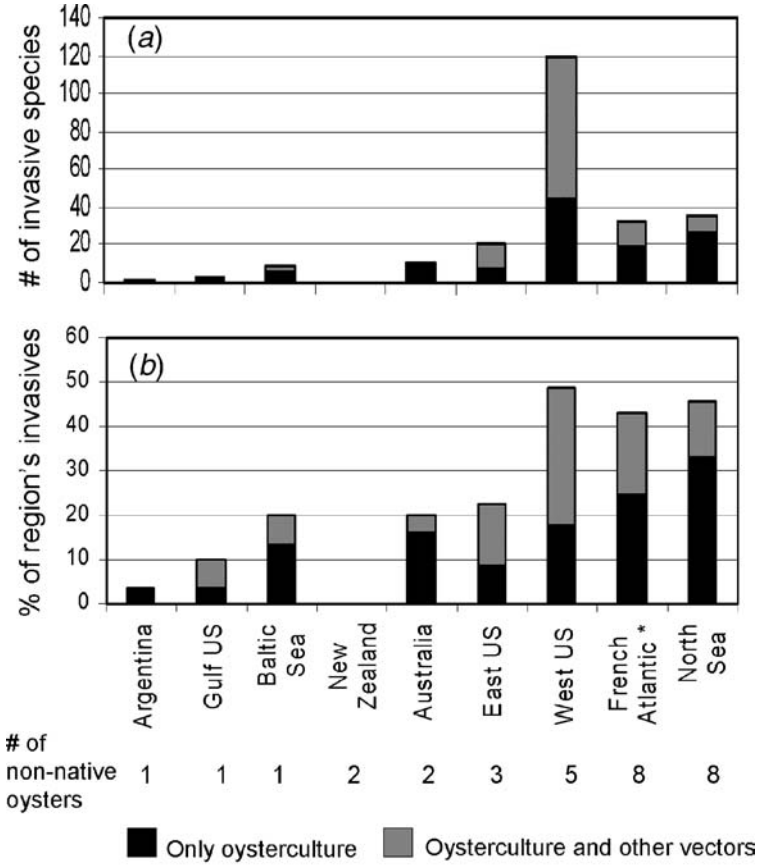
*The French Atlantic refers to the Atlantic and Channel coasts of France, Spain, and Portugal.

Figure 2 The number (*a*) and percentage (*b*) of known introduced species brought into different global regions exclusively through the culturing of oysters (black) or via oyster culture and some other vector such as shipping (gray). Established non-native oysters are included in these data. The regions are ordered by the number of non-native oyster species cultured in that region, from least to most. (Cranfield et al. 1998, Goulletquer et al. 2002, Olenin et al. 1997, Orensanz et al. 2002, Pollard & Hutchings 1990, Reise et al. 1999, Ruiz et al. 2000.)

invertebrates, and protozoa were introduced to the nine regions solely through the culturing of non-native oysters. If we include species with multiple vectors of introduction (oyster imports and some other vector such as shipping), then 46% of the introduced species in northern Europe and 20% in Australia likely entered with oyster aquaculture. The contribution of oyster aquaculture to invasion in coastal

systems of the United States varies by region: 10% on the Gulf Coast, 20% on the East Coast, and 49% on the West Coast. Not unexpectedly, regions where a wider variety of oyster species have been cultured tend to have a greater number (Figure 2*a*) and percentage (Figure 2*b*) of hitchhiking non-native species.

Many of the species brought in with aquaculture present problems for the continued production of oysters in addition to potentially interacting with native species and altering the structure and function of surrounding communities and ecosystems (White et al. 1985, Wilson et al. 1988). Some invasives outcompete and ultimately displace native species. *Batillaria attramentaria*, an Asian snail introduced to the U.S. West Coast with *C. gigas*, outcompetes the mud snail *Cerithidea californica*, which has caused local extinction of the native snail in a number of estuaries (Byers 2000). Other hitchhikers alter the community structure in surrounding areas. In Great Britain, *Crepidula fornicata*, introduced with *C. virginica*, is found in densities greater than 4,000 individuals per m^2 and has positive effects on abundance, biomass, and species richness of the macrozoobenthos (de Montaudouin & Sauriau 1999). In Elkhorn Slough, a central California estuary, 38 of 58 known marine invasives were likely introduced through oyster culture (Wasson et al. 2001). In addition to free-living hitchhikers, parasites of introduced oysters can infest other native species. For example, the shell-boring sabellid polychaete, *Terebrasabella heterouncinata*, introduced with *C. gigas* in California, infested cultured red abalone, *Haliotis rufescens*, with great economic consequences to growers before it was successfully eradicated (Kuris & Culver 1999). Additionally, some hitchhikers provide structural habitats that can host a variety of other species. *Caulacanthus ustulatus*, an Asian turf-forming red alga also introduced with *C. gigas*, forms monospecific stands in the intertidal of Sao Miguel Island, Azores, and Elkhorn Slough, California, that are inhabited by both native and introduced invertebrates (Neto 2000, K. Heiman, unpublished data). With nearly 50% of the species invading some geographic regions attributed, at least in part, to the culturing of oysters (Figure 2), hitchhiking species must factor into assessments of further movement of oysters around the globe.

We have discussed oyster introductions to replace native species and, until now, paid little attention to the role of disease. However, disease is clearly a key factor in understanding both causes and consequences of oyster introductions. Introductions of oyster diseases via imported oysters have caused major ecological changes and economic loss in many estuaries worldwide. Aquaculture of native species may have been able to support high yields, but for high mortality caused by diseases in two high-profile examples: diseases that devastated *O. edulis* in Europe and separate diseases that affect *C. virginica* in North America. These diseases contributed to the decision to introduce *C. gigas* to Europe and to the intense discussion about whether to introduce new oysters to Chesapeake Bay and other eastern U.S. estuaries (Shatkin et al. 1997, MDSG 1991, NRC 2004).

We compiled information on the locations and impacts of 18 oyster diseases. We began with nine taxa recognized by the World Organization for Animal Health and added others reported in published studies (Table 3). Several additional bacterial

TABLE 3 Disease organisms affecting production of cultivated oysters

Disease agent	Disease name	Country	Species infected	Effect	Probable origin	Date	References
Protists							
Bonamia ostreae[a]		United States (USA) (west and east), Europe (e.g., Spain, France)	*O. edulis* (*T. chilensis, O. angasi, C. sikamea*)	70%–80% mortality	USA (east?)	1977, 1979	Chew 1990, Friedman & Perkins 1994, Cochennec et al. 1998, Cigarria 1997
Bonamia sp.		USA (east)	*C. ariakensis* (introduced)	Mortality	Native?	2003	Burreson et al. 2004
Bonamia exitiosa		Australia, Chile, New Zealand	*T. chilensis*	Mortality	Native and introduced?	Periodic (20–30 y)	Hine 1996, Hine et al. 2001
Haplosporidium nelsoni[a]	MSX	USA (west and east)	*C. virginica*	Mortality (S[b]-specific)	Asia	West: 1900s East: 1957	Friedman 1996, Burreson et al. 2000
Haplosporidium costale[a]	SSO	USA (east)	*C. virginica*	Mortality	Native		Sunila et al. 2002
Marteilia refringens		Spain, France, Netherlands	*O. edulis, O. angasi, T. chilensis*	75%–100% mortality (T-specific)	Likely native that spread	1968	Grizel 1979, Berthe et al. 2004
Marteilia sydneyi[a]	QX	Australia	*S. commercialis*	>90% mortality	Likely native that spread	1990s	Nell 2002
Marteilioides chungmuensis		Korean Republic, Japan	*C. gigas*	Reduced fecundity	Native	1990s	Park et al. 2003
Mikrocytos mackini[a]	Denman Island Disease	Canada and USA (west)	*C. gigas, O. conchaphila* (*C. virginica, O. edulis*)	Periodic high mortality (T-specific)	Native	1960	Bower et al. 1997
Mikrocytos roughleyi[a]		Australia, New Zealand	*S. commercialis, T. chilensis, O. angasi*	Mortality (T-specific)	Native?	1926	Nell 2002, Cochennec-Laureau et al. 2003

Organism	Disease	Location	Host	Effect	Origin	Date	Reference
Perkinsus marinus[a]	Dermo	USA (east)	*C. virginica*, (*C. gigas* infected but no losses), *C. ariakensis*	Mortality (T-specific) (S-specific)	Native, but spread	East: 1948 Spread: 1985	Ford 1996, Villalba et al. 2004
Fungus							
Ostracoblabe implexa	Shell disease, maladie du pied	Europe, India, Canada (west, east)	*O. edulis, C. gigas, S. cucullata, C. angulata*	Shell blemish (T-specific)		<1950	Bower 2001
Bacteria							
Proteobacteria	Juvenile oyster disease	USA (east), France	*C. virginica*	Seed mortality (T-specific)	Native in USA	France: 1993	Renault et al. 2002, Paillard et al. 2004
Nocardia crassostreae		USA (west)	*C. gigas, O. edulis*	Heat sensitivity	Asia?	Native: 1945 Introduced: 1956	Friedman et al. 1998, Paillard et al. 2004
Vibrio splendidus		France	*C. gigas* larvae	Summer mortality of spat	Native	1991	Paillard et al. 2004
Viruses							
Iridolike viruses	Virus	France	*C. angulata C. gigas*	Mortality	Asia?	1967	Andrews 1980, Renault & Novoa 2004
Oyster virus velar disease	Virus	USA (west)	*C. gigas*	Larval mortality	Asia?		Elston 1985
Oyster herpesvirus		USA (west), New Zealand, France	*C. gigas, O. edulis* (*C. sikamea* infected but no losses)	Larval, seed mortality (T-specific)	Asia?	1990s	Renault & Novoa 2004

[a]Recognized as one of nine major oyster diseases by the World Organization for Animal Health (OIE), Aquatic Animal Health Code (www.oie.int).

[b]Salinity influence effect.

[c]Temperature influence effect.

and viral diseases not shown in Table 3 occur in larvae. In most cases, the diseases appeared in native oysters, but occasionally, introduced oysters contracted endemic diseases [e.g., *C. ariakensis* affected by *Bonamia* sp. in France and the eastern United States (Cochennec et al. 1998, Burreson et al. 2004)].

Disease theory suggests that pathogens and their hosts evolve toward coexistence, and impacts of native pathogens on native hosts are necessarily low (or the pathogen eliminates its host and goes extinct) (Price 1980). When a new combination of host and pathogen arises, the host may have innate resistance through physiological traits never encountered by the pathogen, or it may be highly susceptible to pathogen attack because selection for resistance has never occurred. Oysters appear to show a pattern similar to many marine species, namely, increased incidence of disease outbreaks and some entirely new (emerging) diseases (Harvell et al. 1999).

Our review of oyster diseases reveals the distressing pattern that oyster introductions or transplants of native species have been a major cause of emerging disease (Table 3). Among the 18 examples, two were definitely associated with introduced oysters (*Bonamia ostreae* and *Haplosporidium nelsoni*), and another five may have been. Three additional disease agents (*Marteilia refringens*, *Marteilia sydneyi*, and *Perkinsus marinus*) were moved via native-oyster transplants, and the pathogens infected naïve subpopulations. *B. ostreae*, a haplosporidian protist that kills three- to four-year-old *O. edulis*, appears to have infected this oyster species when the oyster was introduced to the United States and subsequently infected native-oyster populations when *O. edulis* was transplanted back to Europe (Chew 1990, Wood & Fraser 1996).

Diseases caused by two parasites, *H. nelsoni* (MSX) and *P. marinus* (dermo), are considered major factors in the decline of native *C. virginica* in the eastern United States. Molecular evidence indicated an Asian origin for *H. nelsoni*, which caused high mortality in *C. virginica* in the 1990s [although it was probably introduced with transfers of *C. gigas* much earlier (Burreson et al. 2000)]. In contrast, *P. marinus* probably originated in *C. virginica* along the southwest and Gulf Coast of the United States, but transplants of oysters within the native range spread it to locations where environmental conditions allowed the protist to become much more virulent (Table 1) (Reece et al. 2001). Substantial uncertainty remains in most cases about the origin of disease agents in oysters (Table 3).

CONSERVATION AND RESTORATION

Because oysters are often strong interactors in their native ecosystems, they pose several challenges for conservation. First, they require protection as key species that influence the structure and function of ecosystems. Yet, they are also directly exploited, which partly explains the genuine need for restoration in some places. In the past, oyster productivity has been restored through aquaculture and the introduction of novel species, and these activities can alter the species composition

and ecological processes of coastal ecosystems. Decision makers are, thus, faced with the task of evaluating the costs and benefits of a potential introduction. The NRC (2004) reports an in-depth example of the difficulty of determining the consequences of different introduction decisions, ecologically, economically, and socially, in a book that evaluates the introduction of *C. ariakensis* as a means to recover oyster production in Chesapeake Bay. The approach hinges on ecological risk assessment.

Ecological Risk Assessment for Oyster Introductions

Ecological theory suggests that invasion success is a function of species traits, the recipient environment, the match between the species and the new environment, and effort applied to the introduction (number and size of introductions, often termed propagule pressure). Testing this theory requires data on both successful and failed introductions. Relevant data come from biocontrol releases (Beirne 1975), horticultural plants (Rejmanek & Richardson 1996, Reichard & Hamilton 1997), and imports of birds, mammals, and fishes (Veltman et al. 1996, Blackburn & Duncan 2001, Forsyth et al. 2004, Ruesink 2005). However, answers that emerge from these analyses tend to be idiosyncratic; different factors explain invasion in different taxa and at different scales. Factors also often differ in their predictive value for establishment and impact (Kolar & Lodge 2001).

Emerging ecological risk assessments for introductions embody ecological principles and include reproductive rates, species interactions, and propagule pressure, among others, in their guidelines (Ruesink et al. 1995). One widely accepted protocol for assessment of the risk of marine introductions was developed through the International Council for the Exploration of the Sea (ICES 2003). This protocol emphasizes four points:

1. Probability of colonization and establishment in the area of introduction, which depends on the match between the environment and the species' needs for food, reproduction, and habitat. This section also requires information on resistance to invasion from biotic or abiotic factors in the environment.

2. Probability of spread from the point of introduction, which includes the species' ability to disperse and the extent of suitable environmental conditions.

3. Magnitude of impact on native (especially natural) ecosystems, which includes trophic interactions, habitat transformation, and interactions with native species of concern (threatened or declining).

4. Probability of transport of a harmful pathogen or parasite. This final risk can be mitigated by a variety of methods to inspect and quarantine incoming organisms and release of only their progeny.

The ICES code recognizes two types of risks from introductions, namely, the possible negative impacts of the species itself and the undesirability of bringing in

more hitchhiking species. Methods exist to reduce both of these risks: quarantine to reduce hitchhikers and triploidy to reduce establishment of oysters. The most feared organisms to import with oyster shipments are diseases (versus historical concern about predators) because of potential negative impacts on aquaculture and fisheries. Methods for disease reduction incidentally remove oyster predators and other hitchhikers as well (Barrett 1963, Mann 1983, Utting & Spencer 1992, Spencer 2002, NRC 2004). Non-native oysters are often planted as sterile triploids to prevent escape from cultivation and establishment of self-sustaining populations. However, a small percentage of triploid oysters typically revert toward diploidy with age (Guo & Allen 1994). Even triploid oysters are not completely sterile, although their fecundity relative to diploids is small. Nevertheless, the average triploid female still produces thousands of fertilization-capable eggs every year. A second problem with introductions of triploids is that a small percentage of nontriploids may be inadvertently stocked because of a failure in the screening (Dew et al. 2003).

The ICES (2003) also recommends that the risk assessment generates a hypothesis about the outcome of an introduction, which must be tested through postintroduction monitoring and experiments. We examine the history of introduction of *C. gigas* into western North America as a means of conducting an after-the-fact risk assessment. This species was introduced to Washington state in 1902, and regular imports began about 2 decades later and lasted until the 1970s. Imports of spat were initiated without any risk assessment and before another century of accumulated information on other oyster introductions. What would a risk assessment indicate if the species were only now considered for introduction? Here, we briefly consider each of the four points in the ICES protocol:

1. Because *C. gigas* has successfully established in warm bays on western continental shores (e.g., Europe and South Africa), it also would have a high probability of establishment in western North America. It has successfully colonized both rocky and soft-sediment habitats. However, resistance to invasion would be highly uncertain, because it has not been well studied anywhere.

2. *C. gigas* has planktonic larvae that increase the likelihood of long-distance spread from the point of introduction.

3. Impacts on natural ecosystems seem likely. Established populations in Germany occur at low density (Reise 1998), but high-density populations exist in New Zealand and South Africa (Robinson et al. 2005). Recent work in Argentina indicates community-level changes associated with high-density introduced oysters (up to 250 per m^2) (Escapa et al. 2004). However, the prediction is reasonable that *C. gigas* would occupy a higher tidal elevation than does the native species, *O. conchaphila*, and that, in places where it reached high density, it would transform habitat and increase epifaunal diversity. Thus, it would perform a novel ecosystem role in western North American estuaries. Evidence from other countries suggests that *C. gigas*

could be used to replace the economic production value of the native oyster, but it would not provide a functional replacement.

4. The probability of transporting harmful pathogens or parasites could be reduced by release of second-generation individuals, rather than by direct importation of spat. If this risk assessment had been applied, fewer byproduct introductions would have occurred (Figure 2). The high probability of establishment and uncertain impacts might have prompted greater efforts to protect and restore the native oyster, despite its slower growth and small size for aquaculture.

The ICES protocol can also be used to evaluate the potential ecological consequences of introducing *C. gigas* and *C. ariakensis* as replacement for diminished populations of native *C. virginica* in eastern North America:

1. Both introduced species have a high probability of establishing in bays occupied by *C. virginica*. The introduced species could occupy much of the same areas because of their high tolerance of temperature and salinity variation and because they could colonize remnant reefs created by the native species. However, any oyster introduced into the system will sustain high levels of predation from blue crabs, which will severely limit their recovery or establishment (C.H. Peterson, personal communication). Preliminary results from a multi-million-dollar research project recently initiated by the NOAA-Chesapeake Bay Program indicate that *C. ariakensis* has a thin shell compared with *C. virginica*, so is more vulnerable to crab predation (NRC 2004).

2. Both introduced species have long-lived larvae that would likely invade areas not intended for introduction.

3. Both species would have significant impacts on ecosystem functions. *C. ariakensis* and *C. gigas* filter large volumes of water and, therefore, could replace the biofiltration capacity lost with *C. virginica*, as well as fulfill some of the same functions regarding nutrient cycling. However, neither introduced species creates large subtidal reefs like *C. virginica* does. Therefore, the non-natives would not provide this critical ecological function.

4. Introduction of a harmful pathogen (e.g., *Bonamia* sp., via *C. ariakensis*) is possible.

To summarize, this risk assessment indicates that introductions of the two species into estuaries of the eastern United States are likely to have substantial ecological impacts, that introductions would possibly fail because of deleterious biotic interactions and disease, and that effort at restoration of native species should be increased. Powers et al. (2005), who evaluated the restoration success of 103 *C. virginica* reefs from 12 reef sanctuaries in North Carolina, found that restoration of native oysters has been largely successful from both an ecological and fisheries-productivity standpoint, which highlights the possibility that reintroductions of

native oysters are a better option for ecosystem restoration than introduction of
non-natives.

RESEARCH PRIORITIES

Ecological risk assessments associated with oyster introductions should place
greater emphasis on ecosystem-level effects. Oyster introductions require that
we advance our understanding of the functions and services provided by different
marine species and assemblages. Major gaps in knowledge include how native
and introduced species influence nutrient cycling, hydrodynamics, and sediment
budgets; whether other native species use them as habitat and food; and the spatial
and temporal extent of direct and indirect ecological effects within invaded and
adjacent communities and ecosystems. Lack of information on community-level
and ecosystem-level consequences of oyster introductions is surprising (but see
Escapa et al. 2004), given that these introductions have occurred worldwide for
more than a century. Studies that compare the ecosystem functions and services
provided by native and introduced oysters are important research priorities, and
they provide the framework for recent research projects, such as that supported
by the NOAA-Chespaeake Bay Program to examine *C. ariakensis* and *C. gigas*
introductions. Comparisons between introduced and native species must empha-
size naturalized populations, rather than oysters in aquaculture, although impacts
of aquaculture also warrant examination.

An important area of research is the possible context dependency of the impacts
of oyster introductions. Introduction of the same species could have dramatically
different consequences, depending on local environmental conditions, biological
composition, and additional stressors at different sites. The broad geographic dis-
tribution of introductions of some oyster species, such as *C. gigas*, provides an
opportunity for such spatial comparisons, both within (e.g., among estuaries along
the western coast of the United States) and across regions (e.g., western versus
eastern United States).

Another critical research area is the role of introduced oysters as vectors,
refuges, and resources for other introduced species and diseases (Figure 2,
Table 3). Widespread and unanticipated introductions of nonindigenous species
and novel diseases through oyster introductions raise major concerns about the
ecological and economic consequences of these introductions and call for careful
screening of larvae, juveniles, and adults before introduction. Even introduced reef
habitat could facilitate establishment and persistence of invasives and pathogens.
Facilitation of invaders by species that provide biogenic habitat or other resources
that enhance the recruitment, growth, or survival of the invaders has been proposed
as a mechanism for "invasion meltdowns" in natural ecosystems (Simberloff & von
Holle 1999, Ricciardi 2001). Evidence of invasion facilitation by habitat-creating
invasive species exists for estuarine species, such as the cordgrass *Spartina al-
terniflora* in northern California (Brusati & Grosholz 2005, Neira et al. 2005), the

reef-forming tubeworm *Ficopomatus enigmaticus* in central California (K. Heiman, unpublished data), and the bryozoan *Wateresipora subtorquata* in Queensland, Australia (Floerl et al. 2004). We found no similar evidence for oysters because such research has yet to be conducted.

Considering the large uncertainty about the functional equivalence of different oyster species and possible impacts of oyster introductions on native populations and assemblages (focus of this review), introductions should be considered with caution until further, well-directed, and designed research is conducted. The high potential for unintended consequences of oyster introductions suggests that the deliberate introduction of oysters, although often effective in providing the economic benefits of increased aquaculture production, is unlikely to provide an effective tool for the restoration of ecological functions lost from native oyster decline and habitat degradation.

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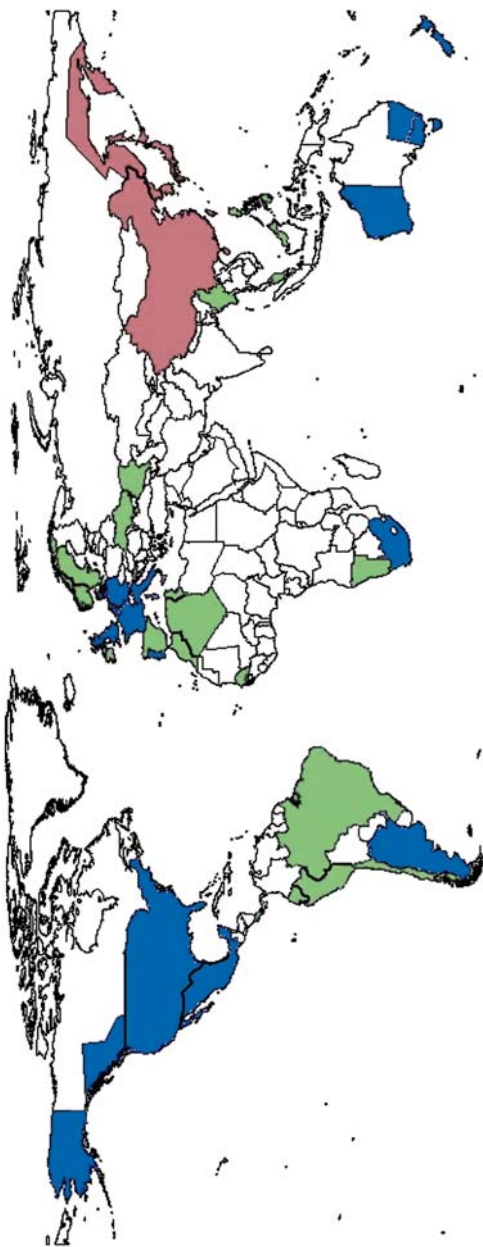
Figure 1 Countries that have received documented introductions of *Crassostrea gigas*. Blue represents countries where *C. Gigas* is known or highly likely to be established; green represents countries where the oyster is not established (in self-sustaining populations) or its status is unknown. Note that the map indicates where introductions have occurred and does not necessarily imply current importations. Also, *C. gigas* was not necessarily planted throughout the whole coastline of marked countries. The map probably underestimates certain areas of distribution where natural spreading or rogue (undocumented) plantings have occurred. The native range of *C. gigas* is colored red. It is worth noting that introductions of *C. gigas* have occurred back to the native range (Table 1), which may influence processes such as gene flow and the introduction of non-native hitchhiking species. Because of their extraordinary size, including coastline that borders several oceans, Canada, Russia, and Australia were broken up into regions/provinces. The United States meets these criteria as well; however, *C. gigas* has been planted along all of its coastlines. The Pacific Northwest is the only area where it is certain that populations of the species have been established (Table 1).

Contents

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