UNIVERSITY OF CALIFORNIA

Los Angeles

Assessing the Importance of Biological Attributes for Invasion Success: Eastern Oyster (*Crassostrea virginica*) Introductions and Associated Molluscan Invasions of Pacific and Atlantic Coastal Systems

A dissertation submitted in partial satisfaction of the requirements for the degree

Doctor of Environmental Science and Engineering

by

Alexander Whitman Miller

2000

SIGNATURE PAGE

The dissertation of Alexander Whitman Miller is approved.

Richard R. Vance

Michael D. Collins

L. Donald Duke

Richard F. Ambrose, Committee Chair

University of California, Los Angeles

2000

DEDICATION

This dissertation is dedicated to my mother, Jessie Barr Miller, who instilled me with an interest in nature and a sense of stewardship, and to my wife, Melissa Hagan, who has always encouraged me to pursue my goals and generously provided support for me to do so.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

LIST OF TABLES

Chapter 2

Chapter 3

Chapter 4

ACKNOWLEDGEMENTS

I would like to give special thanks to my advisor, Richard Ambrose, for his mentoring, insight, and friendship throughout my graduate studies. Gregory Ruiz of the Smithsonian Environmental Research Center provided valuable guidance and critical intellectual input to my research, and generously created an environment in which to pursue it. I would like to thank James Carlton of the Maritime Studies Program of Williams College and Mystic Seaport for his enthusiasm, encouragement, and insight regarding invasion biology. I also wish to thank Paul Fofonoff for stimulating and detailed conversations about natural history and biological invasions. Thanks to my committee members, Richard Vance, Michael Collins, and Donald Duke who each offered essential critiques and suggestions. Thanks to my friends, Karl Klug and Ray Wakeland, for their ready ears and quick wits. Finally, I thank my family. In particular, my father, Frederick M. Miller, who has been a tremendous source of encouragement and humor. F. Hudson Miller and Patricia Kennedy provided a friendly and comfortable haven on many occasions in Los Angeles. I thank my wife, Melissa Hagan, whose grace, caring, and friendship are unparalleled. She offered much needed editorial and graphical expertise and believed in me throughout. Last but not least, I would like to thank my son, Sander, who inspires me through his unmitigated joy of life.

VITA

October 20, 1962	Born, Syracuse, New York
1983-1984	Teaching Assistant Department of Biology Earlham College Richmond, Indiana
1983-1984	Student Research Associate Joseph Moore Museum Earlham College Richmond, Indiana
1984	B. A., Biology Earlham College Richmond, Indiana
1985	Field Research Assistant Hubbard Brook Experimental Forest Department of Biology Dartmouth College Hanover, New Hampshire
1985-1987	Laboratory Technician Department of Biology Boston University Boston, Massachusetts
1988-1990	Data Manager Environmental Chemistry Division Arthur D. Little, Inc. Cambridge, Massachusetts
1990-1992	Staff Research Associate Department of Psychology University of California, Los Angeles
1992-1996	Teaching Assistant Department of Biology University of California, Los Angeles

1993-1997	Staff Research Associate Environmental Science and Engineering Program Department of Environmental Health Sciences University of California, Los Angeles
1995	M. A., Biology University of California, Los Angeles
1997-1998	National Sea Grant Knauss Marine Policy Fellow Office of Senator John Glenn Washington, D. C.
1998-Present	Research Program Coordinator National Ballast Water Information Clearinghouse Marine and Estuarine Invasion Biology Laboratory Smithsonian Environmental Research Center Edgewater, Maryland

PUBLICATIONS AND PRESENTATIONS

Miller, A. W. 1984. Breeding Bird Censuses, American Birds 38:126-127.

Miller, A. W. and D. P. Young 1984. New geographical distribution record for the stinkpot turtle, *Sternotherus odoratus*. Herpetological Review 15(3):77.

Miller, A. W. and D. P. Young 1985. Breeding Bird Censuses, American Birds 39:112.

Cuevas, M. E., A. W. Miller, and G. Callard 1992. Sulfoconjugation of steroids and the vascular pathway of communication in dogfish testis. J. Exp. Zool. 264:119-129.

Miller, A. W. and R. F. Ambrose 1994. Malibu Lagoon Birds. In: Ambrose R. F., I. W. Suffet, and S. S. Que Hee, Enhanced Environmental Monitoring Program at Malibu Creek and Malibu Lagoon, Report to Las Virgenes Municipal Water District.

Miller, A. W. 1997. Senator John Glenn’s floor speech to introduce the Great Lakes Fish and Wildlife Restoration Act of 1997 (S. 659). Congressional Record, Proceedings and Debates of the 105th Congress 143(51):S3735-S3736.

Miller, A. W. and R. F. Ambrose (January 1997). Comparison of sampling design efficiency and effectiveness in rocky intertidal habitats of southern California. Western Society of Naturalists Annual Meeting, La Paz, Baja Mexico.

Miller, A. W. (August 1997). Ecological expertise on the Hill: can ESA make it better? Panel Member. Ecological Society of America Annual Meeting, Albuquerque, New Mexico.

Miller, A. W. (March 1998). The USA National Ballast Water Information Clearinghouse/Ballast research at the Smithsonian Environmental Research Center (SERC). Joint Meeting of the International Council for the Exploration of the Sea/Intergovernmental Oceanographic Commission/International Maritime Organization, The Hague, Netherlands.

Miller, A. W. (April, 1998). Ecological and Economic Impacts of Marine and Estuarine Invasive Species. U.S. Fish and Wildlife Service Forum on Ecological Surveys of Aquatic Nuisance Species, Smithsonian Environmental Research Center, Edgewater, Maryland.

Ruiz, G. M., Miller, A. W., and W. C. Walton 1998. The bi-coastal invasion of North America by the European green crab: impacts and management strategies. Report to the Aquatic Nuisance Species Task Force, 40 p.

Ruiz, G. M., Miller, A. W., Takata, L, and L. Kurzava 1998. The National Ballast Information Clearinghouse: function, design, and implementation, Progress Report I. Report to U.S. Coast Guard and U.S. Congress, 34 p.

Miller, A. W. (January 1999). Measuring ballast water exchange patterns: the National Ballast Survey (NABS). National Conference on Marine Bioinvasions, MIT Sea Grant College Program, Massachusetts Institute of Technology, Cambridge, Massachusetts.

Miller, A. W. (October 1999). Nonindigenous species in the Gulf of Mexico and in Ballast Water. Workshop on Invasive Species and Ballast Water Management in the Gulf of Mexico Region. Gulf of Mexico Program and Louisiana Sea Grant College, New Orleans, Louisiana.

Miller, A. W. (December 1999). Progress Report on the National Ballast Information Clearinghouse. Aquatic Nuisance Species Task Force Meeting, Arlington, Virginia.

Miller, A. W. (May 2000). Marine invasion biology research at the Smithsonian Environmental Research Center. Center for Marine Conservation Workshop, Virginia Beach, Virginia.

Miller, A. W. (June 2000). Living among oysters - the commercial oyster industry as a vector for molluscan introductions: a retrospective analysis of invasion success and failure. Annual Meeting of the American Society of Limnology and Oceanography, Copenhagen, Denmark.

Miller, A. W. and R. F. Ambrose 2000. Sampling patchy distributions: comparison of sampling designs in rocky intertidal habitats. Marine Ecology Progress Series 196:1-14.

Miller, A. W., G. M. Ruiz, Takata, L., Steves, B., and A. H. Hines 2000. Measuring ballast water delivery and management patterns in the United States: the National Ballast Water Information Clearinghouse and National Ballast Survey. Proceedings of the National Conference on Marine Bioinvasions. MIT Press, Cambridge (in press).

Fofonoff, P. W., Ruiz, G. M., Miller, A. W., Steves, B., and J. T. Carlton 2000. Comparison of invasion patterns between the Northeastern Atlantic Coast estuaries and the Great Lakes of North America. Canadian Journal of Fisheries and Aquatic Sciences (in press).

Ruiz, G. M., Miller, A. W., Everett, R. A., Steves, B., Lion, K., Whitcraft, C., Arnwine, A., Collinetti, E., Sigala, M., and D. Lipski 2000. National Ballast Water Information Clearinghouse interim report to the U. S. Coast Guard. Results from the first year of data management and analysis: Shipping industry compliance with mandatory ballast water reporting requirements / shipping industry compliance with voluntary ballast water management guidelines, 30 p.

ABSTRACT OF THE DISSERTATION

Assessing the Importance of Biological Attributes for Invasion Success:
Eastern Oyster (*Crassostrea virginica*) Introductions and Associated Molluscan Invasions
of Pacific and Atlantic Coastal Systems

by

Alexander Whitman Miller
Doctor of Environmental Science and Engineering
University of California, Los Angeles, 2000
Professor Richard F. Ambrose, Chair

Despite a growing body of evidence indicating that biological invasions are increasing, there are very few studies that treat biological invaders themselves or the process of invasion quantitatively. Without such studies, it is impossible to fully understand which biological factors are crucial to the success of invasions. This dissertation employs a retrospective analysis of past marine invasions in an attempt to quantitatively describe how biological invaders differ from non-invaders. The importance of the commercial oyster industry as a vector for conveyance of eastern oysters (*Crassostrea virginica*) and their molluscan associates lies at the center of this research. The discrete spatial and temporal aspects of this vector, in conjunction with the rich history of marine biological investigation from the mid-Atlantic and New England coasts, made this study possible.

The foundation of the present analyses was the compilation of a species pool of potential molluscan invaders. To qualify for inclusion in the species pool, a species had to meet the following two criteria. First, the mollusk had to occur in the waters where eastern oysters were normally harvested for live export to San Francisco Bay or Northwest Europe. Second, all mollusks included were either natural biological associates of eastern oysters or had the opportunity to colonize eastern oysters during packing and shipment (e.g., nestling among oysters during freshening or intertidal storage). The final species pool contained 93 shelled mollusks, 42 bivalves and 51 gastropods.

Discriminant analyses simultaneously compared successful and failed molluscan invaders of San Francisco Bay across 18 ecological, biogeographical, and biological species characteristics. Results indicated significant differences with respect to two attributes: 1) historical species abundance in the source region (propagule pressure) and 2) tolerance of low salinity concentrations. These findings suggest that some mollusks have inherent attributes that render them better invaders than other mollusks. However, comparisons at coastal scales indicate that invasions by the same species proceed differently in different geographic locations. This research indicates that quantitative approaches to invasion biology are possible and can yield information that may be useful for identifying potential invaders.

CHAPTER 1

INTRODUCTION

Biological invasions are a growing problem in the United States and other countries (Soulé 1990, Ruiz et al. 1997, Cohen and Carlton 1998, Mack et al. 2000). Biological invasions can happen through natural dispersion and range expansion, as have occurred for millions of years throughout evolutionary time. Invasions can also take place on ecological time scales when anthropogenic forces breach natural biogeographic barriers (e.g., oceans, mountain ranges, and deserts) (Carlton 1987). During the post-Columbian age, the extent of human-mediated transport of biological organisms outside their native ranges has burgeoned. In fact, the magnitude of species movement in the last 500 years, intentional or otherwise, is unequaled during any single five hundred-year period throughout the history of the earth (Mack et al. 2000).

Nonindigenous species have the potential to alter native ecosystems and biological communities (OTA 1993, Mooney and Drake 1986, Carlton 1996a, Carlton 1999, Mack, et al. 2000). Changes to natural systems may include changes to native biodiversity; alteration of food web patterns; and the destruction of physical and biological components of natural habitats (Carlton 1999, Grosholz et al. 2000). Following habitat destruction, the greatest threat to natural biodiversity is from introduced species (Wilcove et al. 1998). Economic and public health impacts can also result from nonindigenous species entering a new region. These impacts may include the degradation of physical infrastructure (e.g., clogging water pipes or destroying wooden pilings), damage to agricultural production, and reduced yield from fisheries and aquaculture, as well as costs for quarantine, eradication, and control. Cost estimates for such impacts in the United States alone are $137 billion per year (Pimentel et al. 2000). New introductions of disease-producing pathogens pose threats to human populations as well (Ruiz et al. 2000b).

Threats posed by nonindigenous species have received the attention of lawmakers in Washington, D.C. Legislative efforts to address the impacts of invasive species were stepped up in the 1990s. The Non-indigenous Aquatic Species Prevention and Control Act of 1992 (amended and reauthorized as the National Invasive Species Act of 1996) are both federal laws directed at the prevention and management of the spread of nonindigenous species. In February 1999, in recognition of the threats posed by nonindigenous species, President Clinton signed an Executive Order to further prevent, control, and minimize their impacts (Executive Order on Invasive Species, #13112). The Executive Order calls for the formation of an interagency Invasive Species Council that includes the Departments of State, Treasury, Defense, Interior, Agriculture, Commerce, Transportation, and the Environmental Protection Agency. The purpose of the initiative is to develop a national strategy to expand understanding of nonindigenous species so that effective measures can be taken to lessen ecological, economic, and public health consequences.

While invasions of terrestrial habitats have been recognized for many decades, marine and estuarine invasions have gone virtually unnoticed until relatively recently (Elton 1958, Carlton 1989). Scientists have devoted much energy to understanding the adverse effects of weeds and other terrestrial nonindigenous species (OTA 1993), but comparatively few marine and estuarine invaders have been studied well enough to understand their effects on receiving ecosystems. To date, very few studies of invasion biology, terrestrial or aquatic, have employed quantitative techniques to explore the process of invasion. Most investigations are simply presence/absence lists of nonindigenous species. As such, little is known about the biological characteristics of invaders and whether such characteristics are common across taxonomic categories. Understanding such fundamental aspects of invasion and invaders can only be accomplished by the systematic application of quantitative approaches. This dissertation uses quantitative techniques to differentiate successful and failed invaders in the marine environment.

A complicating factor to the study of invasions in marine systems is that much of the global transport of marine species by shipping and commercial fisheries predates the earliest biological surveys of marine and estuarine habitats. Many marine ecosystems once considered pristine have actually harbored nonindigenous species for decades or centuries (Carlton 1989). This situation poses a serious dilemma for biologists and biogeographers since it is sometimes impossible to say with certainty whether a species is native or introduced (Carlton 1996c). Carlton (1999) indicates that as many as one thousand near-shore marine species now considered native are likely introduced species.

The significance is that some of these invaders now dominate ecosystems, having changed the original co-evolved community structure and function without detection by humans. While this loss of biodiversity and ecosystem integrity is now impossible to retrieve, and therefore easily dismissed, overlooking such loss underestimates the historical importance of introduced species as agents of environmental change (Carlton 1996a).

The rate of marine/estuarine invasions is increasing (OTA 1993, Ruesink et al. 1995, Carlton 1996b, Cohen and Carlton 1998, Ruiz et al. 2000a). Higher rates of invasion are believed to be the result of increased rates of introduction by humans as intercontinental trade and travel markets have grown (Jenkins, 1996, Cohen and Carlton 1996). Advancements in transportation technology have shortened travel times and increased traffic between continents, resulting in greater dispersal of nonindigenous species around the world. Currently, the commercial shipping industry is perhaps the most important vector by which marine and estuarine organisms are transported around the globe (Carlton and Geller 1993). Organisms can be entrained while ballast water is pumped into ships, residing either in the ballast water or sediments of ballast tanks, or attaching to ships as fouling organisms on hulls and anchor chains (Carlton 1985, CBC 1995, NRC 1996, Ruiz et al. 2000a). Historically, hull fouling of wooden vessels and dry ballast introductions were dominant modes of intra and inter-oceanic transport of marine species (Carlton and Hodder 1995).

Other dispersal vectors have also played important roles in the spread of marine and estuarine species (Ruiz et al. 1997). These include: 1) engineered canal systems that have connected geologically and evolutionarily separated bodies of water; 2) intentional and accidental releases associated with pet and aquarium trades; 3) intentional and accidental scientific releases; 4) intentional and accidental releases associated with aquaculture and fisheries activities. Of these vectors, the last may be the most important. A particularly good example of this is the introduction of oysters to regions outside their native ranges.

More important than the oysters themselves are the accidental introductions of large numbers of other species that naturally associate with oysters (Carlton 1979, Carlton 1993, Carlton and Mann 1996). The commercial oyster industry has been responsible for the introduction of many oyster-associated fauna (Elton 1958, Carlton 1979). This dissertation focuses on the large scale movements of eastern oysters, *Crassostrea virginica* and their molluscan associates from the western Atlantic Ocean to coastal systems of the northeast Pacific and northeast Atlantic Oceans. This research uses a retrospective analysis to explore: 1) the differential invasion success and failure of molluscan oyster associates and 2) multiple invasions by the same species in geographically disparate locations.

The intentional introduction of the eastern oyster (*Crassostrea virginica*) to estuaries outside its native western Atlantic region provides an excellent opportunity to examine an important, yet spatially and temporally discrete transport vector. Because of the commercial importance of oyster fisheries, the history of oyster transfers and introductions has been well documented. By combining this history with the extensive ecological information available for the mid-Atlantic and New England coastal systems, a list of mollusks that occur naturally with oysters was generated. Since little effort was ever made to extensively clear oysters of their epibiota before shipment, any of these mollusks (and many other invertebrates) could have been moved with the millions of tons of live oysters that were transported during the 19th and early 20th centuries. This list of oyster associates represents a species pool composed of successful and failed invaders. Quantitative comparisons of these subgroups are carried out to determine if invasion success can be statistically linked to biological and biogeographic characteristics, an area of fundamental importance to the study of marine invasion biology (Vermeij 1996, Carlton 1996b).

The contemporaneous introductions of eastern oysters to the eastern Pacific and eastern Atlantic also provide an excellent opportunity to investigate how organisms originating in the same donor region (i.e., western Atlantic) respond in two widely separated regions. This invasion pathway permits the same pool of potential invaders to be compared in two independent systems according to their invasion success/failure and in terms of their geographic patterns of invasion within each location.

This dissertation is divided into five chapters. This chapter, Chapter 1, provides a brief introduction to marine invasions and briefly describes the research undertaken. Chapter 2 is a historical review of the commercial oyster industry of the United States in the 19th and early 20th centuries, the time period when the greatest number of oysters was moved. The practice of oyster fishing and live oyster transport is described and the significance of this industry as a vector for the dispersal of marine organisms is explored. Chapter 3 investigates whether successful invaders can be separated statistically from failed invaders using Monte-Carlo simulations, contingency tests, and discriminant analyses applied to biological and biogeographic attributes of western Atlantic molluscan oyster-associates. Chapter 4 compares the invasion patterns of five mollusk species that originated in the western Atlantic and successfully invaded both eastern Pacific and eastern Atlantic coastal systems. Patterns are described according to their geographic extent and incidence of invasion (i.e., frequency within the invaded range). Chapter 5 provides conclusions and recommendations for future research and management of marine invasions.

LITERATURE CITED

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation. University of California, Davis. 904 p.

Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. Oceanography and Marine Biology: An Annual Review 23:313-371.

Carlton, J. T. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bulletin of Marine Science 41:452-465.

Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conservation Biology 3:265-273.

Carlton, J. T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research 11: 489-505.

Carlton, J. T. 1996a. Marine bioinvasions: the alteration of marine ecosystems by nonindigenous species. Oceanography 9:36-43.

Carlton, J. T. 1996b. Pattern, process, and prediction in marine invasion ecology. Biological Conservation. 78:97-106.

Carlton, J. T. 1996c. Biological invasions and cryptogenic species. Ecology 77:1653-1655.

Carlton, J. T. 1999. The scale and ecological consequences of biological invasions of the World's oceans. In: (eds. O. T. Sandlund, P. J. Shei and Å. Viken) Invasive species and biodiversity management. Based on a selection of papers presented at the Norway/UN Conference on Alien Species, Trondheim, Norway. Kluwer Academic Publisher, Dordrech, 444 p.

Carlton, J. T. and J. B. Geller 1993. Ecological roulette: Biological invasions and the global transport of nonindigenous marine organisms. Science 261:78-82.

Carlton, J. T. and J. Hodder 1995. Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. Marine Biology 121:721-730.

Carlton, J. T. and R. Mann 1996. Transfers and world-wide introductions. In: V. S. Kennedy, R. E. I. Newell, and A. F. Eble (eds.), The eastern oyster, *Crassostrea virginica*, p 691-706. Maryland Sea Grant Program, College Park.

CBC (Chesapeake Bay Commission) 1995. Introduction of nonindigenous species to the Chesapeake Bay via ballast water: Strategies to decrease the risks of future introductions through ballast exchange. Chesapeake Bay Commission Report, Annapolis, MD.

Cohen, A. N. and J. T Carlton 1996. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasion of San Francisco Bay and delta. Report to U.S. Fish and Wildlife Service, Washington, D.C. and National Sea Grant College Program, Connecticut Sea Grant. 246 p.

Cohen, A. N. and J.T Carlton 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555-558.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, England.

Grosholz, E. D., Ruiz, G. M., Dean, C. A., Shirley, K. A., Maron, J. L., and P. G. Connors 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206-1224.

Jenkins, P. T. 1996. Free trade and exotic species introductions. Conservation Biology 10:300-302.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and F. A. Bazzaz 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689-710.

Mooney, H. A. and J. A. Drake 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

NRC (National Research Council) 1996. Stemming the tide: controlling introductions of nonindigenous species by ships' ballast water / Committee on Ship's Ballast Operations, Marine Board, Commission on Engineering and Technical Systems. National Academy Press, Washington, D. C., 154 p.

OTA (Office of Technology and Assessment) 1993. Harmful nonindigenous species in the United States. U.S. Government Printing Office. Washington, D.C. OTA-F-565.

Pimentel, D., Lach, L., Zuniga, R., and D. Morrrison 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53-65.

Ruesink, J. L., Parker, I. M., Groom, M. J., and P. M. Kareiva 1995. Reducing the risks of nonindigenous species introductions: guilty until proven innocent. BioScience 45:465-477.

Ruiz, G. M., Carlton, J. T., Hines, A. H., and E. D. Grosholz 1997. Global invasions of marine and estuarine habitats by nonindigenous species: mechanisms, extent, and consequences. Amer. Zool. 37:621-632.

Ruiz, G. M., Fofonoff, P., Carlton, J. T., Wonham, M. J., and A. H. Hines 2000a. Invasions of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics (in press).

Ruiz, G. M., Rawlings, T. K., Dobbs, F. C., Drake, L. A., Mullady, T., Huq, A., and R. R. Colwell 2000b. Worldwide transfer of microorganisms by ships. Nature 408:49-50.

Soulé, M.E. 1990. The onslaught of alien species, and other challenges in the coming decades. Conservation Biology 4:233-239.

Vermeij, G. J. 1996. An agenda for invasion biology. Biological Conservation 26:3-9.

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., and E. Losos 1998. Quantifying threats to imperiled species in the United States. Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. BioScience 48:607-615.

CHAPTER 2

Historical Review of the Eastern Oyster (*Crassostrea virginica*) Fishery in the United States as a Vector for Accidental Transport of Associated Mollusks

‘O Oysters come and walk with us!’
The Walrus did beseech.
‘A pleasant walk, a pleasant talk,
Along the briny beach:
‘We cannot do with more than four,
To give a hand to each.’

-Lewis Carroll

INTRODUCTION

The contribution of the commercial oyster industry to the introduction of nonindigenous marine species around the world is widely recognized (Carlton 1979, Rosenthal 1980, Andrews 1980, Mooney and Drake 1986, Carlton 1989, Chew 1990, Carlton and Mann 1996). Elton (1958) aptly described the connection between exotic species and the commercial oyster industry:

> But the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture, a very ancient and world-wide craft now turning gradually into an applied science.

Because of the prominence of the eastern oyster (*Crassostrea virginica*) as an important commercial fishery, the history of its movement has been documented more fully than that of most marine species. During the past two centuries, eastern oysters have been transported widely within and outside the United States (Figure 2.1). Although the commercial oyster industry was eclipsed in the 20th century by the shipping industry in terms of vector importance, the movement of oysters is responsible for a large fraction of the nonindigenous invertebrate and algae species living along the coastal United States today (Ruiz et al. 2000).

The purpose of this chapter is to introduce the commercial oyster industry and to highlight important aspects that made it an important vector for the accidental transfer of marine organisms. Because the invasions associated with the trafficking of oysters are historic events, this chapter aims to describe the commercial oyster industry as it was in the late 19th and early 20th centuries.

The most comprehensive treatise on the commercial oyster industry was written in 1881 by Ernest Ingersoll (Ingersoll 1881) as part of a report on the history and condition of the fishing industries of the United States. Ingersoll wrote during the height of the commercial oyster industry, and at the time in history when live oyster exportation was maximal. Other valuable treatments of the commercial oyster industry and its history are also available (e.g., Richardson 1877, Blackford 1887, Hall 1894, Smith 1913, Churchill 1920, Elsey 1933, Bonnot 1935, Kinkaid 1951, Barrett 1963, Kochiss 1974, Carlton 1979, Galpin 1989, Carlton and Mann 1996, Mackenzie 1996, MacKenzie et al. 1997). For the purpose of an assessment of oyster-mediated marine invasions, Ingersoll (1881) provides the greatest historic detail for the time period and geographic regions of interest, and therefore his work was an invaluable resource.

TERMINOLOGY

The commercial oyster business is replete with specialized terminology. Several terms are defined here to assist the reader in later sections. Most definitions are partially or fully extracted from Ingersoll (1881).

Bedding - Transplanting oysters of any size to beds prepared for them, from which they are to be removed before the frosts of the ensuing winter.

Bugeye – A flat-bottomed, center-board schooner of three to fifteen tons, built of heavy timbers, without a frame. A bugeye is always decked over and has a cabin aft. A dredging schooner design used in the Chesapeake Bay.

Cullings – The poorer oysters remaining after larger oysters have been picked out. Also *Cullins*

Cultch - The shells, gravel, fragments of brick, or any other material placed in the water to catch spawn of the oyster.

Cultivate - To raise oysters artificially through spawn, or transplanted young. See *Plant*.

Dredge – An apparatus with a rectangular iron frame and chain bag, attached by a heavy rope to a deck-mounted winch called a "windlas" that is pulled behind a schooner or steam boat for harvesting oysters from the sea bottom.

Fatten – To place oysters on floats or in fresh water, just before marketing.

Float – A platform of planks, upon which oysters are piled and subjected to fresh water, before being taken to market. See *Fatten*.

Freshen – To place oysters in fresh or brackish water over one or more tidal cycles to clear mantle of sediments, shell bits, and sand. Osmotic pressure temporarily increases the volume of the oyster tissue.

London Stock - Oysters culled for the foreign market; about three years old, small, round, and cup-shaped. See *Cullins*.

Plant - To place oysters on artificial beds, intending them to survive the winter, attain full size, and spawn. See *Cultivate.* In Connecticut the term is applied only to southern oysters laid down for summer. See *Bed.*

Seed – Infant or young oysters suitable or intended for transplanted growth in artificial beds. See *Set* and *Plant*.

Sharpie – Long, shallow-drafted, flat-bottomed sailboats used for tonging and dredging, especially in Connecticut.

Shuck – To open oysters.

Skipjack – A v-bottomed oyster dredge boat designed and used in the Chesapeake Bay.

Spat - Larvae that are newly settled out of plankton onto hard substrate.

Tongs – Instrument for gathering oysters from the sea bottom. Similar to two very long handled garden rakes that are hinged near the rake heads. Can be used in 7 to 24 feet of water.

NATURAL HISTORY OF CRASSOSTREA VIRGINICA

Eastern oysters (*Crassostrea virginica*) live in estuarine and marine habitats from the Gulf of Saint Lawrence to the Gulf of Mexico. Oysters exist under a wide variety of environmental conditions over this range. Eastern oysters grow on a variety of substrates from hard rocky bottoms to semihard mud that is firm enough to prevent the animals from sinking and thus inhibiting their ability to filter feed. Oysters cannot survive in conditions with heavy sediment loads or unstable sand or mud bottoms (Galtsoff 1964).

Eastern oysters live in varying salinity regimes (6 ppt to >32 ppt), and temperature regimes (1° C to 31° C), but mass spawning typically requires that temperatures exceed 20° C (Galtsoff 1964). Adult females have the capacity to expel 100,000,000 eggs during a single spawn and likely spawn multiple times during the year (Galtsoff 1964). Swimming planktonic larvae exist in the water column for approximately 2 to 3 weeks before settling to the bottom and becoming attached to the substrate (Thorson 1946, Galtsoff 1964). Shell shapes and sizes vary considerably depending on the environmental conditions in which eastern oysters were reared (Ingersoll 1881, Galtsoff 1964). Ingersoll (1881) reported an adult shell from Maine that measured 14 inches in length.

Since the early 20th century, eastern oysters from Prince Edward Island have suffered increased mortality due to infection by shellfish diseases (e.g., Malpeque Bay disease) (Galtsoff 1964). Since the 1950s, two protozoan parasites (MSX and Dermo) have devastated oysters from Maine to Florida (Burreson et al. 2000). DNA sequencing indicates that the protozoan parasite *Haplosporidium nelsoni*, the causative agent of MSX, was likely introduced to the Chesapeake and Delaware Bays with infected Japanese oysters (*Crassostrea gigas*) shipped from the West Coast (Burreson et al. 2000). These diseases have had devastating effects on the commercial oyster fishery during the past half-century.

HISTORY OF THE EASTERN OYSTER FISHERY

Evidence from shell middens on the shores of the western Atlantic indicate that eastern oysters and other shellfish were consumed and traded extensively by native

Americans for thousands of years before Europeans colonized the North American continent (MacKenzie et al. 1997). Following European settlement in the 1600s, oysters became an important resource in the colonies bordering the Atlantic coast from Chesapeake Bay to New England (Ingersoll 1881, Wallace 1997). Oyster populations and habitats have changed dramatically during the past 300 years as a result of human exploitation and environmental degradation (Rosenfield 1997), and it was not long after Europeans arrived that legal protection of this fishery was required. The earliest ordinance regarding oyster harvest in North America was put into effect by the Dutch Council in New Amsterdam (New York) in 1658 (Ingersoll 1881). As early as the 18th century, oyster resources were so depleted in New England and New York that legislators imposed laws restricting the months of the year in which oysters could be taken (Kochiss 1974, Mackenzie 1996). During the past two centuries numerous state laws governing private and commercial oyster fisheries have been enacted to manage this important fishery (see Ingersoll 1881, Mackenzie et al. 1997 for details).

Important Oystering Locations in the Mid-Atlantic and New England

During the later half of the 19th century, the oyster industry of the United States was unparalleled anywhere in the world. Indeed, the North American catch during 1880-1910 averaged 27 million bushels per year, a volume that has since never been matched (by comparison, oyster production in 1996 was estimated at just 5.9 million bushels) (MacKenzie 1996). Table 2.1 indicates the importance of the oyster industry by state in 1880 in terms of oyster landings, sales value, employees, and vessels used. The most concentrated oyster fishing took place in the mid-Atlantic and New England states. Figure 2.2 identifies many of the most important locations where commercial oystering was present in 1880, as described by Ingersoll (1881).

Due to its enormous expanses of natural oyster beds and reefs, the Chesapeake Bay was a self-sustained fishery during the first half of the 20th century and before. Since estuaries to the north were severely over-harvested as early as the 18th century, they required supplementation with seed oysters taken from the Chesapeake. The seed oyster trade was an important element of the commercial oyster industry that bound these two regions together. The following sections describe the nature of this industry in two of the most prominent commercial oyster centers in the world, Chesapeake Bay and New York.

The Chesapeake Bay Commercial Oyster Industry

The Packing Trade

The Chesapeake Bay was by far the greatest producer of oysters during the 18th, 19th, and most of the 20th centuries, with Maryland and Virginia producing greater volumes than the rest of the country combined. Maryland's oyster industry reached its zenith during the 1880s with as many as 800,000 bushels of oysters per year consumed by the residents of the city of Baltimore (Nichol 1937, Mackenzie 1997). Of the approximately 10,600,000 bushels of oysters harvested from Maryland waters in 1880, 63% were packed inside the state, 18% were consumed locally, and 19% were shipped out of the state for planting in northern waters (Ingersoll 1881). Oysters were packed in one of two ways, either shucked and packed raw in tin cans, glass containers, or specially designed kegs for shipment on ice, or steamed and hermetically sealed in tins and thus preserved indefinitely. Baltimore led all other cities in the nation with respect to the volume of oysters packed from 1865 to 1900 (Nichol 1937). One reason for the success of the canning industry in Baltimore was that during the summer, when oysters were not available, canneries used their facilities to package fruit instead (Nichol 1937, Mackenzie 1997).

The demand for raw oysters was so high that during the height of the oyster season (fall), Baltimore shipped between 30 and 40 rail car loads of raw oysters per day to the interior of the country on the Baltimore and Ohio Railroad (Ingersoll 1881, Stevenson 1894, Churchill 1920). In 1870 a huge shucking industry sprang up in Crisfield, Maryland, a small coastal town on the Eastern Shore of the Chesapeake Bay. Crisfield shucked 700,000 bushels of oysters per year and was connected to Baltimore by a spur railroad build explicitly for transporting shucked oysters to Baltimore (Stevenson 1894). A similar oyster railroad was built between Philadelphia and the small town of Bivalve, New Jersey, on the Delaware Bay. Live oysters were packed in burlap bags at the docks in Bivalve and placed in boxcars for the trip to Philadelphia (MacKenzie 1996).

Oysters in the Shell

Given their remarkable ability to withstand desiccation, live Chesapeake Bay oysters could be piled on the decks of sailing and steam vessels and transported to New York, Boston, and as far north as Portland, Maine. Ingersoll (1881) provides an excellent description of oyster survivorship out of water:

> Southern oysters en route from Chesapeake bay to Boston and Portland are frequently a month out of water, yet do not suffer, and grow well enough when returned to the water, though it is so different a latitude. Stock is frequently kept several weeks in the holds of the “arks” in New York, or in the cellars of wholesale depots, waiting for profitable sale. One gentleman assured me that he kept a quantity of “Blue Points” 107 days in his cellar, losing but a few of them, and these are not generally considered so hardy as some other sorts – those from the East river, for instance. The hardiness of the “Sounds” [from Staten Island Sound, a part of Raritan Bay = New York Bay] is well shown in the article upon the oyster-beds of New York bay, in relating the old custom of peddling them up the Hudson river in fall.

Northbound shipments of live oysters took place during eight months of the year (Ingersoll 1881). The vast majority of live oysters transported this way were laid out in the depleted northern oyster beds during the spring and fall (see below). Given the freezing winter temperatures, especially in embayments north of Wellfleet, Massachusetts, winter shipments of oysters were most often marketed for direct consumption.

In the mid-1800s, the high demand for fresh oysters in Boston and other New England cities was a powerful economic lever that led to the development of one of history’s most important maritime innovations, the Clipper ship. Ingersoll (1881) described the development as follows:

> In the demand for fast sailers, which the oyster-business created, is found the origin of the celebrated model of sailing vessel that made America famous on the seas --the clipper-ship. The first of these were made by Samuel Hall, a noted ship-builder, at his yard in East Boston, and were named Despatch, Montezuma, Telegraph, and Express. They were from 90 to 120 tons, old measurement, and carried an average cargo of 2,500 bushels of oysters. Six months in the year these clippers were devoted to bringing oysters from Virginia. There were thirty-five or forty of these "sail" running, and in summer [when oystering was

> prohibited in most states] they would go fishing. The freight tariff on oysters was then 20 cents, and during the war as high as 25 cents a bushel.

The magnitude of the oyster industry in the Chesapeake Bay in the early 20th century and before is hard to imagine. In the late 1800s, Maryland and Virginia generated 60% of the nation's oysters and 50% of the world's oyster production (Stevenson 1894). Although the Chesapeake Bay was once believed an infinite resource for oysters, over-harvest, destruction of habitat, pollution, and shellfish diseases have proved this notion incorrect (MacKenzie 1996). Today the Chesapeake Bay and most other North American estuaries support only a fraction of the oysters once present before European settlement.

The Commercial Oyster Industry of New York City

Although it did not produce the same volume of oysters as the Chesapeake Bay, New York was an important center for the commercial oyster industry in its own right. The focus of New York City's oyster business was quite different from that of Baltimore and the Chesapeake Bay. While the Chesapeake Bay region led in processing and packing of shucked oysters, and provided large quantities of seed oysters to bolster northern fisheries, New York City was better positioned for the long-distance shipment of live oysters. By virtue of its stature as a leader in international commerce, and the widespread reputation of oysters grown in northern waters, it is not surprising that New York City quickly became the hub for live oyster transport. According to Kochiss (1974):

> By the 1880s New York City had become the center of the northern oyster industry and led the country in over-seas and transcontinental oyster shipments. . . . Fresh oysters came in regularly from nearby Connecticut, Long Island, and Staten Island and to some extent Massachusetts, Rhode Island, Delaware, and Virginia, and here they

> were stored, barreled, opened, sold, and shipped for the local, West Coast, and European trade.

The quantity of oysters handled in New York in 1880 was reported to be 765,000,000 individuals, consisting of 1,634,000 bushels of northern oysters plus 1,065,000 bushels of southern oysters (Ingersoll 1881). Northern stock was dominated by oysters native to the waters of New Jersey, New York, and Connecticut, while southern oysters consisted principally of oysters that originated in the Chesapeake Bay but were cultivated in the oyster beds of New Jersey, New York, and Connecticut.

As early as the 1870s, the viability of southern oysters for long distant export was questioned. An article published in *Scribner's Monthly* (Richardson 1877) described the differences among source oysters:

> As a rule, however, they (Southern oysters) do not maintain themselves more than a single season in the colder northern waters; nor do they bear transplantation to Europe or to California so well as oysters of the North . . . a considerable demand has arisen for northern seed for transportation to England and the Pacific Coast.

Both the southeastern Atlantic coast and the Gulf of Mexico had substantial commercial oyster fisheries at this time, but there is no evidence to suggest that oysters were transported from these regions to the West Coast or relayed to northern beds. Lacking access to the intercontinental railroad system during the late 1800s and the commercial preference for cold-water-adapted oysters probably prevented these regions from participating in the live oyster trade with California.

The international and transcontinental exportation of eastern oysters from New York City in the late 1800s and early 1900s played a crucial role in the dispersal of many marine organisms that naturally associate themselves with oysters. The oyster beds surrounding New York (e.g., Raritan Bay = New York Bay, the East River, Long Island Sound, Great South Bay, New Haven Bay) provided an important source of biota that would ultimately be shipped across the Atlantic Ocean and to California in barrels of live oysters. Understanding the history of the New York oyster industry provides important insight into the prevalence of northwestern Atlantic species as invaders around the world.

Oyster Seed, the Link between Chesapeake Bay and Embayments to the North

Following extensive depletion of native oysters in Massachusetts, Rhode Island, and Connecticut during the late 18th and early 19th centuries, immature oysters (seed oysters) were shipped aboard sailing vessels from the Chesapeake Bay and planted in northern waters (Ingersoll 1881, Mackenzie 1996). This practice was expanded to include New York, New Jersey and Delaware Bay, as oyster beds in these areas were soon depleted. The extent of southern seed transplanted northward was massive. In the 1830s, 150,000 bushels of Chesapeake Bay oyster seed were planted in Delaware per year - this value climbing to 500,000 bushels per year by the 1880s (Mackenzie 1996). As early as 1858, 250 schooners imported 2,000,000 bushels of Chesapeake Bay oysters per year into coastal waters of Delaware and northward, many of these were laid in beds of New Haven Harbor, Connecticut (Ingersoll 1881, Kochiss 1974). In the 1870s, 300,000 bushels of seed oysters per year were relayed to Raritan Bay, New Jersey. Although some native seed stock was used in New Jersey, 75% was brought from the Chesapeake Bay in the 1890s (Hall 1894). During the spring of 1879, 2,178,750 bushels of live oysters were shipped north from Maryland for the purposes of cultivating juveniles and bedding adult oysters for sale the following autumn (Ingersoll 1881). In 1880, 58.6% of the oysters harvested in estuaries from Delaware Bay to Portland, Maine (4,232,800 of 7,222,250 bushels) were derived from oysters originating in the Chesapeake Bay. The process of live seed transport was carried out for a century as the productivity of northern oyster beds continued to decline (MacKenzie 1996). Due to the innovations of Connecticut oyster growers (oyster bed preparation, and spat collection, and native seed production), by 1920 much less Chesapeake Bay seed was planted in Long Island Sound (Churchill 1920).

Oyster Cultivation

In the United States, oysters have been cultivated most commonly in two ways. The first was to raise oysters artificially from spawn by maximizing the amount of larvae that settle out of the plankton. This usually involved providing a hard substrate ("cultch"), for oyster larvae to settle on. The newly settled oyster larvae, or "spat" were then raised to adults and harvested. This kind of cultivation was pioneered in Connecticut in the 1820s when it was discovered that greater spat falls could be expected when high quality cultch was available (Ingersoll 1881, Kochiss 1974). Such discoveries have motivated generations of shellfish researchers and oyster fishermen to investigate the best ways to enhance successful spat fall by trying to understand the relationships among environmental conditions and oyster reproductive physiology. As a result, the eastern oyster (*Crassostrea virginica*) is almost certainly the most studied bivalve on earth.

A second, and more prevalent, method of oyster cultivation was simply the transplantation of small oysters (seed oysters) from one location to another. Cultivated beds, in general, were privately held, and the holder of the lease had exclusive access to the area. Once laid down in a new area, juvenile oysters grew into adults and could be easily harvested. The size and shape of the oyster was dictated largely by the conditions under which it was grown (e.g., how densely oysters were laid and the temperature at which they were grown). Because of the high rate of success with this method, the use of so-called “plants” was extremely popular in the 1800s. When transplanted into beds of Long Island Sound or Raritan Bay, first year Chesapeake Bay seed oysters required roughly three years of growth to attain market size (approximately 3.5 to 4 inches) (Ingersoll 1881).

In addition to small seed oyster transplantation, larger oysters were also laid in northern beds during spring and allowed to grow for one summer before harvest in the autumn. This approach was widespread in Connecticut and practiced exclusively in oyster beds to the north of Wellfleet Harbor where transplanted southern oysters were largely unable to withstand freezing winter temperatures. The transplantation of larger oysters for short growth periods was referred to as “bedding.” When the supply of oysters exceeded demand, surpluses were often dumped into receiving waters for safe storage before sale or on the chance that some would survive the winter.

Table 2.2 summarizes the yield from the important commercial oyster fisheries in the mid-Atlantic and New England on the basis of the volumes of native oysters and Chesapeake plants harvested. From Delaware Bay northward, Chesapeake plants represent a large fraction of the total oysters landed. With the exception of just two locations, Chesapeake plants outnumbered native oysters in all oyster fisheries from New Haven Harbor to Portland, Maine.

The annual flux of Chesapeake Bay oysters to northern locations provided a pathway for the unintentional introduction of southern species, not only to northern waters, but also to the West Coast and Europe. Indeed, there is evidence that many species were moved northward with seed transplants, including the ribbed mussel, *Geukensia demissa* (Gould 1841), the hooked mussel, *Ischadium recurvum,* (= *Modiola hamatus*) (Perkins 1869,Verrill and Smith 1874), and the thick-lipped oyster drill, *Eupleura caudata* (Carriker 1955), but other species were undoubtedly moved. The extensive oyster export business centered in New York provided southern oyster associates a viable two step pathway to other coasts (e.g., Chesapeake Bay to New York and to the West Coast or Northern Europe).

Foreign Export and Intercontinental Transport of Eastern Oysters

Oysters by Ship

Eastern oysters introduced to Europe were shipped from New York City and vicinity (Ingersoll 1881). Europeans preferred oysters that were similar in size and shape to their native oyster *Ostrea edulis.* The so-called “London-Stock” were young eastern oysters (approximately 3 years) that were small and round. Since Americans favored larger oysters, European exports were generally comprised of “cullings,” or oysters that were considered too small for the American market (Ingersoll 1881). Although Europeans preferred certain breeds, these and other oysters from the greater New York area that were shipped to Europe were harvested in waters where southern oysters had also been planted. Ingersoll (1881) describes the European shipments:

> Besides Blue Points, great quantities of oysters from the East river (particularly Rowayton, Norwalk, and Bridgeport), have been shipped, chiefly through J. & J. Ellsworth; a less number from Rockaway and Fire Island; and large quantities from Staten Island waters, under the brand of “Sounds”.

Originally, live oysters were taken a barrel or two at a time by private citizens traveling on steam liners to Europe. By the early 1870s, a commercial market had developed and many barrels were routinely shipped to Europe on steamers. Kochiss (1974) describes the barreling process and indicates the difference between European and California-bound barrels:

> Oysters in the shell were sent in barrels by either of two ways, depending upon their destination. For the European trade they were “double headed,” that is, the top and bottom were identical, and made of wood. A “packer” carefully and closely packed them, hollow shell down, pressing them tightly with a heavy circular weight, and then “headed” or sealed the container with a wooden top the same as the bottom. Packing was so tight that not a single oyster rattled when the barrel was shaken. Dealers believed oysters kept better on the long ocean passage this way because jamming prevented them from opening their shells and consequently they did not lose their precious liquor.
>
> Oysters destined for California or elsewhere in this country were shipped in the same barrels but topped instead with burlap. This necessitated a minimum of skill, was faster, and thus cheaper. Oysters were also transported in one- or two-bushel burlap sacks.

Survivorship in barrels was quite good, especially with the relatively short transit time of steam vessels (less than 12 days) (de Broca 1865). Because of the short voyage time and cool conditions of the hold where barreled oysters were stowed (Ingersoll 1881), no ice was necessary.

The volumes of live oysters shipped to Europe were quite large. According to Ingersoll (1881), 68,140 three-bushel barrels were shipped to Liverpool, England and 2,628 three-bushel barrels to other European ports (e.g., Hamburg, Bremen, Havre, London, Glasgow, Bristol, and Cardiff) during the 12 months between 1880 and 1881. At the close of the 19th century, a reported 100,000 barrels of live oysters were shipped annually to England (Kochiss 1974). Of these, many were bedded for storage and growth in European waters according to Ingersoll (1881):

> To provide against loss in this contingency, the largest dealers own spaces of sea-bottom, where the surplusage is thrown overboard to keep in good condition and drawn upon as required. Some thousands of barrels are sent annually, which are intended to lie and grow there from one to three years.

Of the 50 non-native species of marine flora and fauna documented in British waters (Eno et al. 1997), 21 (42%) are considered possible unintentional introductions with oysters (*Crassostrea virginica*, *Crassostrea gigas*, *Titostrea lutaria*). Of these, 10 (20% of total) algae and invertebrates are potential introductions with *Crassostrea virginica*.

Oysters by Rail

The shipment of live oysters by rail to the nation's interior was extensive, even before the transcontinental railroad. Following the connection of the Union Pacific and

Central Pacific Railroads in 1869, railway passage was open from New York City to San Francisco. Although live eastern oysters were shipped by rail for planting to British Columbia (Taylor 1895, Stafford 1913, Elsey 1933, Quayle 1969, Carlton 1979, Bourne 1997), Washington (Smith 1896, Townsend 1896, Washburn 1903, Kinkaid 1928, Galtsoff 1929, Quayle 1969, Carlton 1979, Lindsay and Simons 1997), and Oregon (Hubbs and Miller 1965, Carlton 1979, Robinson 1997), the vast majority went to San Francisco Bay (Carlton 1979).

Live oyster shipments to the West Coast began in 1869 with 3 carloads of adult eastern oysters shipped to San Francisco by A. Booth & Co. (Collins 1892). Live oysters were shipped by fast freight from New York to San Francisco and were in route from between 8 days and 3 weeks (Washburn 1896, Barrett 1963, Shaw 1997). Shipments were made in the spring and autumn, when oysters were their hardiest (not spawning) (Collins 1892, Barrett 1963). Subsequently, live oyster shipments to the West Coast were composed of several oyster varieties. The following oyster types were shipped to San Francisco between 1874 and 1880: York Bays, Newark Bays, Raritan Rivers, North Rivers, Natural Growth, Blue Points, Sounds, Maurice Rivers, "Virginias, etc." (most likely Chesapeake Bay oysters from Maryland and Virginia), East Rivers, Princes Bays, Rockaways, and Egg Harbors (Ingersoll 1881). Although some of these are listed as being shipped specifically for market rather than planting, market oysters were often bedded down in San Francisco Bay for safe keeping while awaiting sale (Ingersoll 1881). Collins (1892) indicates that surplus oysters from the very first railroad oyster shipments (1869) were stored in the Bay and grew quite well. It should be stressed that even short-term bedding provided oyster-associated fauna the opportunity to colonize.

Based on Carlton's (1979) summary of the literature, the average quantity of oysters shipped from New York City to San Francisco Bay, for the express purpose of planting, was equal to 60 railcars (range = 41 to 76 railcars) x 2500 lbs/railcar = 150,000 lbs/year for the years 1875 to 1880. During the peak years of transcontinental oyster shipment (1887 to 1908), Carlton (1979) estimated an average annual shipment of 125 railcars (range = 72 to 267 railcars) x 2500 lbs/railcar = 312,500 lbs/year of seed oysters.

Of the 212 nonindigenous marine species reported in San Francisco Bay Estuary, 70 (33%) are considered possible unintentional introductions with imported oysters (*Crassostrea virginica*, *Crassostrea gigas*) (Cohen and Carlton 1995). Of these, 52 species (24.5% of total) are potential introductions with eastern oysters, *Crassostrea virginica*.

Oyster Fishery Practices

Oyster Dredging

There were a number of aspects of the commercial oyster industry that likely increased the chances of collateral transfer of marine species. First and foremost was the extensive use of oyster dredges for harvesting oysters. Oyster dredges were made of a rectangular iron frame that supported a bag or net made from iron rings that could hold 2 to 3 bushels. The bottom edge of the frame had iron teeth that projected downward when pulled across an oyster bed. The dredge was attached to a heavy rope that was deployed and retrieved with a deck-mounted winch. In the Chesapeake and Delaware Bays, oyster dredging was done from sailing vessels (primarily schooners, Pungies and Bugeyes, and later Skipjack sloops) (Rolfs 1971). Further north, steam driven vessels were employed as well as schooners and sloops. Oyster steamers had steam driven winches and could hold up to 9500 bushels of oysters on board. Some 8-man oyster steamers could harvest as many oysters in a single day as a 3-man schooner could in close to two and a half months (Galpin 1989).

In the United States, a variety of laws were passed restricting the use of dredges. In Maryland, oyster grounds were legally divided among oyster tonger grounds and oyster dredging grounds. In 1868, because of extensive abuses by dredgers that illegally harvested oyster beds reserved for tonging, an oyster police force was formed (Mackenzie 1996). Despite legal consequences, during the second half of the 19th century, oystermen and the oyster police frequently exchanged gunfire in what were termed the “oyster wars” (Wennersten 1981, MacKenzie 1997). The extensive use of oyster dredges was an important factor in the depletion of oysters in northern waters, and, according to Ingersoll (1881), unregulated dredging was largely responsible for wiping out the native oyster populations (*Ostrea edulis*) in Great Britain and France.

Dredging is a very unselective harvesting method. As a result, tremendous amounts of extra material, including stones and any organisms growing among the oysters, was brought aboard. Although there was a culling process to remove under-sized oysters, by-catch, and other debris, culling was by no means a thorough process. Juveniles and smaller fauna were most certainly not removed, and many were subsequently transported with live oysters.

Oyster Tonging

Prior to the invention of the oyster dredge in the early 1800s, oyster tongs and bull rakes were the principal tools used for harvesting oysters. Tonging could be carried out from small dugout canoes, skiffs, or small sailboats. The most commonly used sailboat in Connecticut was the New England designed "sharpie" (MacKenzie 1997). Oyster tongers would fill their small boats with oysters (seed and adult) and sell them to larger boats at anchor called "buy-boats." Once the buy-boats were loaded, they would set sail for port where the oysters were sold to dealers. Oysters taken with tongs and rakes were also culled, but small and cryptic fauna were nevertheless not sorted out. Although tongers harvested fewer oysters per boat, the vast number of working tonging boats was responsible for a substantial portion of the commercial catch.

Freshening and Storage of Live Oysters

A process called "freshening," "drinking," or "floating" was used to clear the oyster's mantle of any sand, sediment, or other impurities that affected the taste and texture of the meat. Typically, dredged or tonged oysters were brought to shore and dumped into the shallow tidal rivers or onto intertidal river banks and allowed to remain for at least one tidal cycle (Ingersoll 1881, Mackenzie 1996, Ford 1997). Oysters were then removed from the water and sent to market. As sediments were removed, the tissues were also whitened. The osmotic differential between the oyster and the surrounding low salinity water tended to increase the water content of the oyster and therefore increase its apparent volume (Ingersoll 1881, MacKenzie 1996). Although this plumping was only maintained for a few days, the removal of sediments had a lasting effect. It should be noted that with continued urban development, oysters were sometimes placed in polluted waters, causing contamination.

A very popular method for freshening oysters was to place them on shallow floating platforms or barges called “oyster floats.” Oyster floats were constructed from wooden planks and had slotted bottoms that allowed water to flow in and out. The oyster floats were anchored in tidal rivers where they would undergo the freshening process in brackish water before going to market. Oyster boats offloaded oysters directly to oyster floats. Since floats were shallow, the oysters were easily retrieved in bushel baskets after freshening (Ingersoll 1881, Rolfs 1971, MacKenzie 1996). These floats could be moved around according to changing tidal ranges and the desires of oyster wholesalers. Oyster floats also provided an excellent place to temporarily store oysters prior to marketing (Churchill 1920).

From a biological invasion standpoint, the freshening process provided an opportunity for animals not normally associated with oysters to colonize harvested ones. Alternatively, the process may have also excluded some species that were unable to tolerate brackish conditions, but it is unlikely that all barreled oysters underwent the freshening process before shipment. The important point is that a pathway existed by which some non-associated species could have been moved. Given the close contact that oyster floats had with salt marsh and other upper intertidal habitats and structures, even seemingly improbable colonizers such as the pulmonate snails, *Myosotella myosotis* and *Melampus bidentatus* might have ended up in oyster barrels for transport. Furthermore, any other materials and equipment used for processing and moving oysters (e.g., bushel baskets, barrels, burlap bags) that were stored at the water's edge could have promoted the accidental movement of other species as well.

Telling photographs in Rolfs (1971) and Kochiss (1974) illustrate the freshening procedure and indicate the close proximity of oyster floats and equipment to non-oyster habitats. Illustrations in Ingersoll (1881) also demonstrate the close contact that ships, shipping houses (including the famous New York City oyster barges of West Tenth Street on the North River and of Broome Street on the East River), freshening platforms, barrels, baskets, and other materials had with one another and the shore. The opportunity for nestling among these materials and the oysters themselves was certainly present. Contemporary accounts of widespread colonization of modern shipping containers by terrestrial snails, and subsequent invasions to foreign continents (Bishop Museum pers. com. Global Invasive Species Program meeting 1999), provide strong support for nestling as an important mode of nonindigenous species introduction.

SUMMARY

The United States' commercial oyster industry was the largest in the world during the 19th and much of the 20th centuries (Smith 1913). From 1880 to 1910 approximately 27,000,000 bushels of oysters were harvested per year (MacKenzie 1996). A significant proportion of the total landing was sold fresh, in the shell. The popularity of fresh oysters increased their commercial demand and resulted in greater long distance shipment of live oysters and an accelerated depletion of natural oyster beds in the mid-Atlantic and New England states. Many aspects of the commercial oyster industry provided opportunities for repeated, unintentional introductions of oyster-associated flora and fauna to regions outside their native ranges.

From 1869 to 1940, billions of live oysters were shipped in barrels from merchants in New York City to the Pacific coast of North America and to Europe. These oysters were both seed oysters (to be planted for growth and maturation in beds of the recipient region) and adult oysters for direct sale. Both types provided an opportunity for introducing nonindigenous species since many oysters shipped for direct marketing were placed in recipient waters for safe storage or further growth before sale. To compensate for over-harvest, tens to hundreds of millions of bushels of oysters were transplanted from the Chesapeake Bay to more northern estuaries for long-term and short-term growth before sale. Seed oyster shipments provided a pathway for the south to north movement of oyster-associated fauna, and in turn, their exportation to the eastern Pacific and eastern Atlantic coastal systems.

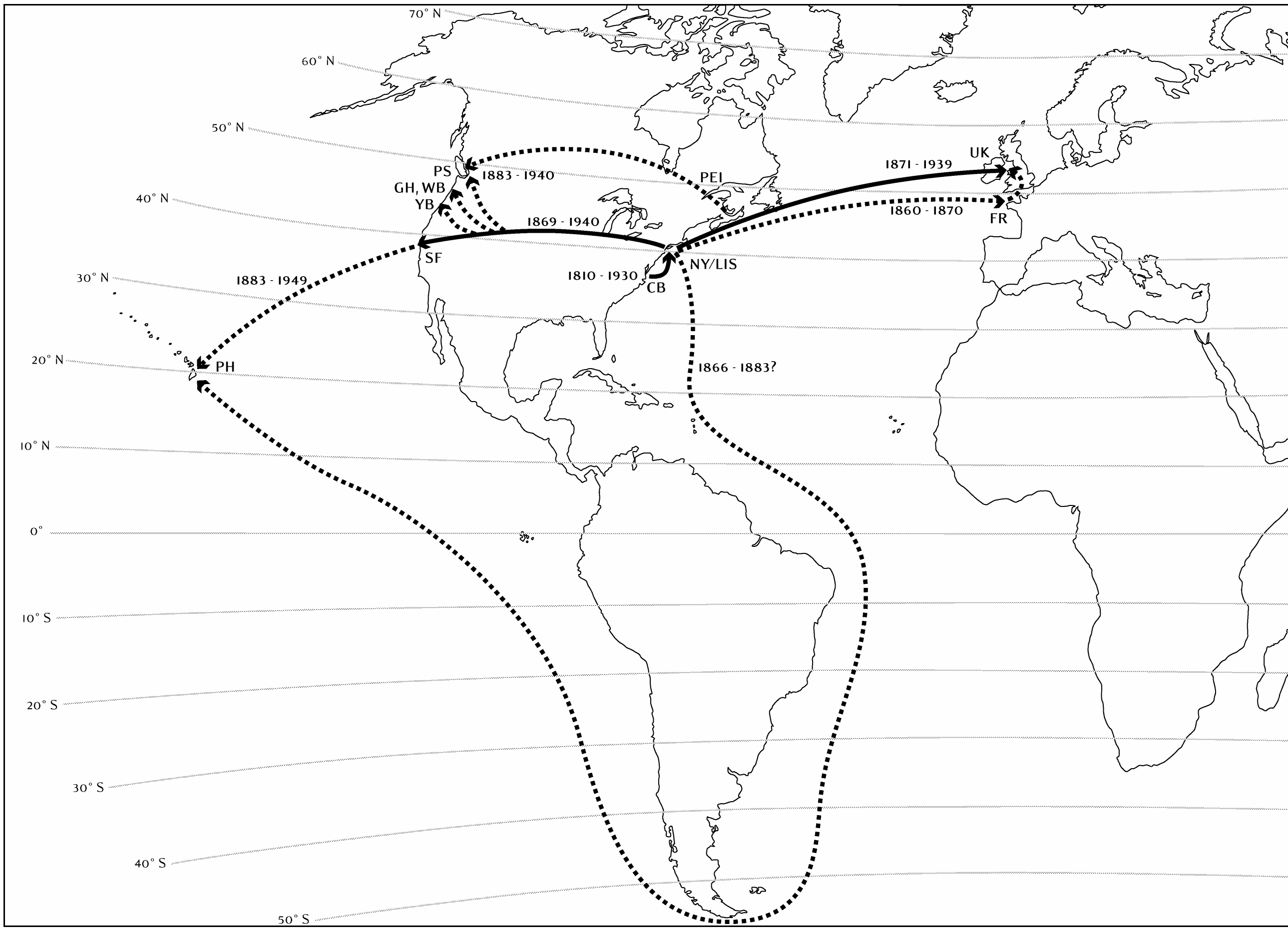


Figure 2.1 Major source and recipient locations of eastern oyster (*Crassostrea virginica*) commercial transport. Solid lines represent routes of highest volumes, dotted lines represent lesser volumes. Approximate time periods of introduction are included. North America: SF=San Francisco Bay/Tomales Bay (1869-1940), PS=Puget Sound and nearby waters of British Columbia (1883, 1890s, 1905-1940), GH=Grays Harbor (1900-1940s), WB=Willapa Bay (1874, 1894, 1897), YB=Yaquina Bay (1872, 1896, 1899-1931, 1943-1944); CB=Chesapeake Bay, NY/LIS=New York and Long Island Sound region; PEI=Prince Edward Island; Hawaii: PH=Pearl Harbor, Oahu (1866, 1883-1949); Europe: UK=United Kingdom (principally Liverpool), FR=France.

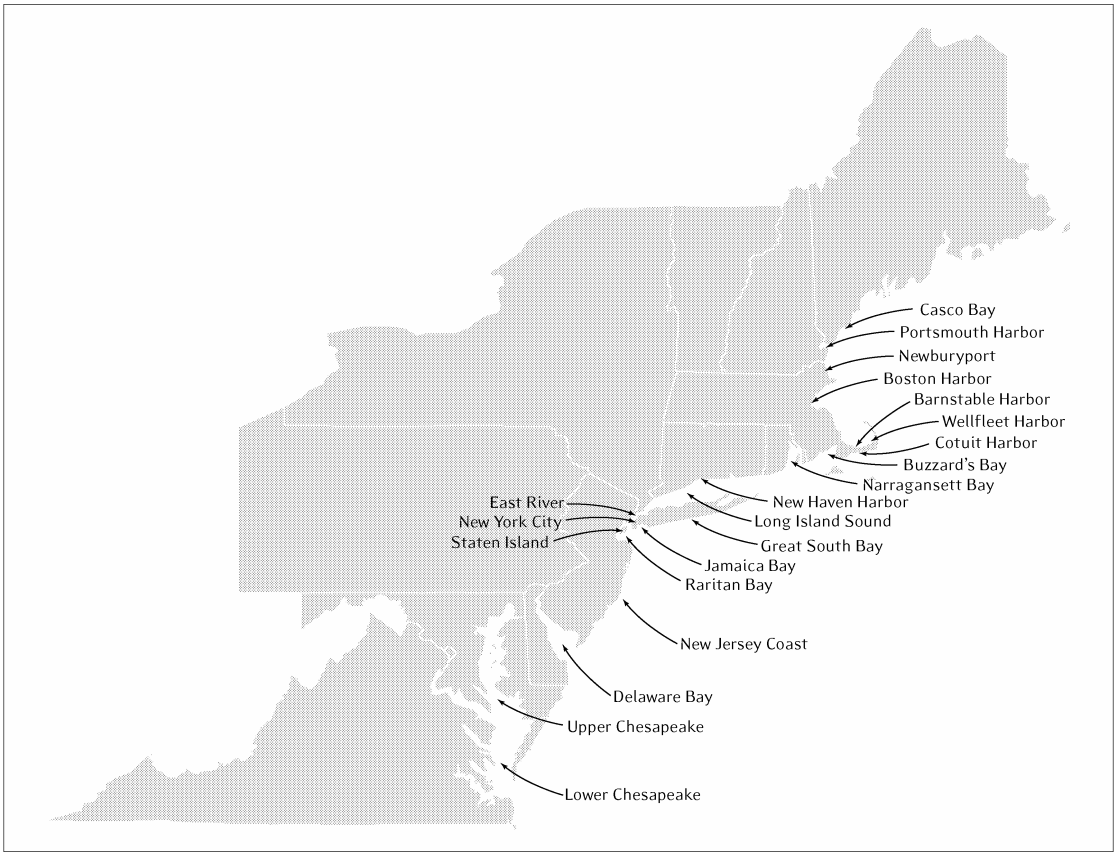


Figure 2.2. Commercially important oystering centers of the mid-Atlantic and northeastern United States.

Table 2.1. Summary of the United States commercial oyster industry (*Crassostrea virginica*) of 1880. Data compiled from Ingersoll (1881).

State	**Native Oysters Produced [bushels]**	**Value of Oysters Sold [dollars]**	**No. Persons Employed**	**No. of Vessels**	**No. of Small Boats**
Maine	--	37,500	15	1	3
New Hampshire	1,000	6,050	9	--	5
Massachusetts	36,000	405,550	896	56	117
Rhode Island	163,200	356,925	650	--	100
Connecticut	336,450	672,875	10,006	100	563
New York	1,043,300	1,577,050	2,724	426	1,714
New Jersey	1,975,000	2,080,625	2,917	575	1,400
Pennsylvania	--	187,500	--	--	--
Delaware	300,000	687,725	1,065	65	300
Maryland	10,600,000	4,730,476	23,402	1,450	1,825
Virginia	6,837,320	2,218,376	16,315	1,317	4,481
North Carolina	170,000	60,000	1,020	90	800
South Carolina	50,000	20,000	185	10	100
Georgia	70,000	35,000	350	--	100
Florida	78,600	15,950	166	--	110
Alabama	104,500	44,950	300	20	42
Mississippi	25,000	10,000	60	--	40
Louisiana	295,000	200,000	1,400	45	120
Texas	95,000	47,300	240	--	70
Washington Territory [a]	15,000	45,000	85	--	40
California [a]	125,000	575,000	75	--	--
Total	**22,320,370**	**14,013,852**	**52,805**	**4,155**	**11,930**

Notes: [a] Oyster volumes refer to eastern oysters (*Crassostrea virginica*) introduced from the Atlantic coast of the United States.

Table 2.2. Commercial oyster (*Crassostrea virginica*) landings from mid-Atlantic coast and New England waters. Harvest values are reported regionally as volumes of native and transplanted oysters. Data compiled from Ingersoll (1881).

Location	**Native Oysters [bushels]**	**Chesapeake Plants [d] [bushels]**
Portland, ME	--	75,000 [e]
Great Bay, Portsmouth, Dover, NH	1,000	7,000
Newburyport, MA	--	3,500
Salem, MA	--	40,000
Boston, MA	15,400 [c]	457,500
Wellfleet, MA	600	6,000
Buzzard's Bay/Vinyard Sound, MA	19,000	7,000
Taunton/Coles Rivers, MA	52,000	--
Narragansett Bay, RI	148,200	274,300
New Haven Harbor, CT	128,250	450,000
Housatonic and Saugatuck Region, CT	9,000	--
East River/Peconic Bay, NY/CT	669,800	--
South Shore of Long Island, NY	400,000	--
Raritan Bay, NY/NJ (excluding NYC)	255,000	175,000
New York City Trade (oysters handled) [a]	1,634,000	1,065,000
NJ (ocean shore)	250,000	77,500
Delaware Bay (NJ/DE)	1,900,000	650,000
Philadelphia [b]	1,740,000	940,000
Maryland	10,600,000	--
Virginia	6,837,320	--
Total	**25,104,295**	**3,638,800**

Notes: [a] These values represent oysters handled in New York City, and thus double-count some fraction of oysters harvested in other states (see Table 2.1).

[b] "Native" oysters to Philadelphia originated in the waters of Delaware Bay, New York Bay, the East River, and Long Island Sound – values double-count some fraction of oysters harvested in other states.

[c] Native oysters had been depleted in Boston by the early 19th century so "Native" refers here to oysters grown in Welfleet, Buzzards Bay, Narragansett Bay.

[d] Chesapeake plants refer to oysters that originated in the Chesapeake but that were planted or bedded in northern waters before harvest.

[e] Many oysters sent for direct consumption but surplus oysters were dumped in Casco Bay for summer keeping.

LITERATURE CITED

Andrews, J. D. 1980. A review of introductions of exotic oysters and biological planning for new importations. Marine Fisheries Review 42: 1-11.

Barrett, E. M. 1963. The California oyster industry. Department of Fish and Game Fish Bulletin 123: 1-103.

Blackford, E. G. 1887. Second Report of the oyster investigation and of survey of oyster territory for years 1885 and 1886. The Argus Company Printers, Albany, New York. 47 p.

Bonnot, P. 1935. The California oyster industry. California Fish and Game 21: 65-80.

Bourne, N. F. 1997. Molluscan fisheries of British Columbia. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 115-130.

Burreson, E. M., Stokes, N. A., and C. S. Friedman 2000. Increased virulence in an introduced pathogen: *Haplosporidium nelsoni* (MSX) in the Eastern Oyster *Crassostrea virginica*. Journal of Aquatic Animal Health 12:1-8.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation. University of California, Davis. 904 p.

Carlton, J. T. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. Conservation Biology 3: 265-273.

Carlton, J. T. and R. Mann 1996. Transfers and world-wide introductions. In: V. S. Kennedy, R. E. I. Newell, and A. F. Eble (eds.), The eastern oyster, *Crassostrea virginica*, p 691-706. Maryland Sea Grant Program, College Park.

Carriker, M. L. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Fish Wildlife Serv. Spec. Sci. Rep. Fish. No. 148, 150 p.

Chew, K. K. 1990. Global bivalve shellfish introductions. World Aquaculture 21:9-22.

Churchill, E. P., Jr. 1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. Appendix VIII, Rep. of U. S. Comm. Fish and Fisheries, 1919, 51 p. Government Printing Office, Washington, D. C.

Cohen, A. N. and J. T. Carlton 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Biological Study. A report for the U. S. Fish and Wildlife Service, Washington, D. C. and the National Sea Grant College Program Connecticut Sea Grant. 272 p.

Collins, J. W. 1892. Report on the fisheries of the Pacific Coast of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1892, 267 p. Government Printing Office, Washington, D. C.

De Broca, P. 1876. On the oyster industries of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1873-1875, 49 p. Government Printing Office, Washington, D. C.

Drake J. A., Mooney H. A, di Castri F., Groves R. H., Kruger F. J., Rejmánek M., and M. Williamson, editors. 1989. Ecology of biological invasions: a global perspective. John Wiley and Sons, New York. 450 p.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, England. 181 p.

Eno, N. C., Clark, R. A., and W. G. Sanderson 1997. Non-native marine species in British waters: a review and directory. Joint Nature Conservation Committee, Peterborough, United Kingdom. 152 p.

Galpin, V. M. 1989. New Haven's oyster industry. The New Haven Colony Historical Society, 78 p.

Galtsoff, P. S. 1929. Oyster industry of the Pacific Coast of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1929, Appendix VIII, Document 1066, 367-400. Washington Printing Office, Washington, D. C.

Galtsoff, P. S. 1964. The American oyster *Crassostrea virginica* Gmelin. Fishery Bulletin of the Fish and Wildlife Service, vol. 64, 483 p. Government Printing Office, Washington, D. C.

Gould, A. A. 1841. Report on the invertebrata of Massachusetts, comprising the mollusca, crustacea, annelida, and radiata. Folsom, Wells and Thurston, Cambridge. 386 p.

Hall, A. 1894. Notes on the oyster industry of New Jersey. Rep. of U. S. Comm. Fish and Fisheries, 1892, 66 p. Government Printing Office, Washington, D. C.

Hubbs, C. L. and R. R. Miller 1965. Studies of cyprinodont fishes. XXII. Variation in *Lucania parva*, its establishment in western United States, and description of a new species from an interior basin in Coahuila, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan No. 127, 104 p.

Ingersoll, E. 1881. The oyster-industry of the United States. In: G. B. Goode (ed.), The history and present condition of the fishery industries, 1879-1880, 251 p. Government Printing Office, Washington, D. C.

International Council for the Exploration of the Sea 1972. Report of the Working Group on Introduction of nonindigenous Marine Organisms. Unpublished, International Council for the Exploration of the Sea. (Cooperative Research Report No. 32).

Kinkaid, T. 1928. Development of oyster industry of the Pacific. Trans. Amer. Fish. Soc. 58: 117-122.

Kinkaid, T. 1951. The oyster industry of Willapa Bay, Washington. Printed by The Tribune, Ilwaco, Washington, 45 p.

Kochiss, J. M. 1974. Oystering from New York to Boston. Mystic Seaport, Inc., Middletown, Connecticut, 251 p.

Lindsay, C. E. and D. Simons 1997. The fisheries for Olympia oysters, *Ostreola conchaphila*; Pacific Oysters, *Crassostrea gigas*; and Pacific razor clams, S*iliqua patula*, in the state of Washington. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 89-113.

MacKenzie, C. L., Jr. 1996. History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. Marine Fisheries Review 58: 1-78.

MacKenzie, C. L., Jr. 1997. The U. S. molluscan fisheries from Massachusetts Bay through Raritan Bay, N.Y. and N.J. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 1. U. S. Dept. of Commer., NOAA Tech. Rep. 127, p 87-117.

MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.) 1997. The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vols. 1-3. U. S. Dept. of Commer., NOAA Tech. Rep. 127,128,129.

Nichol, A. J. 1937. The oyster-packing industry of Baltimore: its history and current problems. Bulletin of the Chesapeake Biological Laboratory, University of Maryland. Contrib. 11, 32 p.

Perkins, G. H. 1869. Molluscan fauna of New Haven. A critical review of all marine, freshwater and land molluscs of the region, with descriptions of many of the living animals and of two new species. Proceedings of the Boston Society of Natural History 13:109-135, 13:139-163.

Quayle, D. B. 1969. Pacific oyster culture in British Columbia. Fisheries Research Board of Canada Bulletin 169, 192 p.

Richardson, J. 1877. American oyster culture. Scribner’s Monthly 15:225-238.

Robinson, A. J. 1997. Molluscan fisheries in Oregon: past, present, and future. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 75-87.

Rolfs, D. H. 1971. Under sail, the dredgeboats of Delaware Bay. Wheaton Hist. Assoc., Millville, New Jersey, 157 p.

Rosenfield, A. 1997. Preface: the past is prologue. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 1. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p v-vi.

Rosenthal, H. 1980. Implications of transplantations to aquaculture and ecosystems. Marine Fisheries Review 42: 1-14.

Ruiz, G. M., Fofonoff, P. W., Carlton, J. T., Wonham, M. J., and A.H. Hines. 2000. Invasions of Coastal Marine Communities in North America: Apparent Patterns, Processes, and Biases. Annual Review of Ecology and Systematics (in press).

Shaw, W. N. 1997. The shellfish industry of California – past, present, and future. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 57-74.

Smith, H. M. 1896. A review of the history and results of the attempts to acclimatize fish and other water animals in the Pacific states. Bull. United States Fish. Comm. For 1895, 15:379-472.

Smith, H. M. 1913. Oysters: the world's most valuable water crop. The National Geographic Magazine 24: 258-281.

Stafford, J. 1913. The Canadian oyster, its development, environment and culture. The Mortimer Co., Ottawa, 159 p.

Stevenson, C. H. 1894. The oyster industry of Maryland. Bulletin of the U. S. Fish Comm. 1892: 203-297.

Taylor, G. W. 1895. Preliminary catalogue of the marine Mollusca of the Pacific coast of Canada. Trans. Roy. Soc. Can. (2) 1:17-100.

Townsend, C. H. 1896. The transplantation of eastern oysters to Willapa Bay, Washington, with notes on the native oyster industry. Rep. U. S. Comm. Fish and Fisheries 21:193-202.

Verrill, A. E. and S. I. Smith 1874. The invertebrate animals of Vineyard Sound and adjacent waters with an account of the physical features of the region. Government Printing Office, Washington, D. C.

Wallace, D. E. 1997. The molluscan fisheries of Maine. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 1. U. S. Dept. of Commer., NOAA Tech. Rep. 127, p 63-86.

Washburn, F. L. 1896. The eastern oyster on the Oregon coast. A preliminary report to H. D. McGuire, State Fish and Game Commissioner, State of Oregon, Salem. 14 p.

Washburn, F. L. 1903. A review of certain attempts to introduce the eastern oyster into the bays on the Oregon coast. Science 27:248.

Wennersten, J. R. 1981. The oyster wars of Chesapeake Bay. Tidewater Publishers, Centerville, Maryland, 147 p.

CHAPTER 3

Discriminating among Successful and Failed Molluscan Invaders: A Retrospective Analysis of Oyster-mediated Introductions to San Francisco Bay

ABSTRACT

The historic, large-scale movement of the eastern oyster (*Crasssostrea virginica*) from the mid-Atlantic coast to San Francisco Bay and other parts of the West Coast provides a rare opportunity to examine the phenomena of marine biological invasions. Whereas with most invasion vectors it is impossible to reconstruct what organisms were brought from where and when (e.g., the worldwide movement of planktonic stages in ballast water), the commercial introduction of the eastern oyster to the Pacific coast of the United States was a more distinct event. The source and recipient regions are well defined and the time period of oyster transport discrete. Using characteristics of biogeography, life history, and habitat of mid-Atlantic coast molluscan oyster-associate fauna, it was possible to discriminate successful invaders from failed invaders. Overall, successful mollusk invaders of San Francisco Bay had greater tolerance of low salinity habitats and appear to have been historically more abundant in the donor region. These results suggest that oyster-mediated molluscan invaders may have been successful, in

part, due to their abilities to withstand certain environmental demands as well as having been introduced in greater numbers than failed invaders were.

INTRODUCTION

Humans have inadvertently and intentionally moved marine and estuarine species around the globe for centuries (Carlton 1979, Ruiz et al. 1997, Cohen and Carlton 1998, Carlton 1999a, 1999b, Ruiz et al. 2000). Historically, shipping and aquaculture have been two of the most important modes of transport for marine and estuarine species (Ruiz et al. 1997). Shipping is a more diffuse pathway for species movement than is aquaculture, since most shipping introductions are purely accidental rather than purposeful. Furthermore, ship introductions via hull fouling or ballast are complicated by our ignorance of historical shipping patterns and the scale of this industry.

In spite of the directed nature of aquacultural introductions (e.g., well defined source and recipient regions, primary target species of introduction), this practice is in no way free of unintended outcomes. Many species are biologically or physically associated with primary target species and have been introduced to new ecosystems concurrently. Nowhere is this more true than with the commercial introduction of eastern oysters (*Crassostrea virginica*) around the world (Elton 1958, Carlton 1999b). The commercial oyster industry provides a rare opportunity to study marine/estuarine invasion biology, since there is a rich history and good documentation of the practice.

Oyster reefs have long been recognized as complex and species-rich habitats. Indeed, the ecological concept of biological community was born from Karl Möbius' observations on species assemblages of oyster reefs, what he termed the "biocönose" (Möbius 1877). With the introduction of *Crassostrea virginica* to different parts of the world came dozens of associated benthic organisms that normally coexist with oysters in the western Atlantic. Although some of these oyster associates successfully colonized San Francisco Bay and other Pacific coast locations (Carlton 1979, Carlton 1992, Cohen and Carlton 1995), most did not.

Enlisting the well-documented (Carlton 1979, Cohen and Carlton 1995) molluscan invasions of San Francisco Bay as a case history, this study aims to understand why some western Atlantic mollusks have been successful invaders while others have not. The approach was to determine whether successful and failed molluscan invaders could be differentiated according to their biological characteristics. Carlton (1992) and Cohen and Carlton (1995) identify five bivalves, *Gemma gemma* (Totten, 1844), *Geukensia demissa* (Dilwyn, 1817), *Macoma balthica* (Linne, 1758), *Mya arenaria* Linne, 1758, and *Petricolaria pholadiformis* (Lamarck, 1818), and seven gastropods, *Boonea bisuturalis* (Say, 1821), *Busycotypus canaliculatus* (Linne, 1758), *Crepidula convexa* Say, 1822, *Crepidula plana* Say 1822, *Myosotella myosotis* (Draparnaud, 1801), *Ilyanassa obsoleta* (Say, 1822), and *Urosalpinx cinerea* (Say, 1822), as invading mollusks that were likely introduced with eastern oysters from the western Atlantic. Single variable and multivariate approaches were used to search quantitatively for salient biological differences between successful and failed invaders and to see whether similar patterns emerged among bivalves and gastropods. Because of the comparatively small invader sample sizes (5 bivalves and 7 gastropods) and hence lack of statistical power, it was not feasible to create a precise multivariate model using a subset of the data and test the model with the remainder. This approach has been employed effectively with invasive plants where sample sizes were larger (Goodwin et al. 1998, Reichard and Hamilton 1997, Rejmánek and Richardson 1996, Rejmánek 1999). Given the current limitations of marine invasion data in general, the development of detailed prescriptive tools for invader prediction and conservation management is not yet possible. However, efforts to quantify biological differences between successful and failed invaders are critical steps in this direction (Rejmánek and Richardson 1996).

By marshaling information compiled by observers of the commercial oyster industry with data and observations collected by marine biologists and natural historians from the past two centuries, a species pool of potential molluscan invaders of the West Coast was generated. This species pool was characterized according to each member's biogeography, habitat preference, and life history. Using data from modern investigations of invasion biology (e.g., Carlton 1979), successful oyster-mediated invaders were compared with failed invaders. The present analyses indicate that successful invaders of San Francisco Bay had 1) statistically lower salinity limits and 2) occurred in greater abundance in the donor region during the late 1800s (when live oysters were being shipped west) than did failed invaders.

Crassostrea virginica - A vector for invertebrate introductions

During the past two centuries, eastern oysters (*Crassostrea virginica*) have been transported widely within and outside the United States (Carlton and Mann 1996) (Figure 3.1). Because of the eastern oyster's prominence as an important commercial fishery, the history of its movement has been documented more fully than most marine species.

Oyster transport has occurred within and outside its native geographic range. The focus of this study is the introduction of *Crassostrea virginica*, and its molluscan associates, from the mid-Atlantic to San Francisco Bay, but eastern oysters were also introduced to other embayments in California, Oregon, Washington, British Columbia, as well as Hawaii, and Northwestern Europe (Figure 3.1).

South to North Seed Oyster Transplantation

As described in Chapter 2, from the early 1800s onward, seed oysters were dredged from oyster beds in the Chesapeake Bay, piled on the decks of sailing vessels, and shipped to the depleted beds of New York and New England, where they were laid out for maturation (Ingersoll 1881). Because of the intense fishing pressure in New England and New York, this transfer of so-called southern oysters to northern oyster grounds was carried out every year to replenish stocks (Ingersoll 1881).

Westward Shipment of Live Oysters by Rail

The introduction of eastern oysters to the West Coast was discrete in both time and space. Although canned oysters were shipped under sail from Baltimore to San Francisco as early as the 1840s, live eastern oysters were not imported from the East Coast to San Francisco until the completion of the transcontinental railroad in 1869 (Ingersoll 1881, Barrett 1963, Bourne 1997). Adult oysters were originally packed in barrels and transported from east to west on refrigerator cars for direct sale in San Francisco markets (Ingersoll 1881, Barrett 1963). It was soon discovered that oysters grew well in San Francisco Bay and that it was more economical to ship larger numbers of smaller seed oysters rather than adult market oysters. Not only could more seed oysters be shipped per barrel, but also in-route mortality was lowered with smaller oysters (Barrett 1963). Shipments of seed oysters were removed from rail cars and placed in the Bay for grow-out and harvest in subsequent years.

The westward shipment of live eastern oysters continued from 1869 until the mid-20th century. At its height in the 1890s, the commercial oyster industry was shipping an average of 125 rail carloads of eastern oysters to San Francisco per year (Carlton 1979). At roughly 90 barrels per car and from 4,000 to 8,000 seed oysters per barrel (Barrett 1963) the number of oysters introduced to San Francisco was astronomical (from 450,000,000 to 900,000,000 oysters in the 1890s alone).

Following widespread failure of oyster seed growth in San Francisco Bay after 1910, seed was no longer shipped to California, but adult oysters were transported again to San Francisco Bay and Tomales Bay beds for holding until sale (Bonnot 1935, Barrett 1963, Shaw 1997). Bonnot (1935) indicates that following the 1910 failure no attempt was made to grow oysters in California waters until 1931 when the California Division of Fish and Game and the U.S. Bureau of Fisheries began experimenting with oyster culture (including *Crassostrea virginica*). Kornicker (1975) reports continued importation of adult oysters from Gardiner's Bay, Long Island to Tomales Bay until at least the 1970s.

Oyster Export from the Mid-Atlantic Coast (New York/Long Island Sound)

The delineation of the source region for *Crassostrea virginica* in this study is based on historical accounts describing locations from which westbound oysters originated. While *Crassostrea virginica* occurs in appropriate habitats in west Atlantic estuaries and coastal embayments from the Gulf of Saint Lawrence south to the Gulf of Mexico (48° N to 26° N), only oysters from part of this latitudinal range were introduced to the West Coast.

The source region for westbound live oysters was confined strictly to latitudes north of Cape Hatteras, North Carolina (Carlton 1979). New York City and vicinity was the center for live export to inland states, the West Coast, and Europe (see Chapter 2). According to Ingersoll (1881) "The oysters sent to California are all procured from beds in the neighborhood of New York, and are sent exclusively by the firm J. & J. W. Ellsworth . . . ." Although Baltimore was certainly an important export center for oysters, the focus of this market was the shipment of fresh (shelled) and preserved oysters rather than live oysters (Churchill 1920).

Townsend (1893) stated "Eastern oysters have for the past twenty-five years been brought to California in the form of seed and kept in the Bay for three or four years until grown to a large size." The first shipments of seed oysters came from New York and were imported by the San Francisco-based Morgan Oyster Company in 1869 (Barrett 1963). Barrett (1963) summarized the oyster donor regions as follows:

> One and 2-year-old seed oysters were brought from the east coast in the spring and fall of the year, from mid-March to mid-May and from mid-October to mid-November, the two periods when they are in peak condition. Most of these came from bays and estuaries of New York and northern New Jersey, principally Newark Bay and the North River, but also Raritan River, New Jersey, and Prince Bay, Staten Island. Oysters from the east side of Manhattan Island (Blue Points, East Rivers, York Bays, Staten Island Sounds, Rockaways) were preferred for flavor, but they did not survive the cross-country journey so well.

Although some oysters from Chesapeake Bay were planted in Willapa Bay, Washington as part of an experiment, the number was small (12 of 80 barrels planted between 1896 and 1900) (Townsend 1896). Hubbs and Miller (1965) cite the planting of 2 barrels of Chesapeake oysters in Yaquina Bay, Washington in 1878. There is no indication that any significant numbers of California-bound oysters came directly from the Chesapeake Bay.

To define the source regions for oysters, reports on the commercial oyster industry were invaluable (e.g., Ingersoll 1881, Collins 1892, Galtsoff 1929). In addition to outlining the magnitude of the oyster fishery in various geographic locations up and down the Atlantic coast, such reports often indicated the major markets for oysters and oyster products. Descriptions of the market often outlined the route by which oysters were moved, including transport by rail to the West Coast. Perhaps the most important features of these reports were the in-depth descriptions, procedures, and practices used. Ingersoll's (1881) comprehensive treatment of the commercial oyster industry of North America describes all aspects of oystering from its earliest history and development, to the most technical aspects employed by oyster fishermen and retailers.

METHODS

Molluscan Oyster Associates

Membership in the oyster community was determined by reviewing the marine ecological literature from the past 200 years. A mollusk was considered an oyster associate if there was strong evidence that the species had been found alive on oyster beds or in barrels of oysters taken for live shipment. In this study, the term oyster associate does not indicate a strict biological relationship with oysters, but instead signifies that a species has been found living in the same habitat as oysters. This definition is a functional one that attempts to describe those molluscan species with the highest likelihood for capture as oysters were dredged or otherwise taken. The species described in this study were confined to oyster beds in the mid-Atlantic and farther north, since southeastern and Gulf of Mexico oysters were not part of the West Coast trade.

Oyster associate species were documented in the following seven studies: (1) *The Fauna of Oyster Beds, with Special Reference to the Salinity Factor* by Wells (1961). This is perhaps the most comprehensive study of oyster fauna of North America's Atlantic coast. The location of this study was just south of Cape Hatteras in Beaufort, NC (34°45′ N). To ensure all species named had the potential to be found in oyster beds farther north, where oyster exports originated, only molluscan species known to live at higher latitudes, north of Cape Hatteras, were included on the list of oyster associates. Of the 303 species of invertebrates Wells found on oyster beds, 99 were mollusks. Of these, 31 shelled gastropods and 20 bivalves were included in the present analysis. (2) *The Benthic Macrofauna Associated with the Oyster Reefs of the James River Estuary, Virginia, U.S.A.*, by Larsen (1985). Larsen reported 16 shelled gastropods and 13 bivalves. The Atlantic rangia, *Rangia cuneata* (G. B. Sowerby I, 1831), although present in Larsen's study, was not included in the list of potential oyster associates because it extended its range northward into the Chesapeake Bay only in the 1960s (Hopkins and Andrews 1970, Pfitzenmeyer and Drobeck 1964). (3) *Oyster Bars of the Potomac River,* by Frey (1946). Frey lists 6 shelled gastropods and 10 bivalves. (4) *The Biology of the Oyster Community and its Associated Fauna in Delaware Bay*, by Maurer and Watling (1973a). Maurer and Watling report 21 shelled gastropods and 20 bivalves in the Delaware Bay oyster community. (5) *Mollusks found in the Oyster Beds of Cocagne, N.B. and Bedeque and Summerside, P.E.I.*, by Winkley (1888), who listed 17 shelled gastropods and 12 bivalve species. Interestingly, Winkley compiled his list from specimens he took directly from 38 barrels of oysters dredged from the waters of New Brunswick and Prince Edward Island. (6) *The Invertebrate Animals of Vineyard Sound and Adjacent Waters, with an Account of the Physical Features of the Region, Section III.3, Animals Inhabiting Oyster-Beds in Brackish Waters*, by Verrill and Smith (1874). Verrill and Smith list 14 shelled gastropods and 8 bivalves. (7) *Estuarine Vegetated Habitats as Corridors for Predator Movements* by Mitcheli and Peterson (1999). Micheli and Peterson list 6 shelled gastropods and 10 bivalves from the Cape Hatteras vicinity whose northern ranges reach into the region of study. *Crassinella lunulata*, *Zirfaea crispata*, *Laevicardium mortoni*, *Hiatella arctica*, *Littorina littorea*, and *Nucella lapillus* did not appear in this literature as oyster associates, but are known to be so, and were thus included (J. T. Carlton, pers. comm.).

The compiled list of oyster associates is composed of 93 mollusk species, 42 bivalves and 51 gastropods (Tables 3.1 and 3.2). So as not to inflate the oyster community with inappropriate species, great care was taken to include only those species that have been explicitly observed coexisting with oysters, with the following exceptions. Although neither of the two pulmonate snails *Myosotella myosotis* or *Melampus* *bindentatus* lives directly among oyster beds, these snails are common nestlers of intertidal areas and likely had access to dredged oysters awaiting shipment. The primary habitat of both snails is the extreme upper intertidal, especially in salt marshes. Each species is submerged during maximum spring tides (McMahon and Russel-Hunter 1981, Capaldo 1983, Berman and Carlton 1991), but both species can also be found in lower elevations of the intertidal zone. How could pulmonate snails be associated with oysters? The opportunity for nestling was certainly present as oysters were "freshened" on shallow barges in lower salinity intertidal creeks. Oysters were removed from barges or boats and piled for culling or stowed in shipping houses while waiting to be barreled for shipment by rail or ship. The storage of oysters and the equipment and materials associated with oystering and shipment near the shore provided ample opportunity for these high littoral zone species to wander into oyster groups later barreled for transport.

Biogeographical, Life History, and Habitat Characteristics of Oyster Associates

After compiling the list of probable oyster associates from the coastal waters of the mid-Atlantic states, New England, and Canadian Maritime provinces, members of this list were characterized by their biological, ecological, and biogeographical attributes (see Appendices 3.1 and 3.2). The natural history of each member of the oyster associate list was summarized through a review of the scientific literature from the early 19th century to the present. The biological, ecological, and biogeographical characteristics used for analysis were limited to those traits for which reliable information was available.

With the exception of widely studied species such as commercially important bivalves (*Crassostrea virginica, Mya arenaria, Argopecten irradians*) and certain numerically dominant gastropods (e.g., *Ilyanassa obsoleta, Littorina littorea*), the complete natural history is not known for most of the molluscan oyster associates considered here. In particular, there is a lack of detailed information concerning the biology of larval life stages for many species. As a result, the characteristics analyzed in this study are limited primarily to the adult stages of the organisms. Although this practice limits the scope of the study, it accurately reflects the extent of our current knowledge of this fauna.

Historical Accounts

Every effort was made to gather data that were relevant to the time period under consideration, 1869-1939. Limiting the time period was especially important for characterizing relative abundance values for the species included. Although, in general, one would expect membership of the oyster community to remain relatively stable through time, abundance values can fluctuate due to changes to the physical and biological environment. The invasion by a nonindigenous species can sometimes have such an impact. For example, the introduction of a single species, the common periwinkle (*Littorina littorea*) to Nova Scotia (followed by a southward spread to the mid-Atlantic coast) in the 19th century has significantly altered habitat (Bertness 1984) and affected intertidal dynamics and composition (Carlton 1992, Lubchenco 1978). In particular, the numerical dominance of the native eastern mud snail (*Ilyanassa obsoleta* =

Nasarrius obsoletus) appears to have been adversely affected by *Littorina littorea* (Brenchley and Carlton 1983). Consequently, when species abundance estimates were used for analysis in this study, only estimates made during the pertinent time period were included.

Categorical Variables

Salinity Range Classes

Typically, organisms do not span the entire salinity spectrum from 0 to =35 ppt. Instead, some species are confined to estuaries (true estuarine species) while others are primarily marine or freshwater organisms that stray into parts of the estuary. Animals are often described as stenohaline (occurring in a narrow range of salinities) or euryhaline (occurring in a wide range of salinities). In this paper, species have been assigned to four categories based on each one's range of salinity tolerance and whether the organism is confined to estuarine conditions. The four categories are: 1) stenohaline-marine (a salinity range spanning 15 ppt or less and including marine conditions of 32 ppt or more, 2) stenohaline-estuarine (a salinity range spanning 15 ppt or less, but confined to estuarine conditions, 3) euryhaline-marine (a salinity range spanning 16 ppt or more, including marine conditions), and 4) euryhaline-estuarine (a salinity range spanning 16 ppt or more, but confined to estuarine conditions).

Developmental Mode

Each species was categorized according to its developmental mode. Bivalves and gastropods were listed as either planktonic developers (i.e., with planktonic eggs and/or larvae) or direct developers that lack a planktonic stage.

Feeding Mode

Bivalves were divided into suspension feeders, deposit feeders, or suspension and deposit feeders (i.e., organisms that can feed both ways). Feeding modes varied more among gastropods. Gastropods ranged from carnivores and ectoparasites to herbivores, detritivores, and suspension feeders.

Substrate

Mollusks were divided into three substrate utilization categories: hard, soft, or both hard and soft substrates. Each species was assigned to only one of the three categories.

Vertical Distribution

The occurrence with respect to tidal height was categorized for each molluscan species as intertidal, subtidal, or both intertidal and subtidal. Each species was assigned to only one of the three categories.

Benthic Placement

Each bivalve species was designated as either infaunal or epifaunal. Being mobile organisms, gastropods were not categorized for benthic placement.

Biogeographical Faunal Provinces of Origin

Oyster associates were classified into 3 categories, according to their biogeographical faunal provinces of origin. These faunal provinces are based on the west Atlantic shallow water mollusk categorizations of Franz and Merrill (1980a, 1980b). Franz and Merrill's Boreal and Arctic categories have been combined here as "Northern." The three faunal provinces used are as follows: 1) Northern = species whose northern and southern geographic boundaries lie to the north of Cape Cod, MA and Cape Hatteras, NC, respectively. The Northern category encompasses species that are considered arctic or boreal. 2) Northern Transhatteran = species ranging to the north of Cape Cod and to the south of Cape Hatteras, NC. 3) Southern Transhatteran = species with northern limits do not extend north of Cape Cod and southern geographic boundaries that extend south of Cape Hatteras. Tables 3.1 and 3.2 summarize the faunal groupings of bivalves and gastropods.

Amphi-Atlantic Distribution

Species whose natural distribution includes the eastern and western Atlantic are called amphi-Atlantic species. Each species was categorized as either amphi-Atlantic or not. Species believed non-native to the western Atlantic (i.e., introduced by humans in historical times) are not treated as amphi-Atlantic species.

Invasion Success Elsewhere

Each species from the oyster associate list was categorized as a successful or failed invader to San Francisco. Those species that failed to establish populations in San

Francisco, but which successfully invaded another location in the world, were also specified.

Continuous Numerical Variables

Species Latitudinal Distributions

The spatial distribution along the western Atlantic coast was determined for each of the molluscan species analyzed; southern limit, northern limit are reported in terms of degrees latitude (Tables 3.1 and 3.2). In general, the geographic extents of bivalve species were based on distribution descriptions from Abbott (1974). Northern and southern geographic ranges were converted to latitude for analysis. The latitudinal ranges of gastropods were taken from the Academy of Natural Science of Philadelphia's online database Malacolog 2.0 (ANSP 1996), edited by the Academy's Gary Rosenberg. In a few instances, published accounts of a species' range that superseded the above references were used. Native distributions of each of the 12 San Francisco invaders are presented in Figures 3.2a-3.2l.

In cases in which the geographic location of a range boundary was not specified precisely (e.g., Nova Scotia), the named location's northern and southern limits were averaged, and this was operationally considered as the species' range boundary. It is important to keep in mind that most geographic ranges are neither static nor necessarily fully known. Instead, range limits depend in part on where and when scientists have concentrated their search efforts. The ranges of some mollusks may actually be greater than those reported since not all latitudes have been equally studied. Mollusks and other marine faunal ranges presumably have some between-year variation, perhaps dependent on ocean temperature and current characteristics. For example, Wells and Gray (1960) describe the expanding and contracting range of *Mytilus edulis* around Cape Hatteras, attributing this fluctuation to changes in water temperature and current characteristics. Throughout this paper the terms “range limit,” “northern limit,” and “southern limit” are used to indicate the current best knowledge of range extents, not absolute boundaries. Unlike most marine invertebrates, the mollusks leave their hard shells after death. Because of the widespread interest in seashells by professionals and amateurs, much of the natural history of mollusks has been well described when compared to other marine phyla.

Salinity

The lower salinity limits for the adult stages of bivalves and gastropods were gleaned from the literature. Care was taken to report only lower salinity ranges experienced by organisms in their native habitats rather than in laboratory situations. The extreme variability of acclimatization regimes and tolerance endpoints (e.g., LD50, loss of ciliary movement) made comparisons among laboratory based experiments untenable. Each species’ lower salinity tolerance limit was reported in parts-per-thousand (ppt). Although field distributions do not necessarily indicate absolute tolerance limits, they probably reflect natural conditions that are most suitable for successful growth and reproduction. Data on salinity ranges of larval stages are far too fragmentary for use in this study.

Shell Size

Maximum adult shell size was estimated in millimeters. Shell sizes were obtained primarily from Abbott (1974), Gosner (1971, 1978), Rehder (1997) and Malacolog II online database (ANSP 1996). Shell sizes were log transformed to approximate better a normal distribution before analysis.

Substrate and Depth Diversity

In addition to the general categorical substrate designation (soft, hard, soft & hard substrates), the diversity of substrates where each species naturally occurs (a continuous variable) was compiled and the range of substrates approximated by numerical index (1-5). Species with very narrow substrate requirements received low numbers and generalists were assigned higher index values.

Similarly, an index for depth diversity was assigned to each species (1-4). Subtidal species with broader depth ranges were given higher rankings than subtidal species with narrower depth distributions. Diversity scores are based on presence in various depth intervals. Species were given 1 point for each of the following categories: intertidal, 0-25m depth, >25-100m depth, >100m depth (e.g., a species that occurs intertidally and subtidally to a depth of 35m receives a depth diversity index of 3).

Historical Molluscan Abundance in New York and Long Island Sound Vicinities

To estimate the relative abundance of oyster associate fauna, data were compiled from the scientific literature. To avoid applying potentially inappropriate abundance values, data were taken from the time period under study, namely 1869 to 1910. Such data were available from the following oyster-producing areas: Eastern Long Island (Smith 1862); Staten Island (Hubbard and Smith 1865, Smith 1887); New Haven, Connecticut (Perkins 1869); Long Island embayments (Smith and Prime 1870); Cold Spring Harbor, Long Island (Balch 1899). Since field biologists of the 19th century were primarily descriptive in their research, they rarely quantified organisms explicitly. The studies included here are somewhat atypical in that each attempted to describe the relative abundance of the benthic fauna observed. A comment by Balch (1899) indicates his concern that abundance be recorded for future comparisons : “Too vague to serve as an absolute measure it is yet to be hoped that it will prove accurate enough in relative terms to enable some future student to determine what changes in distribution . . . might prove a useful reference-point for future comparisons.”

In general, species abundance was ranked qualitatively as “absent,” “rare,” “uncommon,” “common,” and “abundant.” Modifiers such as “very,” “extremely,” “moderately,” and “locally” were also sometimes applied. Although not identical, these categorical designations were similar across studies. It is impossible to know how closely calibrated various authors’ qualitative estimates were, but all authors did use ranked categories to characterize the relative abundance of species. As the author of four of the six studies, Sanderson Smith {Smith (1862), Hubbard and Smith (1865), Smith and Prime (1870), Smith (1887)} likely brings consistency to the Staten Island and Long Island region estimates.

A numerical ranking system was developed to describe each of the abundance categories used. The numerical rankings range from 0 (absent) to 10 (extremely abundant). When multiple locations were described in a single study, the rankings for each site were averaged to reflect evenness of species abundance over space. Abundance values were compiled for all species in each study and then averaged (arithmetic mean) across studies. Since averaged values are integrated across the geographical location and the time period of interest, they are assumed to approximate the relative abundance of oyster associates.

To test the sensitivity of statistical analyses to ranking and abundance estimation, ranking was approximated on a scale from 1 to 11 and the composite abundance calculated from the geometric mean. Statistical results from geometric means were compared with those of arithmetic means and shown to yield similar results.

Statistical Tests

To fully characterize potential differences between successful and failed invaders, both univariate and multivariate statistics were used. This multivariate approach allowed all characters, both discrete and continuous, to be considered simultaneously and the results displayed graphically. Although multivariate statistics can simultaneously indicate statistical differences attributable to multiple variables and their interactions, separate univariate analyses sometimes included larger sample sizes than was possible with multivariate methods. Additionally, univariate methods individually compared the biological characteristics of successful invaders with the entire species pool, while the purpose of the multivariate analyses was to discriminate among three subgroups: San Francisco Invaders, Non-San Francisco Invaders, and Failed Invaders (see below).

Univariate Tests

Contingency Tests of Independence

In instances where data were reported as nominal variables (i.e., qualitative attributes), contingency tests of independence were used to compare attribute frequencies of successful invaders with those of the entire species pool of oyster associates. Row and column tests of independence using G-tests were employed (Sokal and Rohlf 1981) to determine whether species attributes such as the presence of planktonic development, benthic placement, or membership in certain biogeographical faunal types had bearing on successful invasion or not. Frequency tables were comprised of rows (species attributes) and columns (successful invader or failed invader) and varied in size from 2x2 to 4x2. G-values were compared with the ?^{2}-distribution with (row-1)(column-1) degrees of freedom. Statistically significant outcomes indicate that successful invaders differ from the species pool as a whole with respect to their biological attributes.

Statistical Power Analyses for Contingency Tests of Independence

Post-hoc statistical power analyses for ?^{2}-tests were performed using G*Power statistical software (Faul and Erofelder 1992). Statistical power was calculated by specifying sample size (n), degrees of freedom (df), effect size (w), and alpha (a=0.05). Effect size (w) increases as the discrepancy between distributions specified by the alternative and null hypotheses increase and was calculated by the program from the observed and expected frequencies (i.e., where frequencies are defined by the contingency table cell values) for each test according to Cohen (1977):

$$w = \sum_{i=1}^{m} \sqrt{\frac{(P_{1i} - P_{0i})^2}{P_{0i}}} \, ,$$

where **P_{0i}** = the proportion of cell **i** posited by the null hypothesis (i.e., expected, random distribution),

P_{1i} = the proportion in cell **i** posited by the alternative hypothesis (i.e., observed distribution),

m = the number of cells in the contingency table.

All expected cell values were calculated by multiplying the row total by the column total and dividing by the grand total (Snedecor and Cochran 1980).

Re-Sampling Techniques

Monte Carlo simulations (re-sampling statistics) were used to test hypotheses regarding successful versus failed molluscan invaders of San Francisco Bay. For the purposes of these analyses, it must be noted that “failed” or “unsuccessful” do not imply a species positively lacks the capacity to invade, only that, to date, it has not become established in San Francisco Bay. In general, re-sampling allowed the group of successful invaders to be compared with subsets containing the same number of species that were randomly sampled from the entire list of probable oyster associates. Specifically, this procedure tested whether or not the average values of biological and biogeographical characteristics from the assemblage of successful invaders could be expected to arise from the available population purely as a matter of chance.

For traits that were expressed as continuous variables, the mean value for invaders was compared to a distribution of permuted means taken at random from the entire list of oyster associates. To simulate the full spectrum of potential combinations available from the population, a subset of 10,000 random grabs was used to build a sample frequency distribution (Manly 1992). The mean invader value for some variable (e.g., maximum body size) was then compared to the 95th percent confidence interval of the sample distribution (n = 10,000). If the mean invader maximum body size fell outside the 95th percent confidence interval of the re-sampled distribution, this result was taken as statistical evidence that invaders, on average, differed from the rest of the community with respect to that maximum body size.

Multivariate Tests

Discriminant Analysis

Linear discriminant analysis was used to simultaneously test the importance of multiple biogeographic, life history, and habitat characters for classifying oyster associates as 1) “San Francisco Bay invaders,” 2) “Failed invaders,” or 3) “Non-San Francisco Bay Invaders” (i.e., successful invaders of some localities, but which failed in San Francisco Bay). Individual species were plotted in canonical discriminant space to visualize separation among groups. Statistical significance of classifications was tested using Wilk’s lambda (Wilkinson et al. 1996). The discriminant function’s stability was tested using a jackknifed classification method. Stepwise analyses were used to systematically winnow the least important variables (those adding least to discriminating power) from the discriminant model. Discriminant analyses included all 18 biological and biogeographical characters. Continuous numerical data were analyzed directly, while categorical data were assigned dummy variables before analysis.

RESULTS

Univariate Analyses

Biogeography

Biogeographical attributes focus primarily on the native ranges of oyster associate species. Invasion success to locations other than San Francisco Bay, biogeographical faunal provinces of origin, latitudinal range, northern limits, southern limits, and amphi-Atlantic native distribution, were investigated.

As a group, mollusk invasions to other parts of the world were more common among successful San Francisco Bay invaders than the rest of the group (p=0.004, n=93, power=0.96). The extent of invasion by bivalves to other parts of the globe was higher among successful San Francisco Bay invaders than among other bivalve oyster associates (p=0.02, n=42, power=0.88). No such distinction could be drawn for gastropods, probably because the statistical power to detect a difference was exceedingly low (p=0.121, n=51, power=0.06).

Of the species on the oyster associate list, 48 species (51.6%) have Northern Transhatteran distributions, 34 species (36.6%) have Southern Transhatteran distributions, and 11 species (11.8%) have Northern distributions (Tables 3.1 and 3.2). Among the 12 San Francisco Bay invaders, 11 (91.7%) are either Northern or Northern

Transhatteran. When all mollusks were compared, a difference in invasion success due to a biogeographical faunal province effect was suggested (p=0.087, n= 93, power = 0.46), but a lack of statistical power precluded a conclusive result (Table 3.3). Invaders could not be statistically separated from failed invaders according to native faunal province for either bivalves (p=0.087, n=42, power=0.45) or gastropods (p=0.630, n=51, power=0.12). Of the gastropods, *Busycotypus canaliculatus* does not normally range to the north of Cape Cod, although there are records of its presence in Casco Bay, Maine (Perkins and Larsen 1975). Whether or not this species reproduces north of Cape Cod could not be determined. Given the historic movement of live oysters to Maine from more southern locations (Ingersoll 1881), it is likely that this species was introduced by this mechanism. Categorizing *Busycotypus canaliculatus* as Southern Transhatteran or Northern Transhatteran made no difference to statistical outcomes.

Species with natural amphi-Atlantic distributions did not invade more or less readily for any of the groups. Statistical power was extremely low, so possible differences may not have been discernible. None of the other biogeographical attributes considered (latitudinal range, northern limit, or southern limit) conferred greater invasion success for bivalves, gastropods, or mollusks as a group (Table 3.3).

Habitat Preferences

Among the shelled mollusks as a whole, invaders differed from failed invaders according to their vertical distribution (p=0.006, n=92, power=0.70), salinity zonal distribution (i.e., stenohaline estuarine, euryhaline estuarine, euryhaline marine, stenohaline marine) (p=0.042, n=77, power=0.46), and low salinity limit (p=0.018, n=75). No differences were observed for any of the other habitat preference factors.

The vertical distribution (i.e., intertidal, subtidal, or both habitat types) of invading bivalves did not differ statistically from that of failed invaders (p=0.085, n=41, power=0.80). Interestingly, all San Francisco invaders were either exclusively intertidal or live in the intertidal and subtidal – none are subtidal specialists. This pattern is also true among the gastropods; there were no subtidal specialists that successfully invaded San Francisco Bay. No differences between invaders and failed invaders were observed with regard to bivalve salinity zonal distributions, but bivalves that successfully invaded San Francisco Bay have lower average salinity limits than do failed invaders (p=0.019, n=36) (Table 3.3). Bivalve invaders of San Francisco Bay occur over larger salinity ranges than non-invading bivalve oyster associates (p=0.020, n=36). There were no differences between bivalve invaders and failed invaders for salinity range, substrate preference, substrate diversity, or depth diversity.

Successful and failed gastropod invaders could not be separated statistically on the basis of any of the habitat preference variables investigated (Table 3.3). But, statistical power was quite low for most habitat preference with the exception of vertical (tidal) distribution. Test results for the remaining habitat preferences were obtained with resampling techniques that incorporated 10,000 replications and should therefore be statistically robust.

Life History Traits

The proportion of direct developers among invaders appears higher than among mollusks that failed to invade. Of 12 molluscan invaders of San Francisco Bay, 5 (41.7%) were direct developers and 7 (58.2%) were planktonic developers (Tables 3.4 and 3.5). Of the 81 species for which developmental mode was available, 16 (19.8%) were direct developers and 65 (80.2%) were planktonic developers. When bivalves and gastropods were analyzed together, the overall developmental mode pattern of invading species differed significantly from that of the group as a whole (p=0.037, n=81, power=0.67). However, among successful San Francisco Bay invaders, neither bivalve nor gastropod developmental mode patterns deviated significantly from failed invaders (i.e., invasion success within each group is independent of developmental mode).

There was no detectable difference between invading and non-invading mollusks (as a group), bivalves, or gastropods with respect to adult shell size, nor could bivalves be differentiated on the basis of benthic placement (infaunal versus epifaunal) (Table 3.3).

When 19th century species abundance estimates were ranked across multiple oyster producing locations in the Long Island Sound and New York/New Jersey region, invading mollusks were more abundant by far than non-invading oyster associates. Invading bivalves ranked 2 (*Geukensia demissa*), 3 (*Mya arenaria*), 5 (*Gemma gemma*), 8 (*Macoma balthica*), and 14 (*Petricolaria pholadiformes*) of 42 species. Successful gastropod invaders ranked 1 (*Ilyanassa obsoleta*), 4 (*Crepidula plana*), 8 (*Busycotypus canaliculatus*), 9 (*Crepidula convexa*), 13 (*Urosalpinx cinerea*), 18 (*Boonea bisuturalis*), and 23 (*Myosotella myosotis*) out of 51 species. These differences were highly significant for bivalves (p=0.004, n=42), gastropods p=0.002, and both mollusk types together (p=0.0002). Although source abundance appears to have been important for invasion of San Francisco Bay, it was not sufficient for successful invasion, as evidenced by the presence of failed invaders in upper abundance ranks (e.g. *Mercenaria mercenaria*, *Nucula proxima*, *Bittiolum alternatum, Littorina saxatilis,* see Tables 3.1 and 3.2).

Discriminant Analyses

Linear discriminant analyses were used to differentiate successful invaders from failed invaders across biological characteristics. The goal of discriminant analysis, like principal components analysis, is to identify orthogonal axes that best explain the greatest amount of variance contained in a data set. Discriminant functions define derived axes, where each is comprised of a linear combination. Discriminant functions are weighted by the magnitude of each constituent variable's coefficients. Thus, the greater the coefficient, the more important its is variable for explaining variance. Wilkinson et al. (1996) provides a review of linear discriminant analysis.

Bivalves

Invading bivalves were differentiated from failed invaders on the basis of their biological characters (Wilk's Lambda=0.477; approximated F=7.17, df=4, 64, p=0.0001). A stepwise linear discriminant analysis systematically removed all factors except lower salinity limit and historical source abundance from the discriminant model. Biological factors were removed according to each one's discriminating strength and correlation with more powerful discrimination factors. Of the two parameters included in the model, lower salinity limit had the highest discriminating power (F-to-remove = 9.21), followed by source abundance (F-to-remove = 6.12). The bivalve discriminant model (Figure 3.3) incorporated the following two canonical discriminant functions:

Function 1=0.284(Source Abundance)-0.153(Low Salinity)+1.049 and Function 2=0.275(Source Abundance)+0.100(Low Salinity)-2.353. Lower salinity limit and source abundance accounted for 97.2% of the total dispersion in the model. All San Francisco Bay invaders and non-San Francisco Bay invaders (with the exception of *Mytilopsis leucophaeta*) occur in the San Francisco Bay invader 95th percent confidence ellipse (Figure 3.3). Clustering is also evident in a simple linear scatterplot of lower salinity limit and historical source where both San Francisco Bay invaders and non-San Francisco Bay invaders are confined to the lower right quadrant of the scatterplot (Figure 3.4).

Although statistically significant, discrimination was not perfect. Overall, the model classified 4 of 5 (80%) San Francisco Bay invaders correctly, 25 of 28 (89.3%) failed invaders correctly, and 1 of 3 (33.3%) non-San Francisco Bay invaders correctly based on a species' nearness to a group centroid. Interestingly, 2 of the 3 non-San Francisco Bay invaders (*Crassostrea virginica* and *Mercenaria mercenaria*) fell solidly within the 95th percent confidence ellipse of the San Francisco Bay invader centroid as well as within the non-San Francisco invader confidence ellipse (Figure 3.3). Likewise, the invader *Petricolaria pholadiformes* fell within the San Francisco Bay invader confidence ellipse, but lies closer to the failed invader centroid and was thus considered misclassified. Six failed invaders also fell within the invader confidence ellipse.

As discussed above, univariate tests also statistically separated bivalves according to historical abundance and tolerance of low salinity conditions.

Gastropods

The power to discriminate among invading and non-invading species was much less among gastropods than among bivalves. Initially, when an automated stepwise linear discriminant analysis was performed using the same criterion for factor removal (F-to-remove = 3.9) for gastropods as for bivalves, no factors had adequate discriminating power for inclusion in the model. When lower salinity limit and historical source abundance were manually included in the analysis, the model discriminated successful invaders from failed invaders (Wilk's Lambda=0.725; approximated F=3.06, df=4, p=0.022). Although the lower salinity limit fell short of the threshold for inclusion by the stepwise analysis (F-to-remove=1.41), when combined with historical source abundance, a strong discriminating factor (F-to-remove=4.99), the San Francisco Bay invader and failed invader clusters were statistically separable (Figure 3.5). The discriminant model was parameterized by the following discriminant functions: Function 1=0.377(Source Abundance)-0.089(Low Salinity)-0.121 and Function 2=0.180(Source Abundance)+0.149(Low Salinity)-2.916. All San Francisco Bay invaders and non-San Francisco Bay invaders, except *Littorina littorea*, occurred in the 95th percent confidence ellipse for San Francisco Bay invaders (Figure 3.5).

A linear scatterplot shows that the invading gastropods were more abundant historically than failed invaders (Figure 3.6). All San Francisco Bay gastropod invaders, except the pulmonate snail *Myosotella myosotis*, clustered together at high historical abundance and similar lower salinity limit (Figure 3.6). Additionally, one of the two non-San Francisco Bay invaders, *Crepidula fornicata*, also grouped closely with San Francisco Bay invaders. Although average lower salinity limit is less among bivalves than gastropods, the salinity range is approximately equal (approximately10 to 12 ppt). Contingency tests of independence determined that successful and failed invaders differed significantly with respect to source abundance, but that they could not be separated on the basis of their tolerance of lowered salinity (Table 3.3).

Mollusks

When bivalves and gastropods were combined, lower salinity limit and historical abundance were shown to be the most powerful discriminators of invader and failed invader mollusks (F-to-remove = 8.38 and 11.29, respectively) (Figure 3.7). Molluscan invaders, as a group, tolerate lower salinities and occurred at higher abundances in their source region than failed invaders (Wilk's Lambda= 0.622; approximated F=9.49, df=4, p =0.00005), yielding the following canonical discriminant functions: Function 1=0.330(Source Abundance)-0.123(Low Salinity)+0.529 and Function 2=0.247(Source Abundance)+0.125(Low Salinity)-2.702). When all mollusks are graphed according to their historical abundance and tolerance of low salinity, all but 1 (*Myosotella myosotis*) of the 12 San Francisco Bay invaders clustered together. Additionally, 3 of the 5 non-San

Francisco invaders (*Crepidula fornicata, Crassostrea virginica*, and *Mercenaria mercenaria*) also grouped closely with successful invaders (Figure 3.8).

Univariate tests demonstrated significant differences for vertical distribution, salinity zonal distribution, and developmental mode (Table 3.3) but these characters did not contribute appreciably to the multivariate discrimination among mollusks.

DISCUSSION

Differentiating Successful and Failed Invaders

While often discussed on theoretical grounds, there have been few attempts to quantify biological differences between species that do and do not successfully colonize regions outside their native ranges (Lodge 1993). The majority of such studies have been restricted to terrestrial systems (Rejmánek and Richardson 1996, Rejmánek 1999, Reichard and Hamilton 1997), with few or none concentrating on marine systems.

In this retrospective analysis of the historic commercial oyster trade (*Crassostrea virginica*) between the mid-Atlantic coast and San Francisco Bay, California, successful invaders and failed invaders were effectively differentiated according to two biological characteristics, 1) tolerance to low salinity and 2) historic abundance in the donor region. This pattern held true for bivalves and the mollusks as a whole, but was less evident, yet statistically significant, for gastropods. Linear discriminant analysis was shown to be an effective analytical tool for identifying biological factors that differentiate successful invaders from failed invaders.

Tolerance to Low Salinity

It has been long understood that distributions of marine and estuarine benthic species are governed in part by salinity (Yonge 1949, Wells 1961, Richer 1985, Kennish 1990, Bulger et al. 1993). Estuaries range from fresh and oligohaline waters (0-2 ppt) at their upper reaches to full marine conditions (≥35 ppt) at their mouths. All successful invaders were tolerant of conditions typical of estuaries, and, as a group, tolerated lower salinities than did failed invaders. Invading bivalves, on average, tolerate lower salinities than invading gastropods.

Source Region Abundance

The notion that species with higher abundance in source regions tend to have an increased incidence of invasion raises questions about the role of abundance in the invasion process. One explanation is that higher abundance elevates the size of inoculation and therefore increases the probability of successful colonization and successful sustained reproduction. If inoculation size were the whole story, over the course of 40 years of intense introductions (followed by another 20 to 30 years of diminished introductions) it would seem that more mollusks might have reached the West Coast in sufficient numbers to colonize. Moreover, despite vast quantities of live oyster introductions to European coastal waters, the number of oyster-associated mollusk invaders there is much lower (see Chapter 4). Although the connection between inoculation size and invasion success has been demonstrated with other taxonomic groups (plants: Levine 2000, birds: Veltman et al. 1996) the relationship does not appear to have been tested previously in marine systems. An alternative explanation is that invading species are those with the inherent capacity to become numerically dominant in their native regions. In this way, invasion success might not be linked with the inoculation size, per se, but instead be a reflection of a species' typical ecology.

Issues of Diversity, Categorization, and Invading Ability

Within the Mollusca, the gastropods and bivalves are both numerically rich taxonomic groups, containing approximately 35,000 and 150,000 described, extant species, respectively (Barnes 1987). When the marine and estuarine bivalves and gastropods are compared biologically, the gastropods are by far the more diverse and specialized group (e.g., trophic status and reproductive biology).

Taxonomic and ecological diversity was certainly higher for the gastropods than for the bivalves included in this study. An offshoot of this higher gastropod diversity is that both successful and failed invaders tended to overlap to a greater degree than bivalves did for the characteristics observed. This result suggests that separating gastropods into two discrete groups (i.e., successful and failed invaders) on the basis of a handful of attributes may be more difficult than separating bivalves this way. Among gastropods, a greater diversity may underlie a greater variety of potential invasion strategies that are not fully reflected by the biological and ecological traits analyzed here. In other words, gastropods may have a greater number of options available to them for mounting a successful invasion and may not always be constrained by the same environmental factors that bivalves are (i.e., invading gastropods may be less similar to one another than are bivalves.) For example, bivalves are less mobile and must be able to survive in a single place, but most gastropods can move to more favorable locations. Therefore, bivalve invaders may be more stereotypical (able to invade new regions for the same reasons) than gastropods and thus more easily distinguished from non-invaders than are gastropods. In spite of the potential differences between gastropods and bivalves, historical abundance and tolerance of low salinity were two attributes with which successful and failed invaders could be clearly distinguished for taxonomic groups in a similar way (Figure 3.8).

Implications of Imperfect Discrimination

The presence of failed invaders and non-San Francisco Bay invaders inside the San Francisco Bay invader state space begs further interpretation and study. Although linear discriminant analysis statistically separated invaders from failed invaders, the discrimination was not perfect and some species fell into both categories. In such cases, robust classification is impossible without further information. The gastropods *Acteocina canaliculata, Neverita duplicata, Astyris lunata, Nassarius trivittatus, Melampus bidentatus, Littorina saxatilis, Eupleura caudata,* and *Costoanachis avara* share fairly similar tolerances to low salinity and had abundance similar to successful invaders (Figures 3.6). Likewise, the bivalves *Mulinia lateralis, Anomia simplex, Anadara transversa, Laevicardium mortoni* were similar to successful invaders along these lines (Figures 3.4).

The fact that some failed invaders group closely with successful invaders suggests that salinity and source region abundance, though important, are not the only critical factors determining invasion success. Given the complexity of interaction between organisms and their physical and biological environment, it is not surprising that complete discrimination between successful invaders and failed invaders could not be performed with only 2 or 3 factors. Conversely, the presence of failed invaders in the successful invader cluster may indicate likely future invaders, given continued introduction. Again, these analyses only included attributes of adult life stages but invasion ability may also be limited by larval attributes as well.

Without doubt, the physical and biotic environments are important to invasions (Moyle and Light 1996), but no specific features of source and recipient regions were included here. Unfortunately, comparisons of many environmental characteristics such as salinity, substrate availability, turbidity, or the presence of significant competitors or predators are difficult, if not impossible, in retrospective analyses.

In the absence of historical baseline data, backcasting a full century using present day conditions, although interesting in theory, runs the real risk of imposing irrelevant parameters upon and ignoring relevant factors to past invasion events. Faced with the certainty that marine invasions will not abate in the future, greater attention should be paid to proper monitoring of the environment, so that meaningful inference with respect to habitat matching is possible.

Non-Adult Life Stages

When compared to the adult form, non-adult life stages of mollusks have not been studied extensively, and for the most part, lay beyond the scope of this study. Although larval characteristics and tolerance limits are likely important for the establishment of reproductive populations, little comparable information could be gleaned from the literature for most species on the oyster-associate list. At a coarse level, when developmental mode was compared among successful and failed invaders of San Francisco Bay, proportionally more direct developers invaded than planktonic developers {5 of 16 (31.2%) direct developers and 7 of 65 (10.8%) planktonic developers successfully invaded San Francisco Bay}.

One explanation for this pattern is that direct development enhances the likelihood of successful recruitment in localized inocula, which consist of but a few individuals (Johannesson 1988). Planktonic developers may experience poorer recruitment if their larvae and/or gametes are carried by tides and currents to inappropriate habitats, or to areas where no mates can be found. It is also possible, but not documented here, that larval stages may be more susceptible to novel toxicity and perturbation regimes encountered during transport and inoculation into new regions than are immature direct developers, perhaps conferring greater invasion success to direct developers. Although the direct developer *Littorina saxatilis* did not invade San Francisco Bay through oyster introductions, this species clusters closely with successful gastropod species (Figures 3.5 and 3.6). Recently, *Littorina saxatilis* has colonized a small intertidal area in San Francisco Bay, most likely by disposal of bait packing materials (Carlton and Cohen

1998). It will be interesting to see whether this small colony is able to persist and expand its range on the West Coast.

Possible Effects of Desiccation on Invasion

Among the twelve successful molluscan invaders to San Francisco Bay, none are exclusively subtidal species – all can be found living in the intertidal zone (Tables 3.4 and 3.5). The same is true of non-San Francisco Bay invaders (*Crassostrea virginica, Mercenaria mercenaria, Mytilopsis leucophaeta, Littorina littorea, and Crepidula fornicata*). Certainly most of the oysters shipped to the West Coast were dredged from subtidal beds, so why are no subtidal specialists represented? Desiccation is a well-known environmental stressor that influences the vertical distribution of near-shore marine organisms. The question remains as to whether desiccation influences the invasion success of molluscan oyster associates, either during transport or following introduction to the West Coast.

This study has focused almost exclusively on biological attributes of successful invaders and failed invaders. No formal effort has been made to characterize the conditions experienced by molluscan fauna after dredging, as they were being prepared and shipped west in refrigerated railroad cars. Without detailed records, such conditions can, at best, only be inferred.

For long distance rail transport, oysters were typically packed in barrels for protection and to minimize desiccation. In New York City oyster houses, oysters were packed in seaweed and stored alive in basements throughout the winter months (Ingersoll

1881). To avoid spoilage from excessive heat and desiccation, refrigerator railcars ("reefers") of the time were insulated, packed with ice blocks, and vented to maintain cold temperatures (White 1986). The ice was replenished at several locations on the trip west. Indeed, it may have been advantageous for invading species to be able to withstand the cold temperatures experienced in these reefer cars. Interestingly, mating stacks of *Crepidula fornicata* (a failed invader of San Francisco Bay, but a successful invader of the northeastern Atlantic where oysters were not shipped on ice) have been observed to disintegrate and the individuals to freeze among oysters stored on ice in seafood markets (A. W. Miller, pers. obs.).

Since high survivorship was imperative for economic gain, it can be assumed that every effort was made to optimize transport conditions (see Chapter 2). These efforts must have conferred increased survivorship to associated oyster fauna as well. Presumably, oyster associates (and their egg masses) took refuge in empty valves and other moist and muddy interstices. Although bivalves probably closed their shells and went hungry, most gastropods had access to biofilms, vegetative matter, and other macrofauna for sustenance.

Several subtidal specialist bivalves were among the 20 most abundant bivalves in the New York, Long Island Sound and vicinities in the 1800s: *Nucula proxima* (4), *Anadara transversa* (6), *Mulinia lateralis* (11), *Anadara ovalis* (16), *Argopecten irradians* (17), *Lyonsia hyalina* (18), and *Tellina agilis* (19). Of these, the shells (non-living specimens) of *Anadara transversa* (=*Arca transversa*) and *Argopecten irradians* have both been recorded in San Francisco Bay (Packard 1918, Wicksten 1976)). *Anadara transversa* and

Mulinia lateralis cluster tightly with successful bivalve invaders (Figures 3.3 and 3.4). The only exclusively subtidal gastropods that ranked among the 20 most abundant species were *Astyris lunata* (11) and *Costoanachis avara* (19). Interestingly, these species cluster tightly with successful gastropod invaders (Figures 3.5 and 3.6).

Given the limited scope of the data presented in this paper, nothing definitive can be said of the effects of desiccation on invasion. But the apparent patterns seen among invaders and non-invaders suggest that desiccation (as inferred by their vertical distributions in nature) may have affected mollusks' abilities to invade San Francisco Bay. If desiccation were shown to be a limiting factor for oyster associate invasions, it could come into play either during transit or in the recipient region, especially if oysters were bedded primarily in intertidal rather than subtidal areas, as was the case in San Francisco Bay (Ingersoll 1881).

Two Notable Invasion Failures

Ironically, despite countless attempts and tremendous inoculation, *Crassostrea virginica* never developed long-term sustainable populations in San Francisco Bay. In some years spawning and larval settlement were recorded (Scofield 1928), but reproduction was so sporadic that true colonization was never possible. Similar failures have occurred along all locations but one on the West Coast and Northwestern Europe where the eastern oyster was introduced. The only known colonies of *Crassostrea virginica* living outside their native region have been those reported from Boundary Bay, British Columbia (Turgeon et al. 1998) and Pearl Harbor, Oahu, HI (Coles et al. 1999, Carlton and Mann 1996).

Crassostrea virginica's failure in San Francisco Bay and most other locations where it has been introduced illustrates the inadequacy of low salinity tolerance and donor region abundance (and inoculation size) to fully explain marine/estuarine invasions by mollusks. Clearly, other factors must be important to the invasion process. It is nevertheless interesting that the vast majority of molluscan invaders, including three of the five non-San Francisco Bay invaders (*Mercenaria mercenaria, Crassostrea virginica, and Crepidula fornicata*) group so closely with San Francisco Bay invaders (Figures 3.7 and 3.8). The overall concordance among successful invaders with respect to these two factors implies their importance to invasion, yet clearly does not fully explain the phenomenon.

Another non-San Francisco invader, the common periwinkle *Littorina littorea,* fell well outside the San Francisco Bay invader state space (Figures 3.7 and 3.8). *Littorina littorea,* a native of northwest Europe and possibly the boreal northwest Atlantic, is now a dominant invader of the Atlantic coast of the United States. Despite *Littorina littorea's* prolific range expansion in the western Atlantic during the last 150 years, it has failed to invade San Francisco Bay or other portions of the Pacific coast with oyster introductions. The history of this snail in the western Atlantic is well documented and may shed light on its failure to invade the Pacific coast.

Littorina littorea's status as indigenous to North America or introduced by Vikings is debatable (Ganong 1886, 1887, Clarke 1963, Spjeldnaes and Henningsmoen 1963, Vermeij 1982). Pre-Columbian *Littorina littorea* shells were found in a Micmac Indian site in Halifax, Nova Scotia and subsequently radiocarbon dated to 700 ± 225 years before present (Clarke and Erskine 1961). A single fossil specimen from Nova Scotian sediments has been dated to 40,000 years before present and specimens reported by Bird (1968) were found in pre-Viking strata in Newfoundland. *Littorina littorea* was missing from the western Atlantic fauna from the 13th to the early 19th century when it was reestablished in Nova Scotia. Whether or not *Littorina littorea* is native or introduced to the Canadian Maritime region, there is no evidence to suggest that it occurred southward before the middle of the 19th century (Vermeij 1982).

Wells (1965) traces *Littorina littorea's* southward expansion from Pictou, Nova Scotia (1840), to Halifax, Nova Scotia (1857), St. John, New Brunswick (1861), Portland, ME (1870), Cape Cod (1870-1872), Woods Hole (1875), New Haven, CT (1879), Staten Island (1888), Atlantic City, NJ (1888), Cape May, NJ (1928), and Ocean City, MD (1959). *Littorina littorea* reached Wachapreague, VA in 1978 (J. Carlton, pers. comm. in Bertness 1984).

Littorina is recognized as one of the most successful and dramatic molluscan invaders of the western Atlantic. Following reintroduction into the Canadian Maritime Provinces, *Littorina* rapidly attained dominant status in the intertidal community (Bertness 1984) and is thought to have partially displaced the former dominant herbivorous gastropod, the mud snail (*Ilyanassa obsoleta*), and altered the trophic structure of intertidal communities (Lubchenco 1978). Brenchley and Carlton (1983) have demonstrated *Littorina's* capacity to outcompete *Ilyanassa obsoleta* for habitat.

Bertness (1984) showed that as *Littorina littorea* forages, it removes soft sediments from hard substrates, thereby altering community structure through habitat modification and herbivory.

Given its invasive abilities, *Littorina's* failure to invade San Francisco and other Pacific coastal locations is perplexing. Since the end of east to west oyster transport, both living and dead specimens of *Littorina littorea* have been found in San Francisco Bay and Puget Sound, but these are thought to have been introduced with discarded bait packing materials from the East Coast (Carlton 1979, Miller 1969). The species has never managed to establish a reproducing population in either location (Carlton 1979).

Although *Littorina littorea* was not present in Long Island Sound until 1879 (Wells 1965), it had clearly reached the donor region for westbound oysters well within the window of transcontinental introduction. Inoculation size may have played a role in *Littorina's* inability to colonize the West Coast. In 1887 *Littorina* was still not observed in the molluscan fauna of Staten Island (Smith 1887), but arrived the following year (Bequaert 1943). By the close of the 19th century *Littorina littorea* was listed as "common" in Cold Spring Harbor, a harbor on the northeastern edge of Long Island (Balch 1899). By the early 20th century, the heyday of the oyster trade with the West Coast was winding down and oyster shipments were decreasing.

Today, *Littorina littorea* is one of the most numerically dominant snails of the northern mid-Atlantic, New England, and Canadian Maritime coasts. If *Littorina littorea* is plotted using current abundance values, it falls solidly inside the SF-invader state space (Figures 3.8).

Temperature Considerations

Wells (1965) noted that in its native range, *Littorina littorea* reaches the coast of Portugal but does not extend southward beyond the 21°C mean isotherm for the warmest month of the year. By extension, Wells (1965) hypothesized that in the western Atlantic, *Littorina littorea's* southern range may be restricted by a similar 21°C summer isotherm, which occurs off the Delmarva Peninsula. *Littorina littorea* does not appear to range deeply inside estuaries in New Jersey and to the south where water temperatures are warmer than on the open coast (Alexander 1947).

If *Littorina littorea* is truly warm water limited, this condition has interesting implications for this snail's apparent inability to colonize and develop sustainable populations in San Francisco Bay and other locations on the West Coast. On the West Coast, where oceanic currents and upwelling keep coastal waters cool, the 21°C mean isotherm for the warmest month of the year occurs to the south of Point Conception, California. If Wells' temperature-limiting hypothesis holds, one might expect that *Littorina littorea* could colonize appropriate coastal substrata from Point Conception northward to Alaska. Carlton (1969) suggests this possibility as well, however no reproducing colonies of *Littorina littorea* are known on the West Coast (Carlton 1979).

As an oyster associate, *Littorina littorea* was introduced to embayments rather than open coastal habitats on the West Coast. In San Francisco Bay, eastern oysters (*Crassostrea virginica*) were introduced to fenced beds in the South Bay, primarily on the western side of the Bay from Point San Bruno to the Dunbarton Beds in the Bay's extreme southern end (Townsend 1893, Barrett 1963). Temperature data collected by the

United States Geological Survey from 1969 to the present indicate that surface and subsurface temperatures in the deepest part of South Bay routinely reached 21°C during September, the warmest month of the year (USGS 2000 - Water Quality San Francisco Bay web site). A significant temperature gradient exists from the cool water at Golden Gate at the Bay's mouth to the warmer waters at the Bay's interior. Since all oyster beds were located in depths of 2 m or less (Barrett 1963, Townsend 1893), the summer and early autumn water temperature there certainly surpassed 21°C. According to Wells' hypothesis, these temperatures would be enough to prevent the establishment of a sustainable population of *Littorina littorea*. If elevated temperatures compromise reproduction in this snail, despite *Littorina littorea's* planktonic egg cases and veligers, the opportunity for larval colonization may never have arisen in this system, even in habitats with cooler summer temperatures. Depending on the local conditions of those particular areas along the West Coast where oysters were bedded, high summer temperatures may have contributed significantly to *Littorina littorea's* failure.

Predicting Invasion Success – The Tens Rule

Eastern oyster-mediated mollusk invasions of San Francisco Bay appear to conform, at least partially, to the "tens rule." Seeking to describe the process of invasions statistically, Williamson and Fitter (1996) examined various terrestrial invasions and proposed that roughly 10% (from 5 to 20%) of species are able to survive three critical transitions of invasion. That is, 10% of species imported to a new area will escape cultivation and survive in the wild; 10% of survivors will go on to establish reproducing colonies; and 10% of these colonizing species will become pest species with negative economic effects. Ultimately, 1 in 1000 nonindigenous species imported to a new area will escape cultivation and become a pest.

Molluscan invaders differ somewhat from the plants and animals that Williamson and Fitter (1996) examined in that each was introduced directly to the wild and therefore required no escape from cultivation following importation. Of 93 oyster associates introduced, 12 established reproducing populations (13%). The bivalves and gastropods established at rates of 12% (5 of 42) and 13% (7 of 51) respectively. Oyster-mediated introductions of mollusks would therefore appear to conform to the tens rule for the transition from introduction to establishment.

Concerning the transition from colonizer to pest, of the 12 eastern oyster-mediated molluscan invaders, *Urosalpinx cinerea* and *Boonea bisuturalis* are said to have economic impacts from their predation and parasitism on commercially important shellfish in San Francisco Bay (Cohen and Carlton 1995). Again, this condition conforms to the tens rule (2/12 = 17%).

If the pest species definition is extended and applied from an ecological viewpoint, numerical abundance must be considered an important defining aspect. For example, in San Francisco Bay numerical abundance of the mud snail *Ilyanassa obsoleta* has led to the competitive displacement of the native snail *Cerithidea californica* (Race 1982). The extensive invasion of San Francisco Bay by the Asian clam, *Potamocorbula amurensis* (although not an oyster-mediated invader) appears to have induced large-scale changes to trophic and benthic dynamics (Carlton et al. 1990). Although numerical abundance will not always produce such effects, it stands to reason that substantial changes to community composition and/or biomass should induce some biological or physical effects to the receiving ecosystem.

If numerical dominance is considered integral to the notion of pest species, then the successful molluscan invaders of San Francisco Bay appear to deviate strongly from Williamson and Fitter's (1996) prediction. Of the 12 species, 7 (58%) are considered numerically important in the San Francisco estuarine invertebrate community. Hopkins (1986) lists *Gemma gemma, Ilyanassa obsoleta, Macoma balthica*, *Mya arenaria,* and *Urosalpinx cinerea* among the 24 most commonly encountered invertebrate species of estuarine reaches of San Francisco Bay. *Crepidula sp.* is assumed to be composed partly of *C. plana* and *C. convexa,* since Hopkins lists the *Crepidula* complex as "introduced" to San Francisco Bay. Whether this apparent deviation from Williamson and Fitter's prediction is a function of the invasive qualities of the species, features of the recipient environment, or simply a misinterpretation of the rule cannot be said. However, extending the notion of nuisance species effects beyond economic and human health impacts and into the realm of ecological and environmental impacts is highlighted.

CONCLUSION

This study sought to differentiate statistically the biological attributes of successful from failed invaders. It showed that successful and failed molluscan invaders of San Francisco Bay tend to separate according to differences in tolerance of lowered salinity and in relative abundance in source regions. The inclusion of most "non-San Francisco invaders" (i.e., species that have not invaded San Francisco Bay but which have invaded other locations) within the grouping of successful invaders suggests that these attributes may be important for characterizing invasions to other estuarine systems. Not surprisingly, discrimination of successful and failed invaders was not absolute, indicating that other biological or environmental factors play a role in marine/estuarine molluscan invasions.

Our current understanding of marine and estuarine invasion biology is still not yet adequate to predict invasions or the effects of most biological invaders on receiving ecosystems. Complete understanding of the invasion process is certainly not essential for reducing invasion rates; common sense suggests that changes to many human activities would reduce the number of nonindigenous species introductions around the world. However, as with other large-scale environmental problems (e.g., global warming, loss of biodiversity), it is not enough to document the fact that biological invasions occur; hard evidence of their ill effects on ecosystems and the human population are required before the economics of human behavior will be altered. True understanding of the environmental, economic, and public health impacts of nonindigenous organisms requires that we understand how and why invasions occur. To the extent possible, discovery of the fundamental, and perhaps general, principles that drive the invasion process will enhance our abilities to prevent and manage biological invasions more effectively.

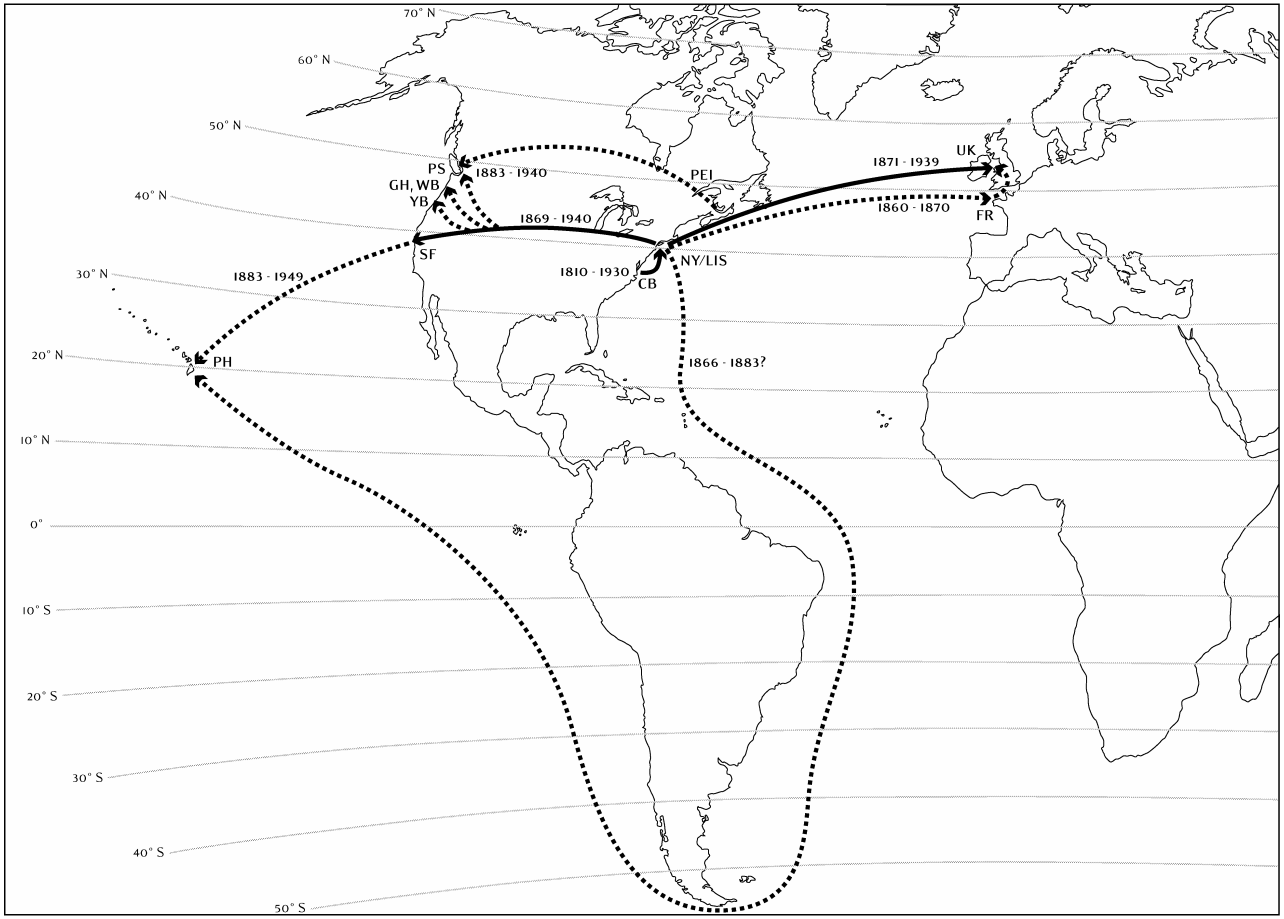


Figure 3.1 Major source and recipient locations of eastern oyster (*Crassostrea virginica*) commercial transport. Solid lines represent routes of highest volumes, dotted lines represent lesser volumes. Approximate time periods of introduction are included. North America: SF=San Francisco Bay/Tomales Bay (1869-1940), PS=Puget Sound and nearby waters of British Columbia (1883, 1890s, 1905-1940), GH=Grays Harbor (1900-1940s), WB=Willapa Bay (1874, 1894, 1897), YB=Yaquina Bay (1872, 1896, 1899-1931, 1943-1944); CB=Chesapeake Bay, NY/LIS=New York and Long Island Sound region; PEI=Prince Edward Island; Hawaii: PH=Pearl Harbor, Oahu (1866, 1883-1949); Europe: UK=United Kingdom (principally Liverpool), FR=France.

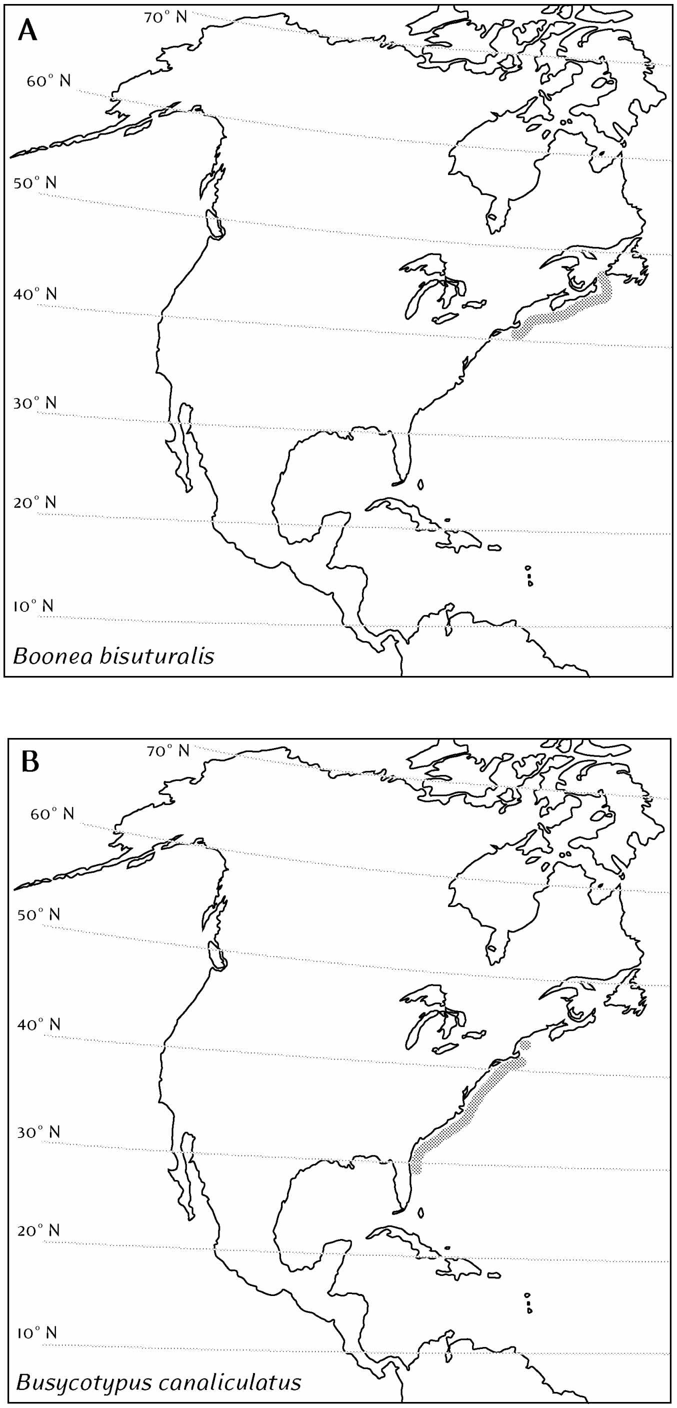
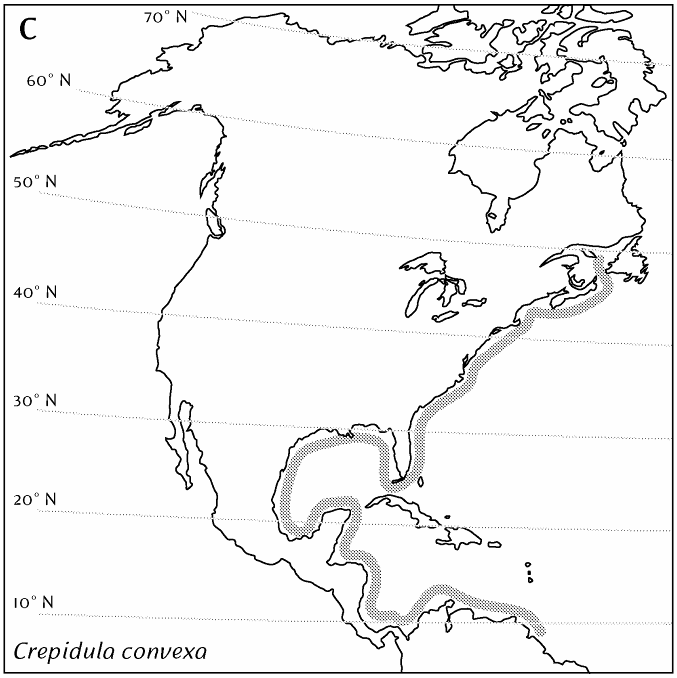


Figure 3.2 Native latitudinal ranges of gastropods in the western Atlantic: (A) *Boonea bisuturalis*, (B) *Busycotypus canaliculatus.*



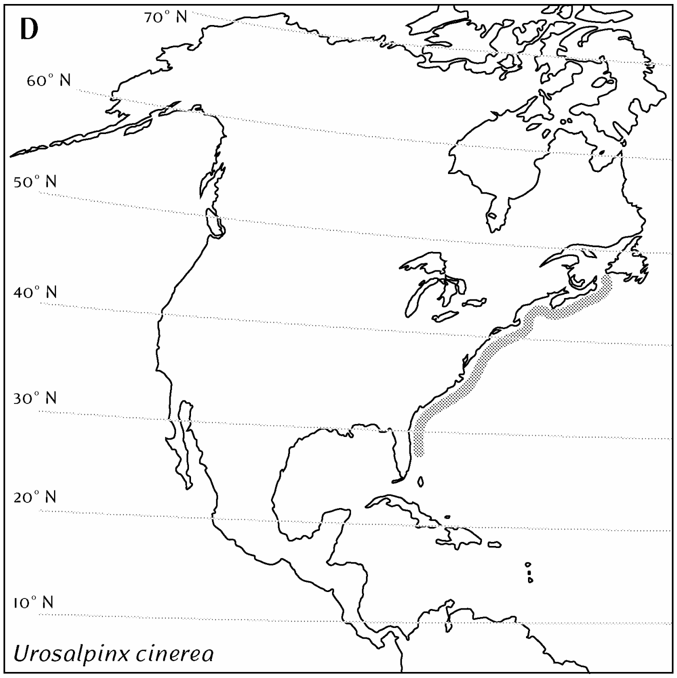


Figure 3.2 cont. Native latitudinal ranges of gastropods in the western Atlantic: (C) *Crepidula convexa*, (D) *Urosalpinx cinerea*.

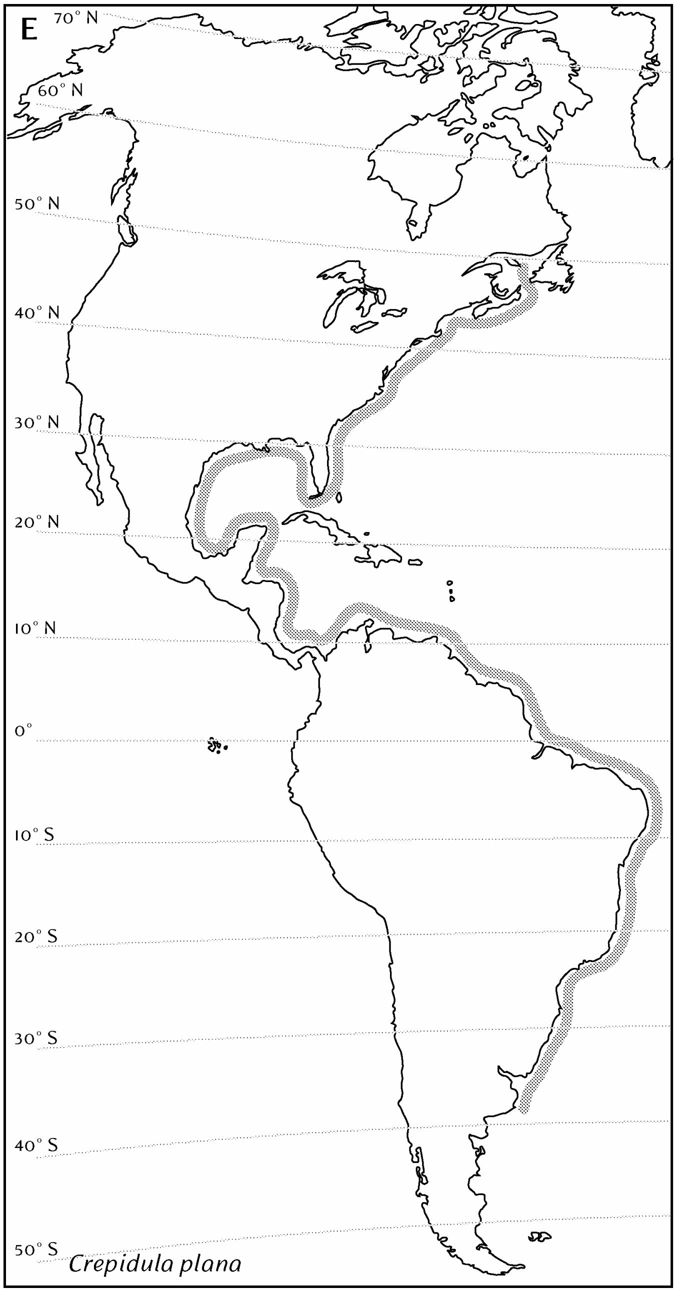


Figure 3.2 cont. Native latitudinal range of gastropods in the western Atlantic: (E) *Crepidula plana*.

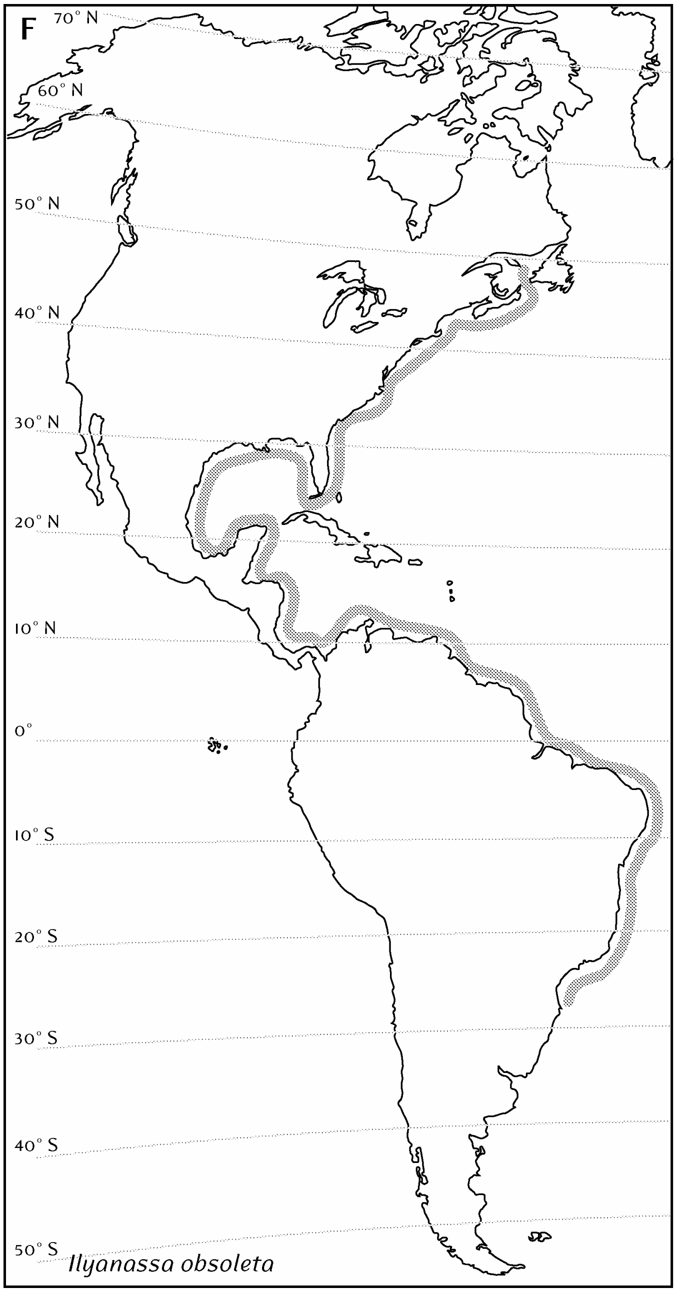


Figure 3.2 cont. Native latitudinal range of gastropods in the western Atlantic: (F) *Ilyanassa obsoleta*.

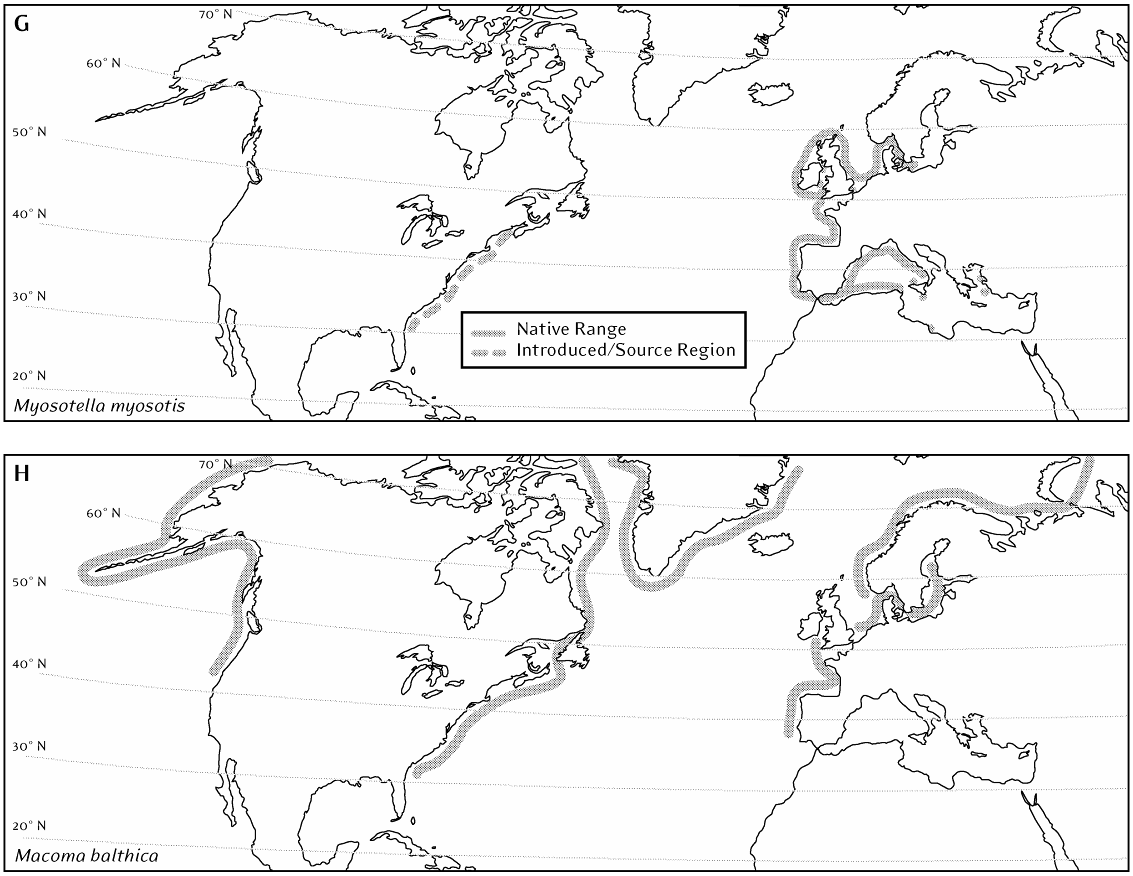


Figure 3.2 Native latitudinal ranges of gastropods, (G) *Myosotella myosotis*, and bivalves, (H) *Macoma balthica*. Note: introduced *Macoma balthica* of San Francisco Bay have been shown to be genetically more similar to western Atlantic populations than to eastern Pacific populations to the north (Meehan et al. 1989).

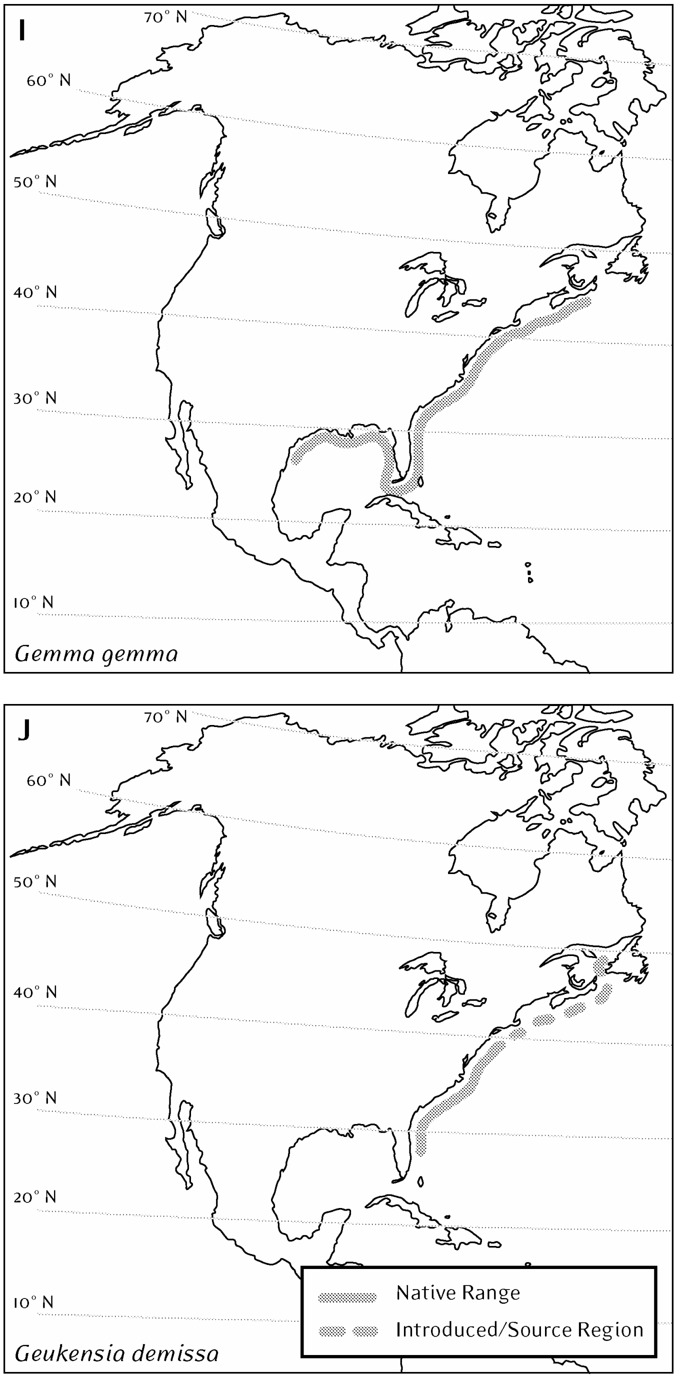


Figure 3.2 cont. Native latitudinal ranges of bivalves, (I) *Gemma gemma*, (J) *Geukensia demissa*.

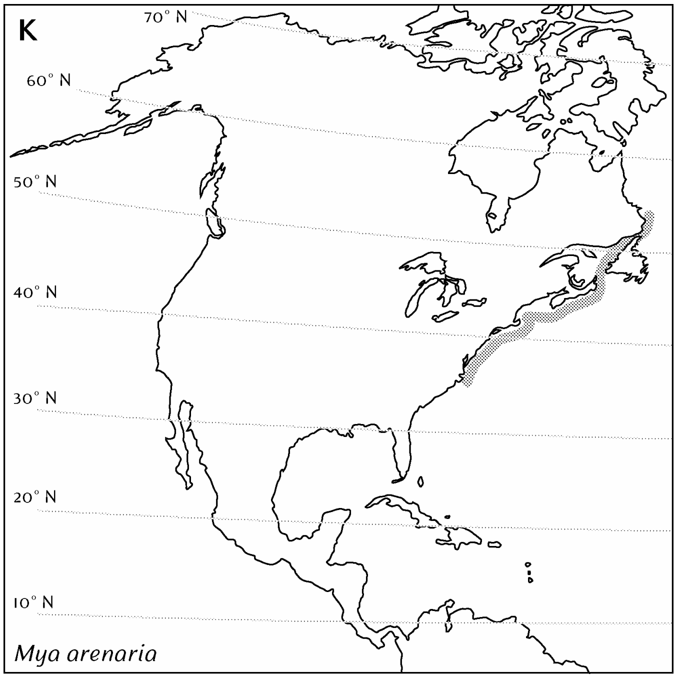


Figure 3.2 cont. Native latitudinal ranges of bivalves, (K) *Mya arenaria*.

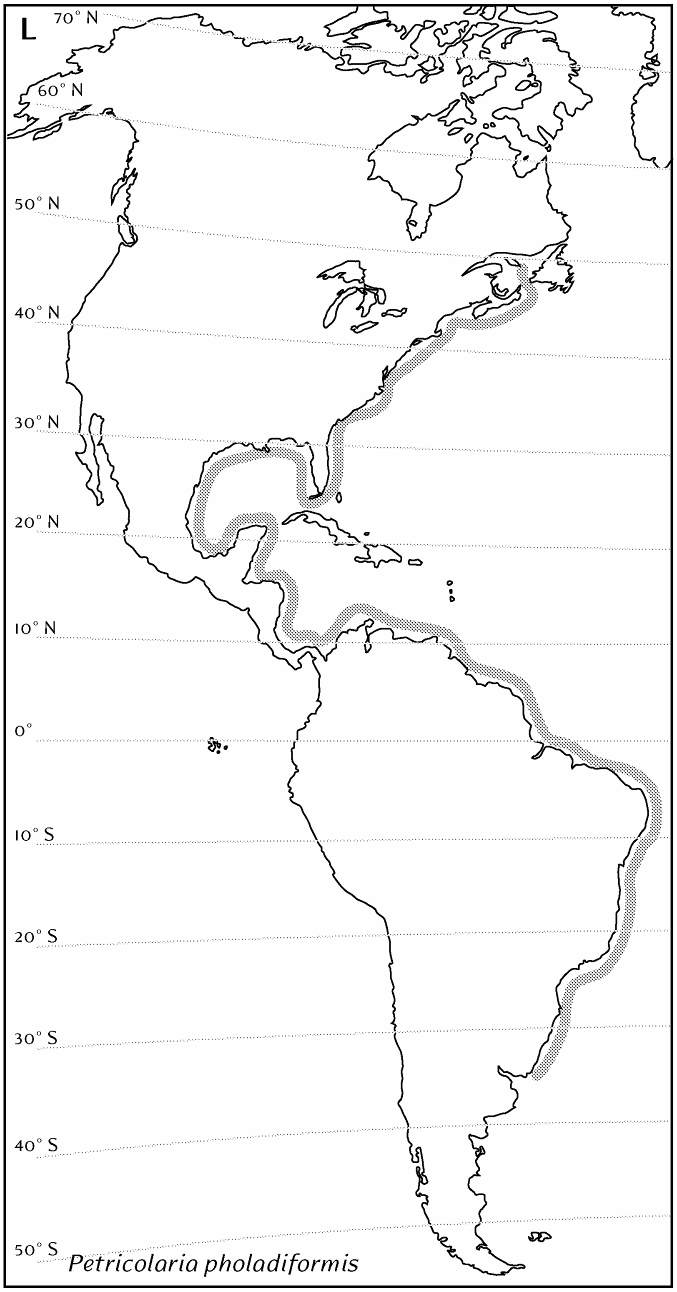


Figure 3.2 cont. Native latitudinal ranges of bivalves, (L) *Petricolaria pholadiformis*.

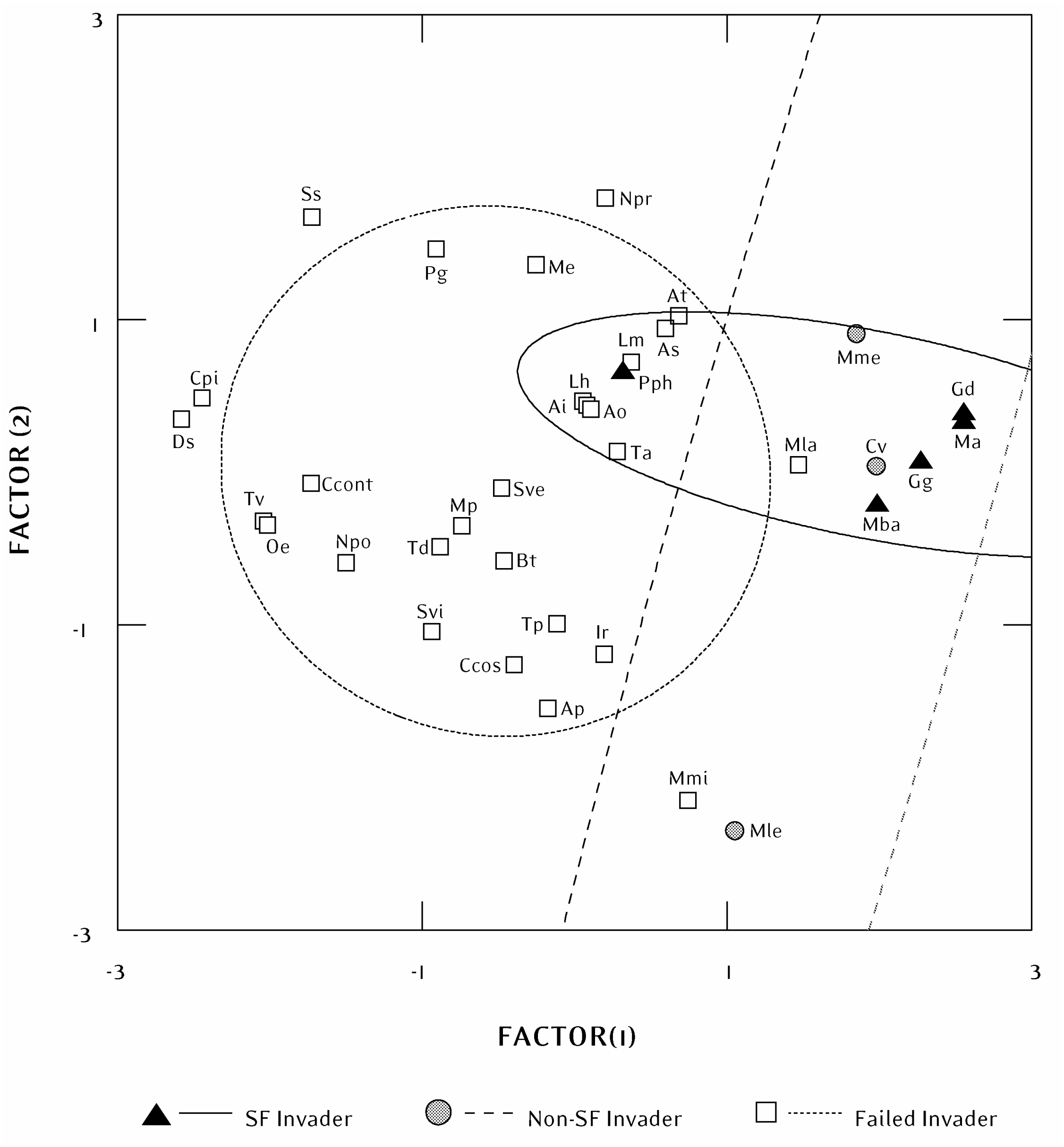


Figure 3.3. Bivalve discriminant analysis biplot. SF Invader=successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. Solid, dashed, and dotted lines represent the 95% confidence ellipse surrounding each of the plotted groups. Factor 1=0.284(Source Abundance)-0.153(Low Salinity)+1.049 and Factor 2=0.275(Source Abundance)+0.100(Low Salinity)-2.353. See Table 3.1 for species label legend.

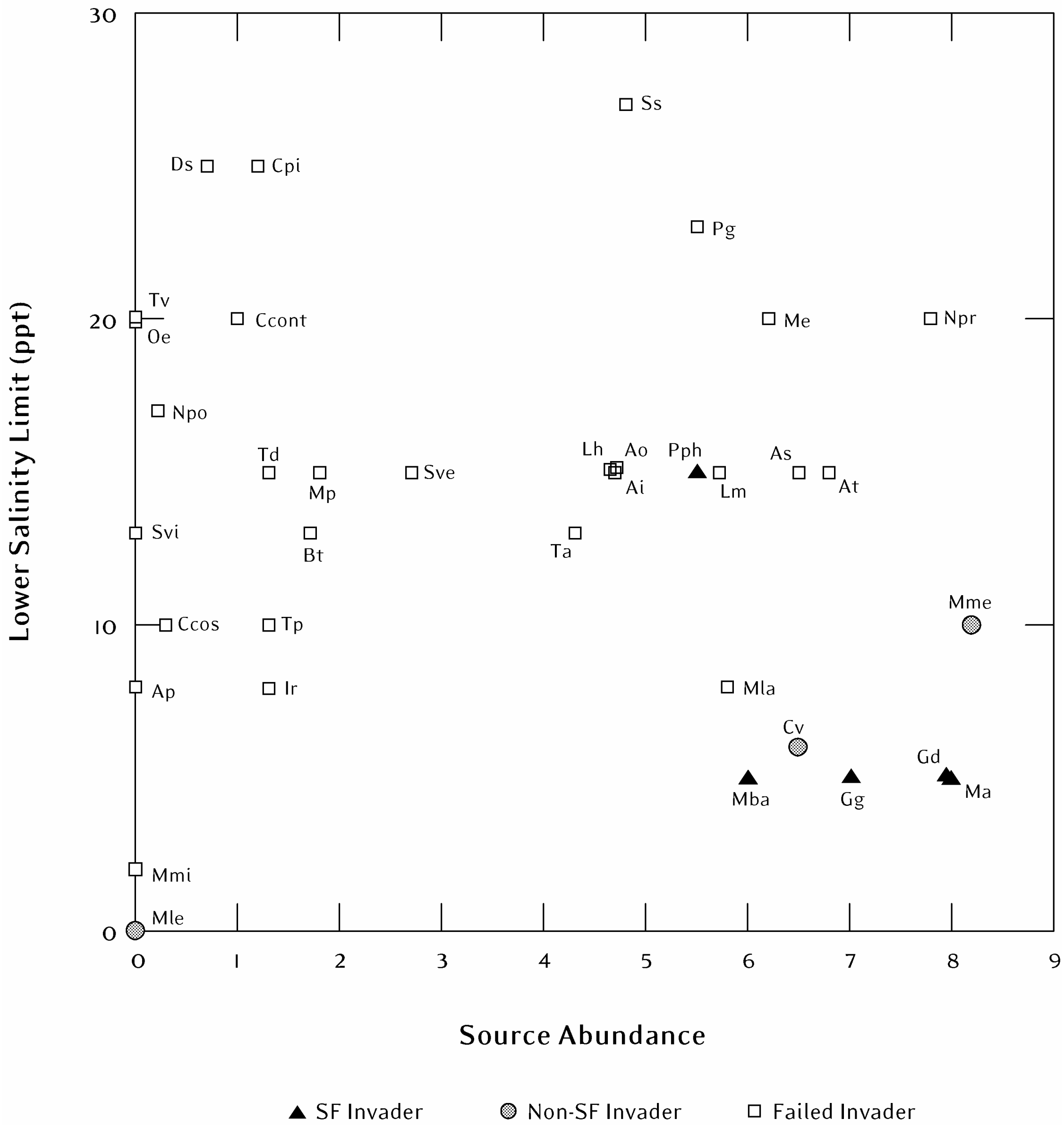


Figure 3.4. Bivalve scatterplot: Source Abundance vs. Lower Salinity Limit of species. SF Invader= successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. See Table 3.1 for species label legend.

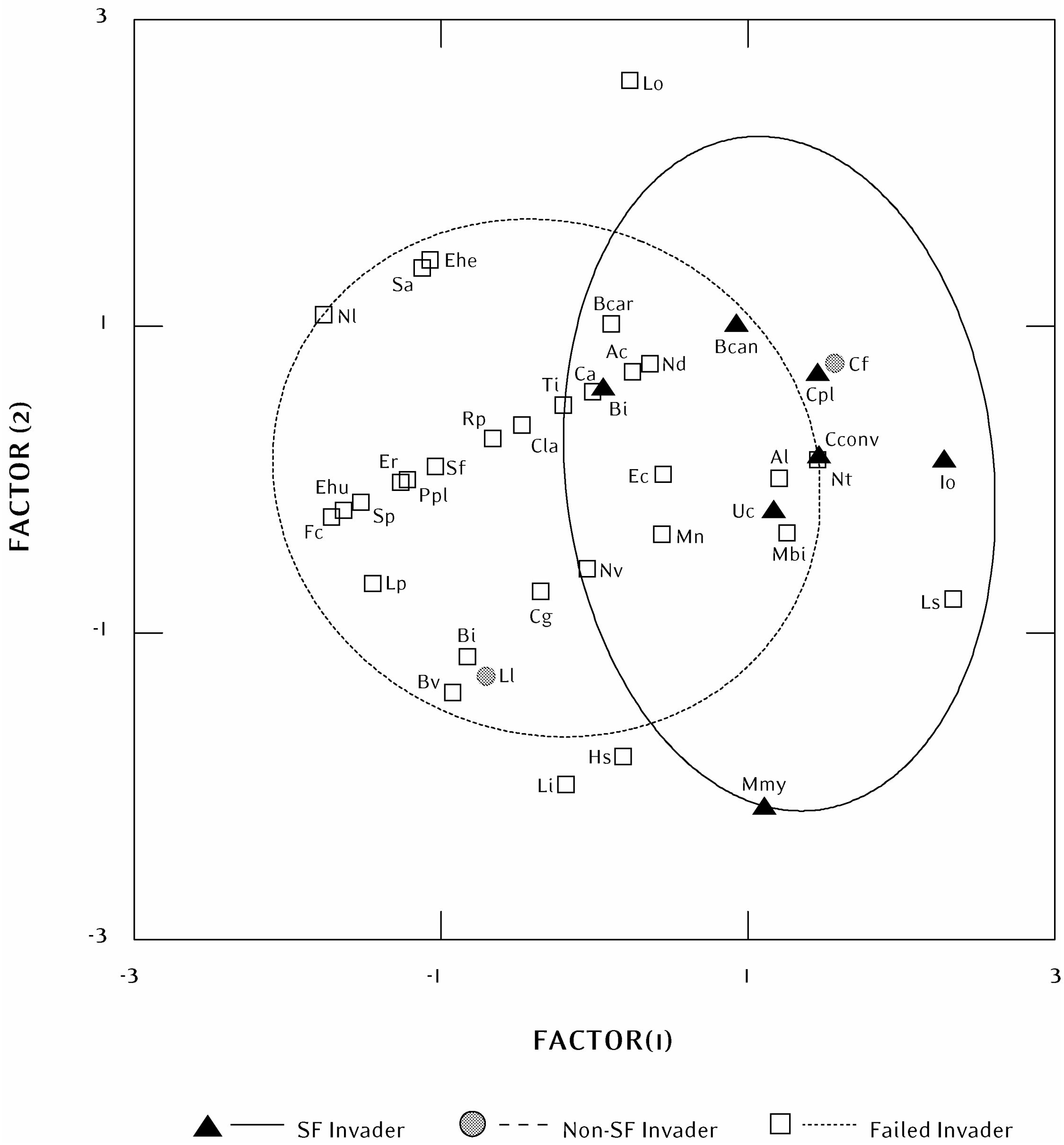


Figure 3.5. Gastropod discriminant analysis biplot. SF Invader=successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. Solid, dashed, and dotted lines represent the 95% confidence ellipse surrounding each of the plotted groups. Factor 1=0.377(Source Abundance)-0.089(Low Salinity)-1.21 and Factor 2=0.180(Source Abundance)+0.149(Low Salinity)-2.916. See Table 3.2 for species label legend.

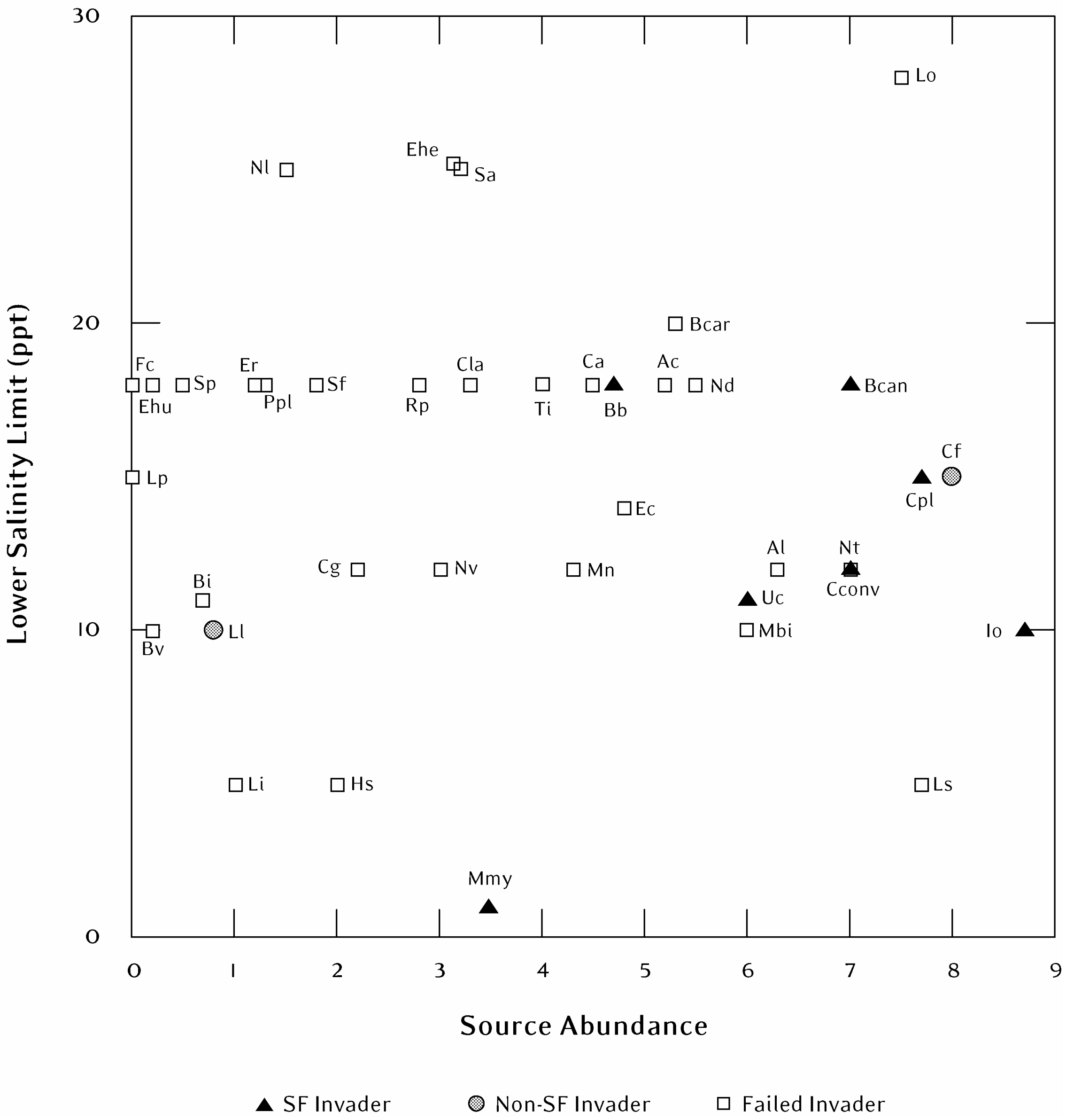


Figure 3.6. Gastropod scatterplot: Source Abundance vs. Lower Salinity Limit of species. SF Invader= successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. See Table 3.2 for species label legend.

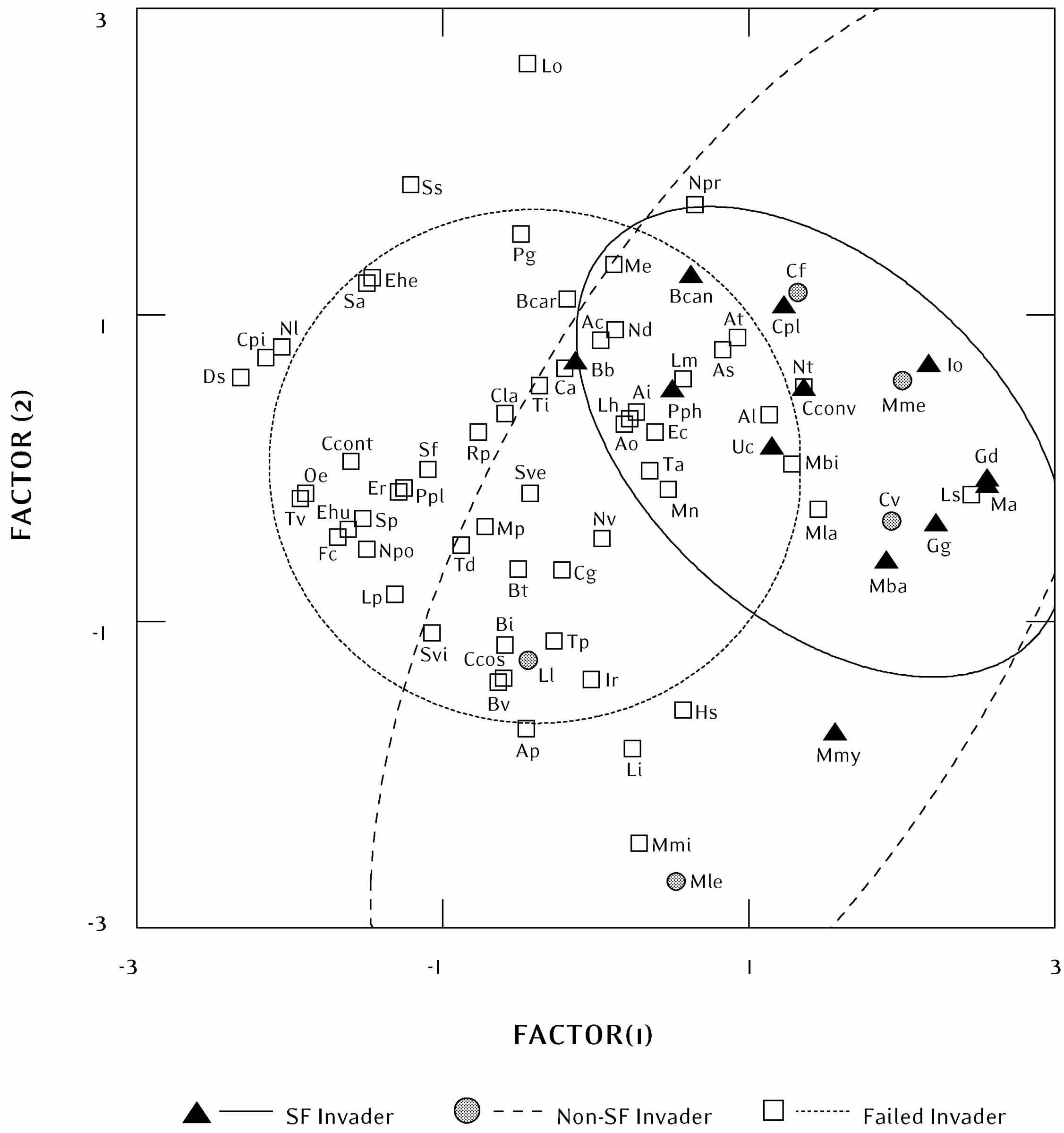


Figure 3.7. Mollusk discriminant analysis biplot. SF Invader=successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. Solid, dashed, and dotted lines represent the 95% confidence ellipse surrounding each of the plotted groups. Factor 1=0.330(Source Abundance)-0.123(Low Salinity)+0.529 and Factor 2=0.247(Source Abundance)+0.125(Low Salinity)-2.702. See Tables 3.1and 3.2 for species label legends.

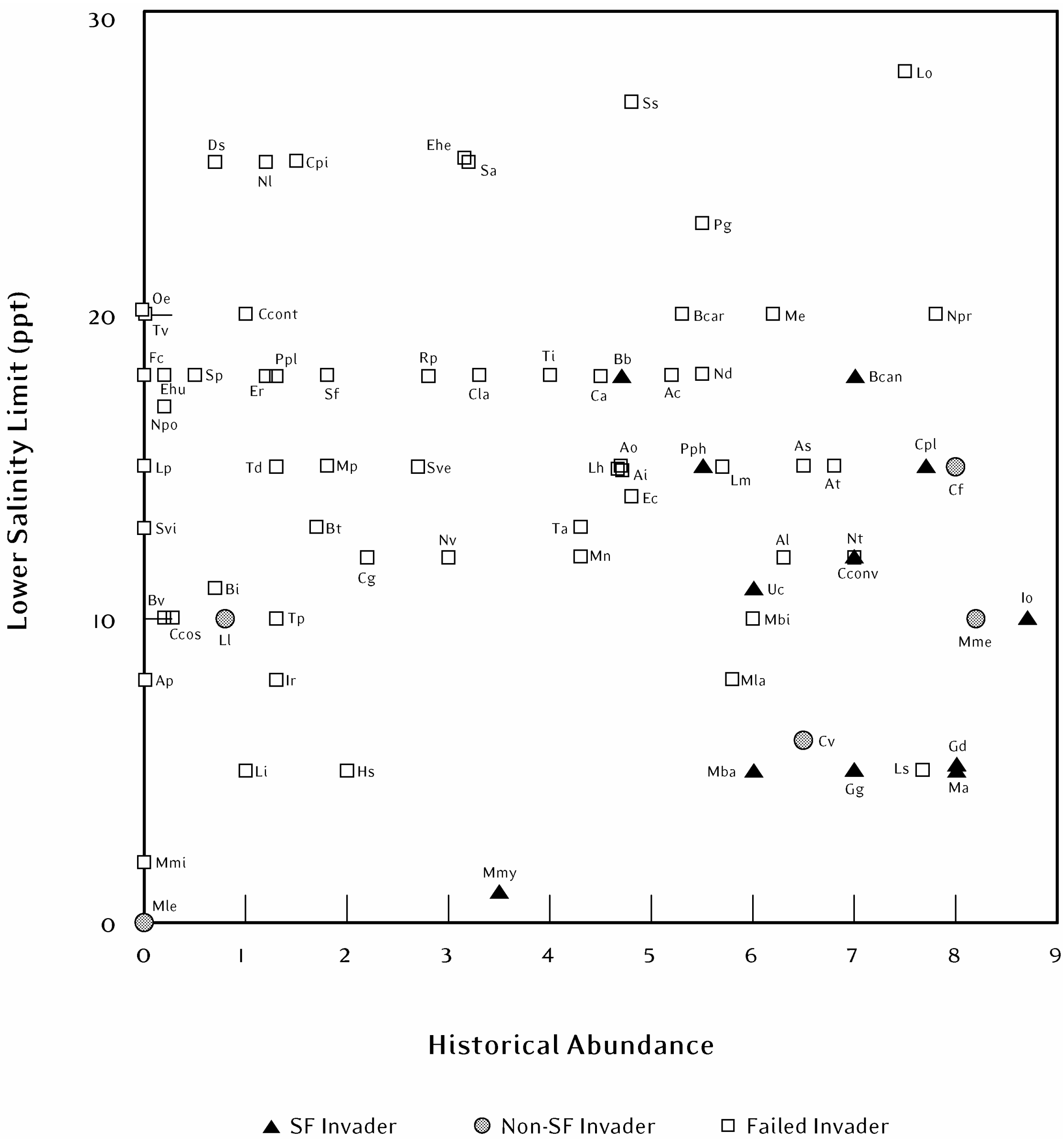


Figure 3.8. Mollusk scatterplot: Source Abundance vs. Lower Salinity Limit of species. SF Invader= successful invader of San Francisco Bay. Non-SF Invader=a species that has successfully invaded somewhere outside its native range, but not in San Francisco Bay. Failed Invader=species that has failed to invade anywhere outside its native range. See Tables 3.1and 3.2 for species label legends.

Table 3.1. Geographic range, native biogeographic faunal group, salinity range, and historical abundance of oyster-associated bivalves of the Western Atlantic. San Francisco Bay invaders in bold.

Family	Species	Label	N-Limit	S-Limit	Fauna	Salinity Distribution	Hist. Abund.
Lyonsiidae	*Lyonsia hyalina* Conrad, 1831	Lh	45N	30N	N-TransHat.	Steno-Estuarine	4.7
	Pandora gouldiana Dall, 1886	Pg	48N	35N	Northern	Steno-Marine	5.5
Nuculidae	*Nucula proxima* Say, 1822	Npr	45N	26N	N-TransHat.	Steno-Marine	7.8
Solemyacidae	*Solemya velum* Say, 1822	Sve	45N	28N	N-TransHat.	Steno-Estuarine	2.7
Arcidae	*Anadara ovalis* (Bruguiere, 1798)	Ao	42N	22S	S-TransHat.	Eury-Marine	4.7
	Anadara transversa (Say, 1822)	At	43.7N	26N	Northern	Eury-Marine	6.8
Noetiidae	*Noetia ponderosa* (Say, 1822)	Npo	37N	26N	S-TransHat.	Eury-Marine	0.2
Anomiidae	*Anomia simplex* Orbigny, 1842	As	45N	22S	N-TransHat.	Steno-Estuarine	6.5
Dreissenidae	*Mytilopsis leucophaeata* (Conrad, 1831)	Mle	41N	22N	S-TransHat.	Steno-Estuarine	0.0
Mytilidae	*Amygdalum papyrum* (Conrad, 1846)	Ap	38N	26N	S-TransHat.	Eury-Estuarine	0.0
	***Geukensia demissa* (Dillwyn, 1817)**	**Gd**	**48N**	**28N**	**N-TransHat.**	**Eury-Estuarine**	**8.0**
	Ischadium recurvum (Rafinesque, 1820)	Ir	42N	26N	S-TransHat.	Steno-Estuarine	1.3
	Mytilus edulis Linne, 1758	Me	83N	33N	N-TransHat.	Steno-Marine	6.2
Ostreidae	*Crassostrea virginica* (Gmelin, 1791)	Cv	48N	26N	N-TransHat.	Eury-Estuarine	6.5
	Ostrea equestris Say, 1834	Oe	37N	22S	S-TransHat.	Steno-Marine	0.0
Pectinidae	*Argopecten irradians* (Lamarck, 1819)	Ai	45N	28N	N-TransHat.	Eury-Marine	4.7
Cardiidae	*Cerastoderma pinnulatum* (Conrad, 1831)	Cpi	53N	35N	Northern	Steno-Marine	1.2
	Crassinella lunulata (Conrad, 1834)	Clu	42N	22S	S-TransHat.	--	1.8
	Laevicardium mortoni (Conrad, 1830)	Lm	42N	26N	S-TransHat.	Steno-Estuarine	5.7
Corbulidae	*Corbula contracta* Say, 1822	Ccont	42N	22S	S-TransHat.	Steno-Marine	1.0
	Corbula swiftiana C. B. Adams, 1852	Cs	42N	26N	S-TransHat.	Eury-Marine	0.0
Hiatellidae	*Hiatella arctica* (Linne, 1767)	Ha	80N	20N	N-TransHat.	--	0.8
Mactridae	*Mulinia lateralis* (Say, 1822)	Mla	44N	26N	N-TransHat.	Eury-Estuarine	5.8
	Spisula solidissima (Dillwyn, 1817)	Ss	45N	33N	N-TransHat.	Steno-Marine	4.8
Montacutidae	*Mysella planulata* (Stimpson, 1851)	Mp	45N	26N	N-TransHat.	Steno-Estuarine	1.8
Myidae	***Mya arenaria* Linne, 1758**	**Ma**	**53N**	**35N**	**Northern**	**Eury-Estuarine**	**8.0**
Petricolidae	***Petricolaria pholadiformis* (Lamarck, 1818)**	**Pph**	**48N**	**35S**	**N-TransHat.**	**Steno-Estuarine**	**5.5**
	Zirfaea crispata Linne, 1758	Zc	53N	39N	Northern	--	3.2
Pholadidae	*Barnea truncata* (Say, 1822)	Bt	42.5N	22S	N-TransHat.	Eury-Estuarine	1.7
	Cyrtopleura costata (Linne, 1758)	Ccost	42N	22S	S-TransHat.	Eury-Estuarine	0.3
	Diplothyra smithii Tryon, 1862	Ds	42N	26N	S-TransHat.	Steno-Marine	0.7
	Cumingia tellinoides (Conrad, 1831)	Ct	45N	30N	N-TransHat.	--	2.5
Semelidae	*Tagelus divisus* (Spengler, 1794)	Td	42N	22S	S-TransHat.	Steno-Estuarine	1.3
Solecurtidae	*Tagelus plebeius* (Lightfoot, 1786)	Tp	42N	22S	S-TransHat.	Eury-Estuarine	1.3
	Solen viridis Say, 1821	Svi	42N	26N	S-TransHat.	Steno-Estuarine	0.0
Solenidae	***Macoma balthica* (Linne, 1758)**	**Mba**	**83N**	**31N**	**N-TransHat.**	**Eury-Estuarine**	**6.0**
Tellinidae	*Macoma mitchelli* Dall, 1895	Mmi	39N	28N	S-TransHat.	Eury-Estuarine	0.0
	Tellina agilis Stimpson, 1857	Ta	48N	31N	N-TransHat.	Eury-Marine	4.3
	Tellina versicolor DeKay, 1843	Tv	42N	26N	S-TransHat.	Steno-Marine	0.0
	***Gemma gemma* (Totten, 1834)**	**Gg**	**45N**	**26N**	**N-TransHat.**	**Eury-Estuarine**	**7.0**
Veneridae	*Mercenaria campechiensis* (Gmelin, 1791)	Mca	40N	26N	S-TransHat.	--	0.0
	Mercenaria mercenaria (Linne, 1758)	Mme	48N	28N	N-TransHat.	Eury-Estuarine	8.2

Notes: Sources include: (Abbott 1974), (Franz and Merrill 1980a, b), (Castagna and Chanley 1973), (Balch 1899), (Smith 1862), (Hubbard and Smith 1865), (Perkins 1869), (Smith and Prime 1870), (Smith 1887), (Jacot 1920), (Maurer et al. 1974), (Barnes 1994), (Lippson and Lippson 1997), (Gosner 1978), (Wass et al. 1972), (Frey 1946), (Larsen 1985), (Maurer and Watling 1973a, 1973b), (Micheli and Peterson 1999), (Wells 1961), (Winkley 1888), (Verrill and Smith 1874), and (J. T. Carlton, pers. comm.).

Table 3.2. Geographic range, native biogeographic faunal group, salinity range, and historical abundance of oyster-associated gastropods of the Western Atlantic. San Francisco Bay invaders in bold.

Family	Species	Label	N-Limit	S-Limit	Fauna	Salinity Distribution	Hist. Abund.
Acteonidae	*Rictaxis punctostriatus* (C. B. Adams, 1840)	Rp	41.6N	6.9N	S-TransHat.	Steno-Estuarine	2.8
Cylichnidae	*Acteocina canaliculata* (Say, 1826)	Ac	46N	6N	N-TransHat.	Eury-Marine	5.2
Haminoeidae	*Haminoea solitaria* (Say, 1822)	Hs	46N	27.8N	N-TransHat.	Eury-Estuarine	2.0
Pyramidellidae	***Boonea bisuturalis*** **(Say, 1821)**	**Bb**	**47N**	**40.5N**	**Northern**	**Steno-Estuarine**	**4.7**
	Boonea seminuda (C. B. Adams, 1837)	Bse	46.5N	35S	N-TransHat.	--	4.2
	Fargoa bartschi (Winkley, 1909)	Fb	45N	30N	N-TransHat.	--	0.0
	Sayella fusca (C. B. Adams, 1839)	Sf	47N	18N	N-TransHat.	Steno-Estuarine	1.8
	Turbonilla interrupta (Totten, 1835)	Ti	47N	35S	N-TransHat.	Eury-Marine	4.0
	Boonea impressa (Say, 1822)	Bi	42N	25N	S-TransHat.	Eury-Marine	0.7
	Fargoa calesi (Bartsch, 1909)	Fc	42N	24S	S-TransHat.	Steno-Estuarine	0.0
	Fargoa dianthophila (Wells & Wells, 1961)	Fd	41.5N	25N	S-TransHat.	--	0.0
Fissurellidae	*Diodora cayenensis* (Lamarck, 1822)	Dc	43.7N	28S	N-TransHat.	Steno-Marine	0.0
Caecidae	*Caecum pulchellum* Stimpson, 1851	Cpu	43N	35S	N-TransHat.	--	1.7
Calyptraeidae	***Crepidula convexa*** **Say, 1822**	**Cconv**	**48N**	**9.4N**	**N-TransHat.**	**Eury-Marine**	**7.0**
	Crepidula fornicata (Linne, 1758)	Cf	48N	25N	N-TransHat.	Eury-Marine	8.0
	Crepidula plana **Say, 1822**	**Cpl**	**48N**	**38S**	**N-TransHat.**	**Eury-Marine**	**7.7**
Cerithiidae	*Bittiolum alternatum* (Say, 1822)	Ba	46N	34.5N	N-TransHat.	--	8.2
	Bittiolum varium (Pfeiffer, 1840)	Bv	38N	34S	S-TransHat.	Eury-Estuarine	0.2
	Seila adamsii (H. C. Lea, 1846)	Sa	41N	35S	S-TransHat.	Steno-Estuarine	3.2
Cerithiopsidae	*Cerithiopsis greenii* (C. B. Adams, 1839)	Cg	46.5N	35S	N-TransHat.	Eury-Marine	2.2
	Cerithiopsis emersonii (C. B. Adams, 1839)	Ce	42N	34.5N	S-TransHat.	--	1.8
Epitoniidae	*Epitonium humphreysi* (Kiener, 1838)	Ehu	41.6N	29S	S-TransHat.	Steno-Marine	0.2
	Epitonium rupicola (Kurtz, 1860)	Er	41N	11N	S-TransHat.	Steno-Marine	1.2
Hydrobiidae	*Hydrobia truncata* (Vanatta, 1924)	Ht	52N	34.5N	N-TransHat.	--	7.3
Littorinidae	*Lacuna pallidula* (da Costa, 1778)	Lp	65.4N	41N	Northern	--	0.0
	Littorina littorea (Linne, 1758)	Ll	53N	38N	Northern	Eury-Estuarine	0.8
	Littorina obtusata (Linne, 1758)	Lo	74N	39N	Northern	Steno-Marine	7.5
	Littorina saxatilis (Olivi, 1792)	Ls	72N	38N	Northern	Eury-Marine	7.7
	Littoraria irrorata (Say, 1822)	Li	44.4N	26.1N	N-TransHat.	Eury-Estuarine	1.0
Naticidae	*Euspira heros* (Say, 1822)	Ehe	51.5N	33N	N-TransHat.	Steno-Marine	3.2
	Euspira immaculata (Totten, 1835)	Ei	49N	18.6N	N-TransHat.	--	0.3
	Neverita duplicata (Say, 1822)	Nd	45N	18.6N	N-TransHat.	Eury-Marine	5.5
Rissoidae	*Onoba aculeus* (Gould, 1841)	Oa	72N	41.2N	Northern	--	1.0
Skeniopsidae	*Skeneopsis planorbis* (Fabricius, 1780)	Sp	69.2N	27S	N-TransHat.	Eury-Marine	0.5
Triphoridae	*Marshallora nigrocincta* (C. B. Adams, 1839)	Mn	46N	23S	N-TransHat.	Eury-Marine	4.3
Columbellidae	*Astyris lunata* (Say, 1826)	Al	48N	28S	N-TransHat.	Eury-Marine	6.3
	Costoanachis lafresnayi (Fischer & Bernardi, 1857)	Cla	44N	16N	N-TransHat.	Eury-Marine	3.3
	Costoanachis avara (Say, 1822)	Ca	42N	20N	S-TransHat.	Eury-Marine	4.5
Melongenidae	***Busycotypus canaliculatus*** **(Linne, 1758)**	**Bcan**	**(43.7N)**	**29.9N**	**S-TransHat.**	**Eury-Marine**	**7.0**
	Busycon carica (Gmelin, 1791)	Bcar	41.5N	29N	S-TransHat.	Steno-Marine	5.3
	Busycon sinistrum Hollister, 1958	Bsi	39N	25N	S-TransHat.	--	0.0
Muricidae	*Nucella lapillus* (Linne, 1758)	Nl	60.7N	40.8N	Northern	Steno-Marine	1.5
	Urosalpinx cinerea **(Say, 1822)**	**Uc**	**46N**	**27.7N**	**N-TransHat.**	**Eury-Marine**	**6.0**
	Eupleura caudata (Say, 1822)	Ec	41.5N	25.7N	S-TransHat.	Eury-Marine	4.8
Nassariidae	***Ilyanassa obsoleta*** **(Say, 1822)**	**Io**	**48N**	**28.5S**	**N-TransHat.**	**Eury-Marine**	**8.7**
	Nassarius trivittatus (Say, 1822)	Nt	48.8N	29.9N	N-TransHat.	Eury-Marine	7.0
	Nassarius vibex (Say, 1822)	Nv	43.2N	27S	N-TransHat.	Eury-Estuarine	3.0
Ovulidae	*Simnialena uniplicata* (G. B. Sowerby II, 1848)	Su	37N	24S	S-TransHat.	--	0.2
Turridae	*Pyrgocythara plicosa* (C. B. Adams, 1850)	Ppl	41.6N	9N	S-TransHat.	Steno-Estuarine	1.3
Ellobiidae	*Melampus bidentatus* Say, 1822	Mbi	48N	18N	N-TransHat.	Eury-Estuarine	6.0
	Myosotella myosotis **(Draparnaud, 1801)**	**Mmy**	**44.7N**	**31N**	**N-Trans Hat.**	**Eury-Estuarine**	**3.5**

Notes: Sources include: (Abbott 1974), (ANSP 1996), (Franz and Merrill 1980a, b), (Castagna and Chanley 1973), (Balch 1899), (Smith 1862), (Hubbard and Smith 1865), (Perkins 1869), (Smith and Prime 1870), (Smith 1887), (Jacot 1920), (Leathem and Maurer 1975), (MacKenzie 1961), (Barnes 1994), Carlton and Cohen 1998), (Lippson and Lippson 1997), (Gosner 1978), (Wass et al. 1972), (Frey 1946), (Larsen 1985), (Maurer and Watling 1973a, 1973b), (Micheli and Peterson 1999), (Wells 1961), (Winkley 1888), (Verrill and Smith 1874), and (J. T. Carlton, pers. comm.).

Table 3.3. Results from univariate resampling and contingency tests of independence comparing successful invaders of San Francisco Bay with the remainder of the oyster-associate applicant pool. Results are reported according to biological character and taxonomic group. Statistically significant p-values ($p<0.05$) are listed in bold. Post-hoc statistical power results are reported for each contingency test.

Attribute Type	Biological Attribute	Bivalves	(n)	Power	Gastropods	(n)	Power	Mollusks	(n)	Power	df	Test
Biogeography	Invasion Success Elsewhere	**p=0.020**	**42**	**0.88**	p=0.121	51	0.06	**p=0.004**	**93**	**0.96**	1	2x2
Biogeography	Biogeographical Fauna	p=0.087	42	0.45	p=0.630	51	0.12	p=0.087	93	0.46	2	RxC
Biogeography	Amphi-Atlantic Distribution	p=0.696	42	0.09	p=0.303	51	0.18	p=0.772	93	0.07	1	2x2
Biogeography	Latitudinal Range	p=0.114	42	r	p=0.810	51		p=0.808	93	r	-	Resample
Biogeography	Northern Latitude Limit	p=0.084	42	r	p=0.766	51		p=0.069	93	r	-	Resample
Biogeography	Southern Latitude Limit	p=0.993	42	r	p=0.896	51		p=0.881	93	r	-	Resample
Habitat	Vertical Distribution (Tidal)	p=0.085	41	0.80	p=0.084	51	0.40	**p=0.006**	**92**	**0.70**	2	RxC
Habitat	Salinity Zonal Distribution	p=0.089	38	0.57	p=0.443	39	0.23	**p=0.042**	**77**	**0.46**	3	RxC
Habitat	Low Salinity Distribution	**p=0.019**	**36**	r	p=0.178	39	r	**p=0.018**	**75**	**r**	-	Resample
Habitat	High Salinity Distribution	p=0.361	38	r	p=0.061	38	r	p=0.627	76	r	-	Resample
Habitat	Salinity Range	**p=0.020**	**36**	r	p=0.166	38	r	p=0.093	74	r	-	Resample
Habitat	Substrate Preference	p=0.271	39	0.35	p=0.885	50	0.07	p=0.601	89	0.16	2	RxC
Habitat	Substrate Diversity	p=0.794	42	r	p=0.210	50	r	p=0.290	92	r	-	Resample
Habitat	Depth Diversity	p=0.437	41	r	p=0.406	51	r	p=0.717	92	r	-	Resample
Life History	Developmental Mode	p=0.251	37	0.72	p=0.126	44	0.42	**p=0.037**	**81**	**0.67**	1	2x2
Life History	Benthic Placement (Epifauna-Infauna)	p=0.820	42	0.06	-	-	-	-	-	-	1	2x2
Life History	Maximum Adult Size	p=0.665	39	r	p=0.650	40	r	p=0.693	79	r	-	Resample
Life History	Historical Abundance NY/LIS	**p=0.004**	**42**	r	**p=0.002**	**51**	r	**p=0.0002**	**93**	r	-	Resample

Notes: The letter “r” in the Power columns indicates a distribution-free resampling test (10,000 iterations) where power is not calculable.

Table 3.4. Biological attributes of bivalve invaders of San Francisco Bay.

Biological Attribute	***Gemma gemma***	***Geukensia demissa***	***Macoma balthica***	***Mya arenaria***	***Petricolaria pholadiformis***
Invasion Success Elsewhere	no	no	no	yes	yes
Biogeographical Fauna	N-TransHatteran	N-TransHatteran	N-TransHatteran	Northern	N-TransHatteran
Amphi-Atlantic Distribution	no	no	yes	no	no
Latitudinal Range [º]	19	20	52	18	83
Northern Latitude Limit [º]	45N	48N	83N	53N	48N
Southern Latitude Limit [º]	26N	28N	31N	35N	35S
Vertical Distribution	Intertidal-Subtidal	Intertidal	Intertidal-Subtidal	Intertidal-Subtidal	Intertidal
Salinity Zonal Distribution	Euryhaline-Estuarine	Euryhaline-Estuarine	Euryhaline-Estuarine	Euryhaline-Estuarine	Stenohaline-Estuarine
Low Salinity Distribution [ppt]	5	5	5	5	15
High Salinity Distribution [ppt]	30	30	25	25	30
Salinity Range [ppt]	25	25	20	20	15
Substrate Preference	Soft Bottom	Hard & Soft Bottom	Hard & Soft Bottom	Soft Bottom	Hard & Soft Bottom
Substrate Diversity [ ]	2.0	4.0	3.0	3.0	3.0
Depth Diversity [ ]	2.0	1.0	2.0	3.0	1
Developmental Mode	Direct	Planktonic	Planktonic	Planktonic	Planktonic
Benthic Placement	Infaunal	Epifaunal	Infaunal	Infaunal	Infaunal
Maximum Adult Size [mm]	3	127	38	140	57
Historical Abundance [ ]	7.0	8.0	6.0	8.0	5.5

Table 3.5. Biological attributes of gastropod invaders of San Francisco Bay.

Biological Attribute	***Boonea bisuturalis***	***Busycotypus canaliculatus***	***Crepidula convexa***	***Crepidula plana***	***Myosotella myosotis***	***Ilyanassa obsoleta***	***Urosalpinx cinerea***
Invasion Success Elsewhere	no	no	no	no	yes	no	yes
Biogeographical Fauna	Northern	S-TransHatteran	N-TransHatteran	N-TransHatteran	N-TransHatteran	N-TransHatteran	N-TransHatteran
Amphi-Atlantic Distrib.	no	no	no	no	no	no	no
Latitudinal Range [º]	6.5	12.1	38.6	86	13.7	76.5	18.3
Northern Latitude Limit [º]	47N	42N	48N	48N	44.7N	48N	46N
Southern Latitude Limit [º]	40.5N	29.9N	9.4N	38S	31N	28.5S	27.7N
Vertical Distrib.	Intertidal-Subtidal	Intertidal-Subtidal	Intertidal-Subtidal	Intertidal-Subtidal	Intertidal	Intertidal-Subtidal	Intertidal-Subtidal
Salinity Zonal Distrib.	Stenohaline-Estuarine	Euryhaline-Marine	Euryhaline-Marine	Euryhaline-Marine	Euryhaline-Marine	Euryhaline-Marine	Euryhaline-Estuarine
Low Salinity Distrib. [ppt]	18	18	12	15	1	10	11
High Salinity Distrib. [ppt]	30	35	35	35	35	32	30
Salinity Range [ppt]	12	17	23	20	34	22	19
Substrate Preference	Hard & Soft Bottom	Soft Bottom	Hard & Soft Bottom	Hard Bottom	Hard Bottom	Soft Bottom	Hard & Soft Bottom
Substrate Diversity [ ]	4	1.5	4	2	3	3.5	4
Depth Diversity [ ]	2	3	2	3	1	2	2
Developmental Mode	planktonic	direct	direct	planktonic	direct	planktonic	direct
Maximum Adult Size [mm]	6	190	19	41	10	32	44
Historical Abundance LIS [ ]	4.7	7.0	7.0	7.7	3.5	8.7	6.0

Appendix 3.1. Biological attributes of molluscan species analyzed.

Species	Invaded Elsewhere	SF Invasion Status	Biogeographical Fauna	Amphi-Atlantic Distribution	Latitudinal Range [degrees]	Northern Limit [degrees]	Southern Limit [degrees]	Vertical Distribution (Tidal)	Salinity Zonal Distribution	Low Salinity Distribution [ppt]	High Salinity Distribution [ppt]	Salinity Range [ppt]	Substrate Preference	Substrate Diversity	Depth Diversity	Developmental Mode	Benthic Pos. (Infaua/epifauna)	Max Adult Shell Size [mm]	Historical Abundance (NY/LIS)	Feeding Mode
BIVALVES																				
Amygdalum papyrum	no	Non-Invader	ST	no	12	38	26	Both	Eury-Estuarine	8	25	17	Both	3	2	Plank.	Infaunal	32	0	Susp.
Anadara ovalis	no	Non-Invader	ST	no	64	42	-22	Subtidal	Eury-Marine	15	35	20	Soft	2	2	Plank.	Infaunal	76	4.7	Susp.
Anadara transversa	no	Non-Invader	NT	no	17.7	43.7	26	Subtidal	Eury-Marine	15	32	17	Hard	3.5	2	Plank.	Epifaunal	32	6.8	Susp.
Anomia simplex	no	Non-Invader	NT	no	67	45	-22	Both	Steno-Estuarine	15	30	15	Both	3	2	Plank.	Infaunal	57	6.5	Susp.
Argopecten irradians	no	Non-Invader	NT	no	17	45	28	Subtidal	Eury-Marine	15	35	20	Soft	3	1	Plank.	Infaunal	102	4.7	Susp.
Barnea truncata	no	Non-Invader	NT	no	64.5	42.5	-22	Both	Eury-Estuarine	13	30	17	Both	4	2	Plank.	Infaunal	70	1.7	Susp.
Cerastoderma pinnulatum	no	Non-Invader	N	no	18	53	35	Subtidal	Steno-Marine	25	35	10	Both	2	3	Plank.	Infaunal	12	1.2	Susp.
Corbula contracta	no	Non-Invader	ST	no	64	42	-22	Subtidal	Steno-Marine	20	35	15	Hard	3	2	N/A	Infaunal	10	1	Susp.
Corbula swiftiana	no	Non-Invader	ST	no	16	42	26	Subtidal	Eury-Marine	5	35	30	Hard	3	2	N/A	Epifaunal	7	0	Susp.
Crassinella lunulata	no	Non-Invader	ST	no	64	42	-22	Subtidal	N/A	N/A	N/A	N/A	Soft	3.5	2	N/A	Infaunal	10	1.8	Susp.
Crassostrea virginica	yes	Inv Non-SF	NT	no	22	48	26	Both	Eury-Estuarine	6	30	24	Soft	4	2	Plank.	Infaunal	203	6.5	Susp.
Cumingia tellinoides	no	Non-Invader	NT	yes	15	45	30	Subtidal	N/A	N/A	N/A	N/A	Hard	3	1	Plank.	Epifaunal	22	2.5	Dep.
Cyrtopleura costata	no	Non-Invader	ST	yes	64	42	-22	Both	Eury-Estuarine	10	30	20	Hard	4	2	Plank.	Epifaunal	203	0.3	Susp.
Diplothyra smithii	no	Non-Invader	ST	no	16	42	26	N/A	Steno-Marine	25	35	10	Both	2	N/A	N/A	Epifaunal	N/A	0.7	Susp.
Gemma gemma	no	SF Invader	NT	no	19	45	26	Both	Eury-Estuarine	5	30	25	Soft	2	2	Direct	Infaunal	3	7	Susp.
Geukensia demissa	yes	SF Invader	NT	no	20	48	28	Intertidal	Eury-Estuarine	5	30	25	Soft	4	1	Plank.	Infaunal	127	8	Susp.
Hiatella arctica	no	Non-Invader	NT	no	60	80	20	Both	N/A	N/A	35	N/A	Both	3	4	Plank.	Epifaunal	76	0.8	Susp.
Ischadium recurvum	no	Non-Invader	ST	no	16	42	26	Both	Steno-Estuarine	8	20	12	Hard	4	2	Plank.	Infaunal	60	1.3	Susp.
Laevicardium mortoni	no	Non-Invader	ST	no	16	42	26	Both	Steno-Estuarine	15	25	10	Soft	3	2	Plank.	Infaunal	25	5.7	Susp.
Lyonsia hyalina	no	Non-Invader	NT	no	15	45	30	Subtidal	Steno-Estuarine	15	30	15	Hard	4	2	Plank.	Epifaunal	25	4.7	Both
Macoma balthica	no	SF Invader	NT	no	52	83	31	Both	Eury-Estuarine	5	25	20	Soft	3	2	Plank.	Infaunal	38	6	Both
Macoma mitchelli	no	Non-Invader	ST	no	11	39	28	Both	Eury-Estuarine	2	25	23	Soft	2	2	Plank.	Infaunal	20	0	Dep.
Mercenaria campechiensis	no	Non-Invader	ST	no	14	40	26	Both	Eury-Marine	10	35	25	Both	1.5	2	Plank.	Epifaunal	152	0	Susp.
Mercenaria mercenaria	yes	Inv Non-SF	NT	no	20	48	28	Both	Eury-Marine	10	35	25	Soft	3.5	2	Plank.	Infaunal	108	8.2	Susp.
Mulinia lateralis	no	Non-Invader	NT	no	18	44	26	Subtidal	Eury-Estuarine	8	30	22	Soft	3	2	Plank.	Infaunal	19	5.8	Susp.
Mya arenaria	yes	SF Invader	N	no	18	53	35	Both	Eury-Estuarine	5	30	22	Soft	3	3	Plank.	Infaunal	140	8	Susp.
Mysella planulata	no	Non-Invader	NT	no	19	45	26	Subtidal	Eury-Estuarine	15	25	20	Soft	3	3	Plank.	Infaunal	4	1.8	Susp.

Appendix 3.1. continued.

Species	Invaded Elsewhere	SF Invasion Status	Biogeographical Fauna	Amphi-Atlantic Distribution	Latitudinal Range [degrees]	Northern Limit [degrees]	Southern Limit [degrees]	Vertical Distribution (Tidal)	Salinity Zonal Distribution	Low Salinity Distribution [ppt]	High Salinity Distribution [ppt]	Salinity Range [ppt]	Substrate Preference	Substrate Diversity	Depth Diversity	Developmental Mode	Benthic Pos. (Infauna/epifauna)	Max Adult Shell Size [mm]	Historical Abundance (NY/LIS)	Feeding Mode
BIVALVES																				
Mytilopsis leucophaeata	yes	Inv Non-SF	ST	no	19	41	22	Both	Steno-Estuarine	0	28	13	Soft	2	2	Plank.	Epifaunal	19	0	Susp.
Mytilus edulis	no	Non-Invader	NT	no	50	83	33	Both	Steno-Estuarine	20	7	7	Both	3	4	Plank.	Epifaunal	102	6.2	Susp.
Noetia ponderosa	no	Non-Invader	ST	no	11	37	26	Subtidal	Steno-Marine	17	35	15	Soft	3	1	Plank.	Infaunal	70	0.2	Susp.
Nucula proxima	no	Non-Invader	NT	no	19	45	26	Subtidal	Eury-Marine	20	35	18	Soft	3	3	Plank.	Infaunal	10	7.8	Dep.
Ostrea equestris	no	Non-Invader	ST	no	59	37	-22	Subtidal	Steno-Marine	20	35	15	Soft	3	3	Plank.	Infaunal	83	0	Susp.
Pandora gouldiana	no	Non-Invader	N	no	13	48	35	Both	Steno-Marine	23	35	15	Soft	2	4	Plank.	Infaunal	38	5.5	Susp.
Petricolaria pholadiformis	yes	SF Invader	NT	no	83	48	-35	Both	Steno-Marine	15	35	12	Soft	3	1	Plank.	Infaunal	57	5.5	Susp.
Solemya velum	no	Non-Invader	NT	yes	17	45	28	Both	Steno-Estuarine	15	30	15	Both	3.5	2	N/A	Infaunal	25	2.7	Both
Solen viridis	no	Non-Invader	ST	no	16	42	26	Both	Steno-Estuarine	13	28	13	Soft	1	2	Plank.	Infaunal	67	0	Susp.
Spisula solidissima	no	Non-Invader	NT	yes	12	45	33	Both	Steno-Estuarine	27	28	15	Hard	4	3	Plank.	Epifaunal	178	4.8	Susp.
Tagelus divisus	no	Non-Invader	ST	no	64	42	-22	Both	Steno-Marine	15	35	8	Both	3	2	Plank.	Infaunal	41	1.3	Both
Tagelus plebeius	no	Non-Invader	ST	no	64	42	-22	Both	Steno-Estuarine	10	29	14	Both	3	2	Plank.	Infaunal	95	1.3	Both
Tellina agilis	no	Non-Invader	NT	no	17	48	31	Subtidal	Eury-Estuarine	13	30	20	Soft	3	2	Plank.	Infaunal	16	4.3	Both
Tellina versicolor	no	Non-Invader	ST	no	16	42	26	Subtidal	Eury-Marine	20	35	22	Soft	2	1	N/A	Infaunal	N/A	0	Both
Zirfaea crispata	no	Non-Invader	N	yes	14	53	39	Both	Steno-Marine	N/A	35	15	Both	4	3	Plank.	Infaunal	89	3.2	Susp.
GASTROPODS																				
Acteocina canaliculata	no	Non-Invader	NT	no	40	46	6.0	Both	Eury-Marine	18	35	17	Soft	2	2	Direct	Epifaunal	6	5.2	Carn.
Astyris lunata	no	Non-Invader	NT	no	76	48	-28.0	Subtidal	Eury-Marine	12	32	20	Both	5	2	Plank.	Epifaunal	6	6.3	Omni.
Bittiolum alternatum	no	Non-Invader	NT	no	11.5	46	34.5	Both	NA	N/A	N/A	N/A	Both	3	3	Plank.	Epifaunal	10	8.2	Detrit.
Bittiolum varium	no	Non-Invader	ST	no	72	38	-34.0	Subtidal	Eury-Estuarine	10	30	20	Soft	2	1	Plank.	Epifaunal	NA	0.2	Detrit.
Boonea bisuturalis	no	SF Invader	N	no	6.5	47	40.5	Both	Steno-Estuarine	18	30	12	Both	4	2	Plank.	Epifaunal	6	4.7	Ecopar
Boonea impressa	no	Non-Invader	ST	no	17	42	25.0	Both	Eury-Marine	11	35	24	Both	3	2	Plank.	Epifaunal	NA	0.7	Ecopar
Boonea seminuda	no	Non-Invader	NT	no	81.5	46.5	-35.0	Both	NA	N/A	N/A	N/A	Hard	2	2	Plank.	Epifaunal	3	4.2	Ecopar
Busycon carica	no	Non-Invader	ST	no	12.5	41.5	29.0	Both	Steno-Marine	20	35	15	Soft	1.5	3	Direct	Epifaunal	229	5.3	Carn.
Busycon sinistrum	no	Non-Invader	ST	no	14	39	25.0	Both	NA	N/A	N/A	N/A	Soft	1.5	3	Direct	Epifaunal	406	0	Carn.

Appendix 3.1. continued.

Species	Invaded Elsewhere	SF Invasion Status	Biogeographical Fauna	Amphi-Atlantic Distribution	Latitudinal Range [degrees]	Northern Limit [degrees]	Southern Limit [degrees]	Vertical Distribution (Tidal)	Salinity Zonal Distribution	Low Salinity Distribution [ppt]	High Salinity Distribution [ppt]	Salinity Range [ppt]	Substrate Preference	Substrate Diversity	Depth Diversity	Developmental Mode	Benthic Pos. (Infaua/epifauna)	Max Adult Shell Size [mm]	Historical Abundance (NY/LIS)	Feeding Mode
GASTROPODS																				
Busycotypus canaliculatus	no	SF Invader	ST	no	12.1	42	29.9	Both	Eury-Marine	18	35	17	Soft	1.5	3	Direct	Epifaunal	190	7	Carn.
Busycotypus canaliculatus	no	SF Invader	ST	no	12.1	42	29.9	Both	Eury-Marine	18	35	17	Soft	1.5	3	Direct	Epifaunal	190	7	Carn.
Caecum pulchellum	no	Non-Invader	NT	no	78	43	-35.0	Subtidal	NA	N/A	N/A	N/A	Soft	3	3	Plank.	Epifaunal	2	1.7	Detrit.
Cerithiopsis emersonii	no	Non-Invader	ST	no	7.5	42	34.5	Subtidal	NA	N/A	N/A	N/A	Hard	1.5	2	Plank.	Epifaunal	19	1.8	Omni.
Cerithiopsis greenii	no	Non-Invader	NT	no	81.5	46.5	-35.0	Subtidal	Eury-Marine	12	32	20	Both	4	1	Plank.	Epifaunal	3	2.2	Omni.
Costoanachis avara	no	Non-Invader	ST	no	22	42	20.0	Subtidal	Eury-Marine	18	35	17	Soft	2	2	Plank.	Epifaunal	19	4.5	Omni.
Costoanachis lafresnayi	no	Non-Invader	NT	no	28	44	16.0	Subtidal	Eury-Marine	18	35	17	Both	2	2	Plank.	Epifaunal	19	3.3	Omni.
Crepidula convexa	no	SF Invader	NT	no	38.6	48	9.4	Both	Eury-Marine	12	35	23	Both	4	2	Direct	Epifaunal	19	7	Susp.
Crepidula fornicata	yes	Inv Non-SF	NT	no	23	48	25.0	Both	Eury-Marine	15	35	20	Hard	3	3	Plank.	Epifaunal	64	8	Susp.
Crepidula plana	no	SF Invader	NT	no	86	48	-38.0	Both	Eury-Marine	15	35	20	Hard	2	3	Plank.	Epifaunal	41	7.7	Susp.
Diodora cayenensis	no	Non-Invader	NT	no	71.7	43.7	-28.0	Both	Steno-Marine	N/A	N/A	N/A	Hard	1	3	Plank.	Epifaunal	44	0	Herb.
Epitonium humphreysi	no	Non-Invader	ST	no	70.6	41.6	-29.0	Subtidal	Steno-Marine	18	32	14	Both	2	3	Plank.	Epifaunal	22	0.2	Carn.
Epitonium rupicola	no	Non-Invader	ST	no	30	41	11.0	Subtidal	Steno-Marine	18	32	14	Soft	1	2	Plank.	Epifaunal	25	1.2	Carn.
Eupleura caudata	no	Non-Invader	ST	no	15.8	41.5	25.7	Both	Eury-Marine	14	32	18	Both	4	2	Direct	Epifaunal	41	4.8	Carn.
Euspira heros	no	Non-Invader	NT	no	18.5	51.5	33.0	Both	Steno-Marine	25	35	10	Soft	2	4	Plank.	Epifaunal	127	3.2	Carn.
Euspira immaculata	no	Non-Invader	NT	no	30.4	49	18.6	Subtidal	NA	N/A	N/A	N/A	Soft	1	2	Plank.	Epifaunal	8	0.3	Carn.
Fargoa bartschi	no	Non-Invader	NT	no	15	45	30.0	Both	NA	N/A	N/A	N/A	Hard	1	3	Plank.	Epifaunal	NA	0	Ecopara.
Fargoa calesi	no	Non-Invader	ST	no	66	42	-24.0	Both	Steno-Estuarine	18	30	12	Hard	1	3	Plank.	Epifaunal	NA	0	Ecopara.
Fargoa dianthophila	no	Non-Invader	ST	no	16.5	41.5	25.0	Both	NA	N/A	N/A	N/A	Hard	1	2	Plank.	Epifaunal	NA	0	Ecopara.
Haminoea solitaria	no	Non-Invader	NT	no	18.2	46	27.8	Both	Eury-Estuarine	5	30	25	Both	3.5	2	Plank.	Epifaunal	13	2	Omni.
Hydrobia truncata	no	Non-Invader	NT	no	17.5	52	34.5	Both	NA	N/A	N/A	N/A	Soft	3	2	N/A	Epifaunal	3	7.3	Detrit.
Ivanassa obsoleta	no	SF Invader	NT	no	76.5	48	-28.5	Both	Eury-Marine	10	32	22	Soft	3.5	2	Plank.	Epifaunal	32	8.7	Omni./Dep.
Lacuna pallidula?	no	Non-Invader	N	no	24.4	65.4	41.0	Subtidal	NA	15	N/A	N/A	Soft	1	1	Direct	Epifaunal	NA	0	Herb.
Littoraria irrorata	no	Non-Invader	NT	no	18.3	44.4	26.1	Intertidal	Eury-Estuarine	5	30	25	Both	2	1	Plank.	Epifaunal	32	1	Herb.
Littorina littorea	yes	Inv Non-SF	N	no	15	53	38.0	Both	Eury-Estuarine	10	30	20	Both	4	1	Plank.	Epifaunal	38	0.8	Herb.
Littorina obtusata	no	Non-Invader	N	yes	35	74	39.0	Intertidal	Steno-Marine	28	35	7	Both	3	1	Direct	Epifaunal	19	7.5	Herb.
Littorina saxatilis	no	Non-Invader	N	yes	34	72	38.0	Both	Eury-Marine	5	35	30	Both	3	3	Direct	Epifaunal	NA	7.7	Herb.

Appendix 3.1. continued.

Species	Invaded Elsewhere	SF Invasion Status	Biogeographical Fauna	Amphi-Atlantic Distribution	Latitudinal Range [degrees]	Northern Limit [degrees]	Southern Limit [degrees]	Vertical Distribution (Tidal)	Salinity Zonal Distribution	Low Salinity Distribution [ppt]	High Salinity Distribution [ppt]	Salinity Range [ppt]	Substrate Preference	Substrate Diversity	Depth Diversity	Developmental Mode	Benthic Pos. (Infaua/epifauna)	Max Adult Shell Size [mm]	Historical Abundance (NY/LIS)	Feeding Mode
GASTROPODS																				
Marshallora nigrocincta	no	Non-Invader	NT	no	69	46	-23.0	Subtidal	Eury-Marine	12	35	23	Both	4	1	Plank.	Epifaunal	6	4.3	Omni.
Melampus bidentatus	no	Non-Invader	NT	no	30	48	18.0	Intertidal	Eury-Estuarine	10	30	20	Hard	1	1	Plank.	Epifaunal	19	6	Detrit.
Myosotella myosotis	yes	SF Invader	NT	no	13.7	44.7	31.0	Intertidal	Eury-Marine	1	35	34	Hard	3	1	Direct	Epifaunal	10	3.5	Detrit./Herb.
Nassarius trivittatus	no	Non-Invader	NT	no	18.9	48.8	29.9	Both	Eury-Marine	12	35	23	Soft	3	3	Plank.	Epifaunal	22	7	Omni.
Nassarius vibex	no	Non-Invader	NT	no	70.2	43.2	-27.0	Both	Eury-Estuarine	12	30	18	Soft	3	2	Plank.	Epifaunal	19	3	Omni.
Neverita duplicata	no	Non-Invader	NT	no	26.4	45	18.6	Both	Eury-Marine	18	35	17	Soft	1.5	3	Plank.	Epifaunal	76	5.5	Carn.
Nucella lapillus	no	Non-Invader	N	yes	19.9	60.7	40.8	Intertidal	Steno-Marine	25	35	10	Both	2	1	Direct	Epifaunal	51	1.5	Carn.
Onoba aculeus	no	Non-Invader	N	yes	30.8	72	41.2	Intertidal	NA	N/A	N/A	N/A	Both	4	1	Direct	Epifaunal	3	1	Detrit./Herb.
Pyrgocythara plicosa	no	Non-Invader	ST	no	32.6	41.6	9.0	Subtidal	Steno-Estuarine	18	30	12	Both	4	1	N/A	Epifaunal	NA	1.3	Carn.
Rictaxis punctostriatus	no	Non-Invader	ST	no	34.7	41.6	6.9	Both	Steno-Estuarine	18	30	12	Soft	2	3	N/A	Epifaunal	6	2.8	Carn.
Savella fusca	no	Non-Invader	NT	no	29	47	18.0	Both	Steno-Estuarine	18	30	12	Soft	3	2	N/A	Epifaunal	NA	1.8	Ecopara.
Seila adamsii	no	Non-Invader	ST	no	76	41	-35.0	Subtidal	Steno-Estuarine	25	30	5	Both	2	2	Plank.	Epifaunal	13	3.2	Detrit./Herb.
Simnialena uniplicata	no	Non-Invader	ST	no	61	37	-24.0	Subtidal	NA	N/A	N/A	N/A	N/A	N/A	1	N/A	Epifaunal	NA	0.2	Carn.
Skeneopsis planorbis	no	Non-Invader	NT	yes	96.2	69.2	-27.0	Subtidal	Eury-Marine	18	35	17	Hard	4	1	Direct	Epifaunal	NA	0.5	Herb.
Turbonilla interrupta	no	Non-Invader	NT	no	82	47	-35.0	Both	Eury-Marine	18	35	17	Both	3	3	N/A	Epifaunal	6	4	Ecopara.
Urosalpinx cinerea	yes	SF Invader	NT	no	18.3	46	27.7	Both	Eury-Estuarine	11	30	19	Both	4	2	Direct	Epifaunal	44	6	Carn.

Notes: Sources include: (Abbott 1974), (Franz and Merrill 1980a, b), (Castagna and Chanley 1973), (Balch 1899), (Smith 1862), (Hubbard and Smith 1865), (Perkins 1869), (Smith and Prime 1870), (Smith 1887), (Jacot 1920), (Maurer et al. 1974), (Barnes 1994), (Lippson and Lippson 1997), (Gosner 1978), (Wass et al. 1972), (Frey 1946), (Larsen 1985), (Maurer and Watling 1973a, 1973b), (Micheli and Peterson 1999), (Wells 1961), (Winkley 1888), (Verrill and Smith 1874), and (J. T. Carlton, pers. comm.), (ANSP 1996), (Leathem and Maurer 1975), (Carlton and Cohen 1998), (MacKenzie 1961), (Chanley and Andrews 1971), (Sullivan 1948), (Galtsoff 1964), (Belding 1912), (Franz 1973), (Mann and Gallager 1984), (Thorson 1946), (Loosanoff et al. 1966), (Scheltema 1984), (Thiriot-Quievreux and Scheltema 1982), (Pechenik 1999), (Carricker 1955), (Morrison 1970), (Weber 1977), (Robertson 1996), (Thiriot-Quievreux 1983), (Rehder 1997).

LITERATURE CITED

Abbott, R. T. 1974. American Seashells, second edition. Van Nostrand Reinhold Company, New York, 663 p.

Alexander, R. C. 1947. *Littorina littorea* on the New Jersey coast. Nautilus 60:73-76.

ANSP (Academy of Natural Sciences) 1996. In: Rosenberg, G. (ed.), Malacolog 2.0: Recent western Atlantic gastropods, online database, Philadelphia.

Balch, F. N. 1899. List of marine mollusca of Coldspring Harbor, Long Island, with descriptions of two new species of nudibranchs. Proceedings of the Boston Society of Natural History 29:133-162.

Barnes, R. S. K. 1994. The Brackish-Water Fauna of Northwestern Europe: a guide to brackish-water habitats, ecology, and macrofauna for field workers, naturalists, and students. Cambridge University Press, Cambridge, UK, 299 p.

Barnes, R. D. 1987. Invertebrate zoology, fifth edition. W. B. Saunders College/Holt, Rinehart and Winston, New York, 902 p.

Barrett, E. M. 1963. The California oyster industry. Department of Fish and Game Fish Bulletin 123: 1-103.

Belding, D. L. 1912. Report upon the scallop fishery of Massachusetts. Wright and Potter Printing Co., Boston, MA.

Bequaert, J. C. 1943. The genus *Littorina* in the western Atlantic ocean. Johnsonia 1:1-27.

Berman, J. and J. T. Carlton 1991. Marine invasion processes: interactions between native and introduced marsh snails. Journal of Experimental Marine Biology and Ecology 150:267-281.

Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65:370-381.

Bird, J. B. 1968. *Littorina littorea*: occurrence in a northern Newfoundland beach terrace, predating Norse settlements. Science 159:114.

Bonnot, P. 1935. The California oyster industry. California Fish and Game 21: 65-80.

Bourne, N. F. 1997. Molluscan fisheries of British Columbia. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 115-130.

Brenchley, G. A and J. T. Carlton 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. Biological Bulletin 165:543-558.

Bulger, A. J., Hayden, B. P., Monaco, M. E., Nelson, D. M., and M. G. McCormick-Ray. Biologically-based estuarine salinity zones derived from a multivariate analysis. Estuaries 16:311-322.

Capaldo, P. S. 1983. Tolerance of the common marsh snail, *Melampus bidentatus*, to submersion. Estuaries 6:176-177.

Carlton, J. T. 1969. *Littorina littorea* in California (San Francisco and Trinidad Bays). The Veliger 11:283-284.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation. University of California, Davis. 904 p.

Carlton, J. T. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. Conservation Biology 3: 265-273.

Carlton, J. T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research 11: 489-505.

Carlton, J. T. 1999a. The scale and ecological consequences of biological invasions of the World's oceans. In: (eds. O. T. Sandlund, P. J. Shei and Å. Viken) Invasive species and biodiversity management. Based on a selection of papers presented at the Norway/UN Conference on Alien Species, Trondheim, Norway. Kluwer Academic Publisher, Dordrech, 444 p.

Carlton, J. T. 1999b. Molluscan invasions in marine and estuarine communities. Malacologia 41:439-454.

Carlton, J. T. and A. N. Cohen 1998. Periwinkle's progress: the Atlantic snail *Littorina saxatilis* (Mollusca: Gastropoda) establishes a colony on a Pacific shore. The Veliger 41:333-338.

Carlton, J. T. and R. Mann 1996. Transfers and world-wide introductions. In: V. S. Kennedy, R. E. I. Newell, and A. F. Eble (eds.), The eastern oyster, *Crassostrea virginica*, p 691-706. Maryland Sea Grant Program, College Park.

Carriker, M. L. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Fish Wildlife Serv. Spec. Sci. Rep. Fish. No. 148, 150 p.

Castagna, M. and P. Chanley 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western Mid-Atlantic Coast. Malacologia 12:47-96.

Chanley, P and J. D. Andrews 1971. Aids for identification of bivalve larvae of Virginia. Malacologia 11:45-119.

Churchill, E. P., Jr. 1920. The oyster and the oyster industry of the Atlantic and Gulf coasts. Appendix VIII, Rep. of U. S. Comm. Fish and Fisheries, 1919, 51 p. Government Printing Office, Washington, D. C.

Clarke, A. H., Jr. 1963. Supplementary notes on pre-Columbian *Littorina littorea* in Nova Scotia. Nautilus 77:8-11.

Clarke, A. H., Jr. and J. S. Erskine 1961. Pre-Columbian *Littorina littorea* in Nova Scotia. Science 134:393-394.

Cohen, A. N. and J. T. Carlton 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Biological Study. A report for the U. S. Fish and Wildlife Service, Washington, D. C. and the National Sea Grant College Program Connecticut Sea Grant. 272 p.

Cohen, A. N. and J. T. Carlton 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555-558.

Cohen, J. 1977. Statistical power analysis for behavioral sciences, revised edition. Academic Press, New York, 489 p.

Coles, S. L., DeFelice, R. C., Eldredge, L. G., and J. T. Carlton 1999. Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. Marine Biology 135:147-158.

Collins, J. W. 1892. Report on the fisheries of the Pacific Coast of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1892, 267 p. Government Printing Office, Washington, D. C.

Daehler, C. C. and D. R. Strong 1993. Predictions and biological invasions. Trends in Ecology and Evolution 8:380.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, England. 181 p.

Faul, F. and E. Erdfelder 1992. G*Power: A priori, post-hoc, and compromise power analyses for MS-Dos [computer program]. Bonn University Dept. of Psychology, Bonn, Germany.

Franz, D. R. 1973. The ecology and reproduction of a marine bivalve *Mysella planulata* (Erycinacea). Biological Bulletin 44:93-106.

Franz, D. R. and A. S. Merrill 1980a. Molluscan distribution patterns on the continental shelf of the middle Atlantic Bight (Northwest Atlantic). Malacologia 19:209-225.

Franz, D. R. and A. S. Merrill 1980b. The origins and determinants of distribution of molluscan faunal groups on the shallow continental shelf of the Northwest Atlantic. Malacologia 19(2):227-248.

Frey, D. G. 1946. Oyster bars of the Potomac River. U. S. Fish and Wildlife Special Scientific Report No. 32, Washington, D. C. p. 1-93.

Galtsoff, P. S. 1929. Oyster industry of the Pacific Coast of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1929, Appendix VIII, Document 1066, 367-400. Washington Printing Office, Washington, D. C.

Galtsoff, P. S. 1964. The American oyster. Fishery Bulletin of the Fish and Wildlife Service. Vol. 64, 480 p.

Ganong, W. F. 1886. Is *Littorina littorea* introduced or indigenous? American Naturalist 20:931-940.

Ganong, W. F. 1887. Is *Littorina littorea* introduced or indigenous? American Naturalist 21:287-288.

Goodwin, B. J., McAllister, A. J., and L. Fahig 1998. Predicting invasiveness of plant species based on biological information. Conservation Biology 13:422-426.

Gosner, K. L. 1971. Guide to identification of marine and estuarine invertebrates – Cape Hatteras to the Bay of Fundy. John Wiley & Sons, New York, 693 p.

Gosner, K. L. 1978. A field guide to the Atlantic Seashore. Houghton-Mifflin, Boston. 329 p.

Gould, A. A. 1841. Report on the invertebrata of Massachusetts, comprising the mollusca, crustacea, annelida, and radiata. Folsom, Wells and Thurston, Cambridge. 386 p.

Grosholz, E. D. and G. M. Ruiz 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78:59-66.

Grosholz, E. D., Ruiz, G. M., Dean, C. A., Shirley, K. A., Maron, J. L., and P. G. Connors 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206-1224.

Hopkins, D. R. 1986. Atlas of the distribution and abundance of common benthic species in San Francisco Bay, California. U. S. Geological Survey Waters Resources Investigations Report 86-4003.

Hopkins, S. E. and J. D. Andrews 1970. *Rangia cuneata* on the East Coast: thousand mile range extension, resurgence? Science 167:868.

Hubbard, J. W. and S. Smith 1865. Catalogue of the mollusca of Staten Island, N. Y. Annals of the Lyceum of Natural History of New York 8:151-154.

Hubbs, C. L. and R. R. Miller 1965. Studies of cyprinodont fishes. XXII. Variation in *Lucania parva*, its establishment in western United States, and description of a new species from an interior basin in Coahuila, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan No. 127, 104 p.

Ingersoll, E. 1881. The oyster-industry of the United States. In: G. B. Goode (ed.), The history and present condition of the fishery industries, 1879-1880, 251 p. Government Printing Office, Washington, D. C.

Jacot, A. 1920. On the marine mollusca of Staten Island, N.Y. The Nautilus 33:11-115.

Johannesson, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*Littorina littorea*)? Marine Biology 99:507-513.

Kennish, M. J. 1990. Estuarine Ecology, vol. II Biological Aspects. CRC Press, Boca Raton, 391 p.

Kornicker , L. S. 1975. Spread of ostracodes to exotic environs on transplanted oysters. Bulletins of American Paleontology. 65:129-139.

Larsen, P. F. 1985. The benthic macrofauna associated with the oyster reefs of the James River Estuary, Virginia, U.S.A. Int. Revue ges. Hydrobiol. 70:797-814.

Leathem, W. and D. Maurer 1975. The distribution and ecology of common marine and estuarine gastropods in the Delaware Bay area. The Nautilus 89:73-79.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288: 852-854.

Lippson, A. J. and R. L. Lippson 1997. Life in the Chesapeake Bay, second edition. The Johns Hopkins University Press, Baltimore, MD, 304 p.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133-137.

Loosanoff, V. L., Davis, H. C., and P. E. Chanley 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia 4:351-435.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and competitive abilities. American Naturalist 112:23-29.

Manly, B. F. J. 1992. Randomization and Monte Carlo methods in biology. Chapman & Hall, London.

Mann, R. and S. M. Gallager 1984. Physiology of the wood boring mollusc *Martesia cuneiformis* Say. Biological Bulletin 166:167-177.

Maurer, D. and L. Watling 1973a. The biology of the oyster community and its associated fauna in Delaware Bay. In: (D. F. Polis, ed.) Delaware Bay Report Series 6:1-97.

Maurer, D. and L. Watling 1973b. Studies on the oyster community in Delaware: the effects of the estuarine environment on the associated fauna. Int. Revue ges. Hydrobiol. 58:161-201.

Maurer, D., Watling, L. and G. Aprill 1974. The distribution and ecology of common marine and estuarine pelecypods in the Delaware Bay area. The Nautilus 88:38-45.

McMahon, R. F. and W. D. Russel-Hunter 1981. The effects of physical variables and acclimation on survival and oxygen consumption in the high littoral salt-marsh snail, *Melampus bidentatus* Say. Biological Bulletin 161:246-269.

Meehan, B. W, Carlton, J. T., and R. Wenne 1989. Genetic affinities of the bivalve *Macoma balthica* from the Pacific Coast of North America: evidence for recent introduction and historical distribution. Marine Biology 102:235-241.

Micheli, F. and C. H. Peterson 1999. Estuarine vegetated habitats as corridors for predator movements. Conservation Biology 13:869-881.

Miller, R. L. 1969. *Ascophyllum nodosum*: a source of exotic invertebrates introduced into west coast near-shore marine waters. Veliger 12:230-231.

Möbius, K. 1877. Die auster und die austernwirthschaft. Verlag von Wiegant, Hempel and Parey, Berlin. Trans. H. J. Rice and published in Fish and Fisheries Annual Report of the Commission for the year 1880, Vol. 3, No. 29, app. H, p. 681-747.

Morrison, J. P. E. 1970. Brackish water mollusks. Malacologia 10(1):55-56.

Moyle, P. B. and T. Light 1996. Biological invasions of fresh water: empirical rules of assembly theory. Biological Conservation 78:149-161.

Packard, E. L. 1918. Molluscan fauna of San Francisco Bay. University of California Publications in Zoology 14:199-452.

Pechenik, J. A.1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Marine Ecology Progress Series 177:269-297

Perkins, G. H. 1869. Molluscan fauna of New Haven. A critical review of all marine, freshwater and land molluscs of the region, with descriptions of many of the living animals and of two new species. Part I. Cephalopoda and Gasteropoda and Part II. Acephala and Bryozoa. Proceedings of the Boston Society of Natural History 13:109-135, 13:139-163.

Perkins, L. F. and P. F. Larsen 1975. A preliminary checklist of the marine and estuarine invertebrates of Maine. TRIGOM Publication, West Boothbay Harbor, ME.

Pfitzenmeyer, H. T. and K. G. Drobeck 1964. The occurrence of the brackish water clam, *Rangia cuneata*, in the Potomac River, Maryland. Chesapeake Science 5:209-212.

Race, M. S. 1982. Competitive displacement and predation between introduced and native mud snails. Oecologia 54:337-347.

Rehder, H. A. 1997. National Audubon Society field guide to North American seashells. Alfred A. Knopf, New York, 894 p.

Reichard, S. H. and C. W. Hamilton 1997. Predicting invasions of woody plants introduced to North America. Conservation Biology 11:193-203.

Rejmánek, M. 1999. Invasive plant species and invasible ecosystems. In: (eds. O. T. Sandlund, P. J. Shei and Å. Viken) Invasive species and biodiversity management. Based on a selection of papers presented at the Norway/UN Conference on Alien Species, Trondheim, Norway. Kluwer Academic Publisher, Dordrech, 444 p.

Rejmánek, M. and D. M. Richardson 1996. What attributes make some plant species more invasive? Ecology 77:1655-1661.

Richer, W. 1985. Distribution of the soft-bottom macrofauna in an estuary of southern Chile. Marine Biology 86:93-100.

Robertson, R. 1996. A little-known Atlantic and Gulf coast American odostomian (Pyramidellidae) and its generic relationships. Amer. Malacol. Bull. 13:11-21

Ruiz, G. M., Carlton, J. T., Hines, A.H., and E.D. Grosholz 1997. Global invasions of marine and estuarine habitats by nonindigenous species: mechanisms, extent, and consequences. Amer. Zool. 37:621-632.

Ruiz, G. M., Fofonoff, P., Carlton, J. T., Wonham, M. J., and A.H. Hines 2000. Invasions of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics (in press).

Scofield, N. B. 1928. Oysters in California. California Fish and Game 14:203-204.

Scheltema, R. S. 1984. Development and planktonic larvae of common benthic invertebrates of the Woods Hole, Massachusetts region: summary of existing data and bibliographic sources. Woods Hole Oceanog. Inst. Tech. Rept. WHOI-84-13.

Shaw, W. N. 1997. The shellfish industry of California – past, present, and future. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2. U. S. Dept. of Commer., NOAA Tech. Rep. 128, p 57-74.

Smith. S. 1862. On the Mollusca of Peconic and Gardiner's Bays, Long Island, New York. Annals of the Lyceum of Natural History of New York 7:147-167.

Smith. S. 1887. Catalogue of the mollusca of Staten Island. Proceedings of the Natural Science Association of Staten Island, Vol. 1, Extra No. 5, p. 53.

Smith, S. and T. Prime 1870. Report on the mollusca of Long Island, N. Y., and of its dependencies. Annals of the Lyceum of Natural History of New York 9:377-407.

Snedecor, G. W. and W. G. Cochran 1980. Statistical Methods, seventh edition. Iowa University Press, Iowa, 507 p.

Sokal, R. R. and F. J. Rohlf 1981. Biometry, second edition, W. H. Freeman and Company, New York, 877 p.

Spjeldnaes, N. and K. E. Henningsmoen 1963. *Littorina littorea*: an indicator of Norse settlement in North America? Science 141:275-276.

Sullivan, C. M. 1948. Bivalve larvae of Malpeque Bay, P.E.I. Bull. Fish. Res. Bd. Can. 77:1-36.

Thiriot-Quiévreux, C. 1983. Summer meroplanktonic Prosobranch larvae occurring off Beaufort, North Carolina. Estuaries 6:387-398.

Thiriot-Quiévreux, C. and R. S. Scheltema 1982. Pelagic larvae of New England intertidal gastropods. *V. Bittium alternatum, Triphora nigrocincta, Cerithiopsis emersoni, Lunatia heros* and *Crepidula plana.* Malacologia 23:37-46.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the sound (Øresound). Medd. Komm. Dan. Fisk. Havunders. (Plankton) 4:1-523.

Townsend, C. H. 1893. Report of observations respecting the oyster resources and oyster fishery of the Pacific coast of the United States. Rep. U. S. Comm. Fish and Fisheries 17:343-372.

Townsend, C. H. 1896. The transplantation of eastern oysters to Willapa Bay, Washington, with notes on the native oyster industry. Rep. U. S. Comm. Fish and Fisheries 21:193-202.

Turgeon, D. D., Quinn, J. F. Jr., Bogan, A. E., Coan, E. V., Hochberg, F. G., Lyons, W. G., Mikkelsen, P. M., Neves, R. J., Roper, C. F. E., Rosenberg, G., Roth, B., Scheltema, A., Thompson, F. G., Vecchione, M., and J. D. Williams 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, second edition. American Fisheries Society, Special Publication 26, Bethesda, Maryland. 535 p.

USGS (United States Geological Survey) 2000. Water quality San Francisco Bay web site (URL: http://sfbay.wr.usgs.gov/access/wqdata/webbib.html).

Veltman, C. J., Nee, S., and M. J. Crawley 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist 147:542-557.

Vermeij, G. J. 1982. Environmental change and the evolutionary history of the periwinkle (*Littorina littorea*) in North America. Evolution 36:561-580.

Verrill, A. E. and S. I. Smith 1874. The invertebrate animals of Vineyard Sound and adjacent waters with an account of the physical features of the region. Rep. U. S. Comm. Fish and Fisheries for 1871-1872, 520 p. Government Printing Office, Washington, D. C.

Wass, M. L., Burrell, W. G., Zwerner, D., Calder, D. G., Van Engel, W. G., and P. A. Sandifer. 1972. Free-living invertebrates: phylum Mollusca. In: A check list of the biota of lower Chesapeake Bay with inclusions from the Upper Bay and the Virginian Sea, Virginia Institute of Marine Science Special Report No. 65, Gloucester, MD.

Weber, H. H. 1977. In: Giese, A. C. and J. S. Pearse (eds.), Gastropoda: Prosobranchia, Reproduction of marine invertebrates, Academic Press, NY.

Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecological Monographs 31:239-266.

Wells, H. W. 1965. Maryland records of the gastropod, *Littorina littorea*, with a discussion of factors controlling its southern distribution. Chesapeake Science 6:38-22.

Wells, H. W. and I. E. Gray 1960. Seasonal occurrence of *Mytilus edulis* on the Carolina coast as a result of transport around Cape Hatteras. Biological Bulletin 119:550-559.

White, J. H. 1986. The great yellow fleet. Golden West Books, San Marino, CA, 186 p.

Whiteaves, J. F. 1901. Catalogue of the Marine Invertebrata of Eastern Canada. Geological Survey of Canada, Ottawa.

Wicksten, M. K. 1976. *Argopecten irradians* (Bivalvia: Pectinidae) in San Francisco Bay, California. The Veliger 18:418.

Wilkinson, L., Blank, G., and C. Gruber 1996. Desktop data analysis with Systat. Prentice Hall, Upper Saddle River, NJ, 850 p.

Williamson, M. and A. Fitter 1996. The varying success of invaders. Ecology 77:1661-1666.

Winkley, H. W. 1888. Mollusca found in the oyster beds of Cocagne, N. B., Bedeque and Summerside, P. E. I. Bulletin of the Natural History Society of New Brunswick 7:69-71.

Yonge, C. M. 1949. The sea shore. Collins Clear-Type Press, London, 350 p.

CHAPTER 4

Comparing Oyster-mediated Molluscan Introductions to the Coasts of the Eastern Pacific and Eastern Atlantic Oceans

INTRODUCTION

Oyster transplantation has been practiced worldwide for centuries (Ingersoll 1881, Elton 1958, Andrews 1980, Chew 1990, Carlton and Mann 1996). The desire for fresh oysters was so great that many varieties of oysters have been introduced intentionally to waters outside their natural ranges. Among these, the eastern oyster (*Crassostrea virginica*) has undergone some of the most massive live export and aquacultural introductions of any marine species. Because of their size and superior flavor, the commercial demand for eastern oysters outside the northwestern Atlantic was tremendous during the latter half of the 19th and first half of the 20th centuries.

Enormous quantities of oysters were relayed for storage, growth, or cultivation in beds on the Pacific coast of the United States (northeastern Pacific) and the waters of northwestern Europe (northeastern Atlantic) (Ingersoll 1881, Kochiss 1974). Independent introductions of oysters and their associates to the West Coast and to northwestern Europe provide the rare opportunity to compare independent marine invasions originating from the same species pool of potential invaders. (See Chapter 3 for detailed description of species pool.)

The fauna closely associated with oysters is extensive, with dozens of species of numerous phyla found on a single shell (Carlton 1979). When this community richness is combined with the sheer quantity of oysters moved around the globe, the number of independent inoculations of non-native species is staggering. *Crassostrea virginica* introductions to the United Kingdom and other northwest European countries provide an opportunity for comparison with the North American oyster introductions reviewed in Chapter 3. Two important parallels exist between these two mass oyster introductions. First, eastern oysters shipped live to the northeastern Atlantic and northeastern Pacific originated from the same region, New York City and vicinity {Raritan Bay, East River, the Long Island Sound estuaries of Connecticut and New York, and the large embayments along the south coast of Long Island (Great South Bay and Jamaica Bay)}. Second, the time periods of the commercial ventures coincide closely. Adult and juvenile oysters were transported to the Pacific coast of the United States primarily between 1869 and 1940. However, smaller subsequent shipments of adult oysters from Gardiner's Bay, Long Island to Tomales Bay, and Drakes Estero, California continued into the late1970s (Kornicker 1975, Carlton 1979). A similar, if not larger scale, transport of eastern oysters took place between 1871 and 1939 between New York and the United Kingdom (Ingersoll 1881, Kochiss 1974, Carlton and Mann 1996).

This chapter begins with a summary of the molluscan invaders into the northeast Atlantic. An analysis comparing the invasions of the northeast Atlantic with those of the northeast Pacific is presented to quantify formally the non-random nature of marine invasions. An account for each of the five molluscan invaders common to the northeastern Pacific and northeastern Atlantic provides detailed information about each species and its invasion history. Comparison of the incidence and geographic range of invasion indicates that invasions proceeded quite differently along European and North American coasts.

Molluscan Invaders of the Northeast Atlantic

Five northwestern Atlantic mollusk species have successfully invaded Europe: *Mya arenaria, Mercenaria mercenaria, Petricolaria pholadiformis, Crepidula fornicata,* and *Urosalpinx cinerea*. These same species, and others, have also invaded the Pacific coast of North America. Based on ecological studies conducted in their native ranges, each of these species is considered to coexist with eastern oysters (*Crassostrea virginica*, see chapter 3). This point is important because the commercial oyster industry is considered the most influential vector by which these species were introduced to the Pacific coast of North America and northwestern Europe (Elton 1958, Carlton 1992). Because of their edibility, the softshell clam (*Mya arenaria*) and the northern quahog (*Mercenaria mercenaria*) were also deliberately introduced to northwestern Europe (Eno et al. 1997) and California (Carlton 1979).

All mollusks originating in the northwest Atlantic that successfully invaded parts of Europe can be found in the United Kingdom (Carlton and Mann 1996). Eno et al. (1997) compiled a list of the non-native marine species in waters of the United Kingdom and describe much of the invasion history of the northwestern Atlantic mollusks. Table 4.1 summarizes the dates of first detection of non-indigenous mollusks and shows that in all but one case, that first detection dates were earlier in Europe than North America. Because dates of first detection do not necessarily correspond directly with dates of first colonization (species can go undetected for many years before being discovered), the order of first invasion cannot be known with certainty.

Repeated Invasions of Multiple Coasts – Are Marine Invasions Random?

Global invasion patterns of oyster-associated mollusks strongly imply that invasion is a non-random process. The group of molluscan eastern oyster associates that have succeeded in other parts of the world, such as northwestern Europe, is a subset of those that have also invaded the northeastern Pacific. Indeed, some oyster associates of the Pacific oyster (*Crassostrea gigas*), a native of the northwestern Pacific, have also repeatedly invaded both the northeastern Pacific and other coastal systems where this oyster was introduced (e.g., *Musculista senhousia* in the Mediterranean Sea and *Tapes philippinarum* in European coastal waters and in the Mediterranean Sea). The fact that the same species repeatedly invade disparate locations around the globe argues that some species are good invaders and others are not.

Probability of Multiple, Random Invasions

Formally testing the likelihood of multiple random invasions by the same organisms to different geographic locations employs a numerical experiment. The experiment requires a calculation using standard mathematical combinations and random selection.

Modeling multiple invasions of separate locations from the same species pool employs the assumption that invasions are independent events (i.e., one invasion does not influence another in the same or a different geographic area). The null hypothesis is that all species, in all environments, share equal invasion abilities.

In the case of oyster-associated mollusk invasions of the northeast Pacific and northeast Atlantic, the Pacific has 15 invaders and the Atlantic has just 5. As mentioned above, the 5 invaders of northeast Atlantic are also invaders of the northeast Pacific. The total number of oyster-associated mollusks that make up the species pool is 93 (see Chapter 3 for details). The question being examined is, "When all invaders arise from the same species pool, what is the probability that the combination of 15 invaders of the northeast Pacific includes the set of 5 invaders of the northeast Atlantic?" Another way of stating this is: "What is the probability that a randomly chosen group of 15 species includes the same individual species in another randomly chosen group of 5 species?"

To address this question, one must think in terms of discrete combinations of 15 species and determine the fraction of total possible 15 species combinations that includes 5 particular species. How are the two parts of the fraction calculated? Taking the denominator first, it represents the total possible unique combinations of 15 species that can be taken from an species pool of 93 species. In the parlance of combinatorial mathematics this is stated, "93 choose 15" (see Appendix for illustrative example of combinations calculation). The number of combinations is calculated using factorial expressions as shown in Equation 1.

Equation 1 $$C(93,15) = \frac{[93!]}{[15!(93-15)!]} = 7.8x10^{16}$$

The numerator must also be thought of in terms of combinations of 15 species, but only the special subset that includes all 5 invaders of the northeast Atlantic. Since all acceptable combinations of 15 species must include the 5 northeast Atlantic invaders, these can be subtracted from both the full 93 species applicant pool (i.e., 93–5) and from the desired combination size (i.e., 15–5) before calculation. Substitution of the modified values into the combinations expression yields Equation 2.

Equation 2 $$C(93-5,15-5) = C(88,10) = \frac{[88!]}{[10!(88-10)!]} = 4.5x10^{12}$$

Equation 3 is simply Equation 2 over Equation 1 and shows the overall probability of a combination of 15 invaders taken from a 93 species applicant pool that is partly composed of 5 exact invaders of another location.

Equation 3 $$\frac{C(93-5,15-5)}{C(93,15)} = \frac{\frac{88!}{10!(88-10)!}}{\frac{93!}{15!(93-15)!}} = 5.78\times10^{-5}$$

The probability of multiple random invasions by the same species to two separate coasts is approximately 6 out of 10,000, so remote that, under the stated assumptions, a random invasion hypothesis must be rejected.

Indeed, the picture is actually a bit more complicated. When analyzed at the level of northeast Pacific and northeast Atlantic coasts, repeated invasions by the same species within a coast are counted just once. If all invasions were counted at the level of individual embayments (e.g., San Francisco Bay, Coos Bay, Puget Sound, English Channel and North Sea embayments), the overall number of invasions would be greater. If repeated invasions to a single coastal system were counted separately, the probability of invasions arising randomly with respect to species' biology and environmental conditions would be even more unlikely than the conservative estimate from above. At least two difficulties prevent such a finely detailed analysis here. 1) The invasion records for individual European embayments are less complete than those of the Pacific coast of North America are. 2) Differentiating discrete, human-mediated inoculation/colonization (i.e., separate invasions) from an invasion event followed by natural dispersal is usually difficult. Among marine invasions to the coastal waters of the United States, with the exception of a few cases, discrete inoculations and single invasions cannot be differentiated (G. Ruiz pers. comm.).

Oyster-mediated Molluscan Invaders of Northwest Europe with Comparisons to Northwest Pacific Invasions

Urosalpinx cinerea

The oyster drill or whelk tingle (*Urosalpinx cinerea*) is a snail that preys on oysters and other bivalves. Orton and Winckworth (1928) first described this species on oyster beds in Essex, England in 1927, and suspected that its introduction actually occurred around 1900. Carriker (1955) provides a comprehensive review of *Urosalpinx cinerea's* biology. Of the 5 northwestern Atlantic mollusks that have invaded Europe, *Urosalpinx cinerea* has the most restricted distribution, occurring only in southeastern England in the adjacent coastal counties of Essex and Kent (Cole 1942, Eno et al. 1997) (Figure 4.1a). With little range expansion in England and the lack of a planktonic larval stage, Cole (1942) concluded that *Urosalpinx cinerea* had limited capacity for natural dispersal and was dependent on oyster-mediated movement for range expansion in Europe. No European range expansion appears to have occurred since the 1940s (Eno et al. 1997).

Although data are limited, *Urosalpinx cinerea* density in English waters appears to be lower than in its native range. Mistakidis (1951) found *Urosalpinx cinerea* densities on subtidal oyster beds in the Rivers Crouch and Roach averaged 2m^{-2} with maximum densities of 6m^{-2}. Similarly, Elton (1958) noted that the Atlantic oyster drill was found at densities of up to 6m^{-2} in England. In Delaware Bay, from 237 to 947 oyster drills m^{-2} were counted in a 500-acre intertidal oyster bed (Stauber 1943). Nelson (1922) reported 29 oyster drills m^{-2} in Little Egg Harbor, New Jersey, and Carriker (1955) measured up to

344 m^{-2} intertidally on Gardiners Island, off the eastern tip of Long Island. Based on the atlas of distribution and abundance of common benthic organisms of San Francisco Bay compiled by Hopkins (1986), introduced *Urosalpinx cinerea* densities range from 1-300 oyster drills m^{-2}. Although San Francisco populations of *Urosalpinx cinerea* are restricted to the South Bay in the vicinity of old *Crassostrea virginica* beds, the highest concentrations of these snails were found in deeper waters of the South Bay (Hopkins 1986).

Elton (1958) states:

> It [*Urosalpinx cinerea*] must be ranked as a really successful invader, living on young oysters as well as other animals, and reaching population densities of five per square yard. Oyster populations in England have suffered severe disasters in recent decades and can ill afford an additional enemy that is able to destroy half the annual increment of an oyster bed.

But given *Urosalpinx cinerea's* inability to spread in the United Kingdom beyond Essex and Kent Counties in over one hundred years, is it accurate to describe *Urosalpinx cinerea* as a "really successful invader?" Carlton (1979) lists six locations on the Pacific coast of North America where *Urosalpinx cinerea* maintains reproductive populations: Boundary Bay, southern Puget Sound, Willapa Bay, Tomales Bay, San Francisco Bay, and Newport Bay. In spite of numerous records from multiple locations (British Columbia, Vancouver Island, Whatcom and Skagit Counties in Washington, Humboldt Bay, Elkhorn Slough, and San Pedro), none of these areas currently support populations of *Urosalpinx cinerea* (Carlton 1979). Carlton concludes that *Urosalpinx cinerea* is not a significant pest species on the Pacific coast. As in England, the poor dispersal of

Urosalpinx cinerea is attributed to the lack of pelagic larvae. Infrequent intra-coastal transport of this species (Carlton 1979) and the possible limitations of suitable hard substrates (Quayle 1964) are also considered potential barriers to dispersal. The low incidence of discrete invasions across a broad latitudinal range (Southern California to British Columbia) suggests numerous individual invasions rather than initial invasion followed by natural dispersal.

Crepidula fornicata

The Atlantic slipper limpet, *Crepidula fornicata,* is found in Sweden and Denmark, one location on the North Sea coast of Norway, Germany, the Netherlands, Belgium, the United Kingdom, Ireland, France, and the Mediterranean (Sjøtun 1997, Eno et al. 1997, AquaSense 1998, de Montaudouin and Sauriau 1999, CIESM 1999) (Figure 4.1b). The best indications are that *Crepidula fornicata* was introduced to England in around 1870-1880 and subsequently spread to other parts of Europe (Chipperfield 1951, Sjøtun 1997). The incidence of *Crepidula fornicata* invasions into European locations is greater than along the west coast of the United States, where Carlton (1979) verified populations in three embayments only: Puget Sound, Grays Harbor, and Willapa Bay. Its absence in San Francisco Bay, where oyster introductions far exceeded all other Pacific coast locations, is curious. Despite *Crepidula fornicata's* planktonic larvae, and perhaps an enhanced ability to disperse naturally or with ship's ballast, this species has failed to spread along the Pacific coast. In Scandinavia, *Crepidula fornicata* is assumed to have dispersed naturally from Denmark to Norway by larval transport (Sjøtun 1997), but given the complexity of commercial oyster movements in Europe and *Crepidula's* failure to colonize widely beyond Pacific coast sites of anthropogenic introduction, alternatives to natural dispersal should be considered.

Interestingly, two other oyster-mediated slipper limpet invaders of the Pacific -- *Crepidula plana* and *Crepidula convexa*, both confined to San Francisco Bay (Carlton 1979) -- have not invaded Europe. In these cases, developmental mode appears to confer no special advantage for invasion or subsequent natural dispersal since *Crepidula plana* is a planktonic developer and *Crepidula convexa* a direct developer.

Crepidula fornicata is a protandic hermaphrodite that lives on hard substrates. This species congregates in mating stacks composed of multiple individuals where the bottommost slipper limpet is a female and is fertilized by multiple overlying males (Gosner 1971). From the standpoint of finding a mate upon arrival to a new location, as long as the mating stack is maintained during transport, this species has the distinct advantage over many since mates are close at hand. Intact mating stacks potentially reduce the effective propagule number needed for successful colonization. Even with the loss of the stack's female, the bottommost male will change sex and provide an opportunity for continued reproduction. If, on the other hand, the mating stack is not maintained and adult individuals are scattered widely, the probability of two individuals finding one another and successfully reproducing is diminished greatly.

Korringa (1951) described *Crepidula fornicata* as a nuisance species in Europe because it can deposit silt and pseudofeces over oyster beds in quantities that prevent successful reproduction by oysters. Korringa also claimed that, as a filter feeder, *Crepidula fornicata* was capable of reducing the rate of successful oyster reproduction through ingestion of oyster larvae. Some investigators consider *Crepidula fornicata* a competitor on oyster beds for food and space (Duggan 1979, Utting and Spencer 1992). However, there is some disagreement about whether *Crepidula fornicata* has had significantly detrimental effects on receiving biological communities. When de Montaudouin et al. (1999) tested whether proliferating *Crepidula fornicata* populations in France depressed benthic biological diversity, they found the exact opposite on muddy sediments. Their results reveal a significant increase in biological diversity in these habitats and that in coarse sand the presence of *Crepidula fornicata* did not affect biomass, biodiversity, or abundance of macrofauna. Additionally, experimental field manipulation has shown that oyster growth, condition index, and mortality were not significantly affected by *Crepidula fornicata* (de Montaudouin and Sauriau 1999). Without a doubt, commercial growers of oysters have experienced financial impacts in the past when forced to clear *Crepidula fornicata* from oyster beds and adjust rearing practices to avoid re-colonization. However, recent evidence establishes that this species has not caused significant ecological detriment to the ecosystems in which it has been introduced.

Petricolaria pholadiformis

Unlike any of the other introduced mollusks described here, the false anglewing, *Petricolaria pholadiformis*, is believed to have had a significant impact on native European species. The extensive decline of the native *Barnea candida* in Belgium and the Netherlands is coincident with, and thought attributable to, *Petricolaria's* population increase (ICES 1972, Vermeij 1989, Eno 1996). Populations of *Petricolaria pholadiformis* are reported from Sweden to Norway, Denmark, Germany, the Netherlands, Belgium, the United Kingdom, and France (AquaSense 1998). *Petricolaria pholadiformis* has been described in the Mediterranean, but is believed not established there (CIESM 1999). Tebble (1966) reports the presence of *Petricolaria pholadiformis* "from south Norway to the Mediterranean and the Black Sea, and along the coast of West Africa to Senegal and the French Congo." Tebble's description suggests a continuous distribution along the European and African continents, but it is unclear whether Spain, Portugal, and all of the coastal West African countries are necessarily included.

Petricolaria pholadiformis has by far the greatest invasion range of any mollusk originating from the northwest Atlantic, spanning 53° latitude (Figure 4.1c). In its native range, *Petricolaria pholadifomis* occurs from the Gulf of Saint Lawrence to Uruguay (Abbott 1974), a range of 83° latitude. Carlton (1979) describes Pacific coast invasions of *Petricolaria pholadiformis* (=*Petricola pholadiformis*) to Willapa Bay, San Francisco Bay, and Newport Bay, CA, noting the relative late detection on the Pacific coast (1927) as a possible indication of a non-commercial oyster vector. Carlton (1999) indicates the potential for members of the family Petricolidae to be hull foulers on wooden vessels and the interstices of metal-hulled vessels, and larval constituents of ballast water. Given the long history of shipping and commercial oyster import to San Francisco Bay, it is curious that *Petricolaria pholadiformis* (apparently) arrived so late. Following widespread eastern oyster failure in San Francisco Bay around 1910, seed oyster shipments ceased and were replaced by adult oyster shipments (Barrett 1963). Whether a change in the nature of oyster import could affect the probability of successful inoculation of *Petricolaria pholadiformis* is unknown.

This literature review found no mention of significant introductions of *Crassostrea virginica* to Africa. The widespread invasion from Scandinavia to the west African coast by *Petricolaria pholadiformis* would seem to require an additional vector to explain its observed distribution. Shipping provides a likely explanation. Despite the enormous native latitudinal range of this clam (if not partly a product of human-mediated introduction itself), natural dispersal from northwest Europe and recent colonization across 53° latitude seems unlikely. Without detailed records describing *Petricolaria's* establishment in west African waters, it is impossible to determine if its range expansion proceeded from multiple invasion loci or was unidirectional. On the Pacific coast of the United States, the spatial discreteness and distance between invasions by *Petricolaria pholadiformis* suggests that natural larval dispersal has not been an effective agent of range expansion there.

Mercenaria mercenaria

The Atlantic hard shell clam or quahog, *Mercenaria mercenaria*, was intentionally introduced to France in the early 1860s (de Broca 1876), where self-sustaining populations still exist in some areas, including Marenne-Oléron Bay and other locations in Southern Brittany (Goulletquer and Heral 1997). *Mercenaria mercenaria* has been reported as a likely accidental introduction with eastern oysters into the Solent, near

Southampton and the Isle of Wight on the southern coast of England in the early 1900s. Although it was probably accidentally introduced to many more locations where *Crassostrea virginica* plantings were attempted, it currently maintains populations only in and around the Solent, in particular in the elevated water temperatures surrounding power plants in the English Channel (Utting and Spencer 1992). Eno et al. (1997) list *Mercenaria mercenaria's* European distribution as: Great Britain, the Netherlands, and France. *Mercenaria mercenaria* is also established in the Mediterranean Sea (CIESM 1999). Figure 4.1d outlines the European regions of invasion of this species. Although natural dispersal of this species has resulted in some range extension, expansion has been quite limited (Eno et al 1997).

Mercenaria mercenaria is reported at just two locations along the Pacific coast of North America: Colorado Lagoon (off Alamitos Bay), California, and Boundary Bay, British Columbia (Murphy 1985 and Turgeon et al. 1998). But it has also been introduced intentionally and unintentionally to numerous locations along the Pacific coast (see Carlton 1979 for details). Benthic sampling of macrofauna in Boundary and Mud Bays by the Canadian Department of Fisheries and Oceans in 1984 (Burd et al. 1987) did not detect *Mercenaria mercenaria* or eastern oysters (*Crassostrea virginica*, also reported from this embayment). While small populations could certainly have been missed, the status of these populations should continue to be monitored to document persistence or failure through time.

Of all eastern oyster-associate bivalves to invade the Pacific coast of the United States, *Mercenaria mercenaria* certainly has the most curious and limited distribution.

The two sites of colonization are quite different physically and hydrographically. Colorado Lagoon is a small body of water (<0.2 km^2) located in a highly urbanized coastal setting in the warm Mediterranean climate of Southern California (33° 45’ N). The lagoon itself has been extensively engineered by humans and is connected to the Marine Stadium and Alamitos Bay by culverts and tide gates. Colorado Lagoon experiences heavy urban runoff, sometimes producing conditions that exceed public health standards for water quality (Murphy 1985). Bottom temperatures and salinities ranged from 12 to 24° C and 17 to 33 ppt during 1978-1980 (Murphy 1983). *Mercenaria mercenaria* is quite tolerant of desiccation, living 8 weeks out of water (Greene and Becker 1977) and highly tolerant of elevated nitrogenous nutrients (Epifanio and Srna 1975). Murphy lists these aspects, together with a requirement for water temperatures of between 22 and 28° C for spawning, and proposes these as critical factors to this species’ success in Colorado Lagoon.

The much larger Boundary/Mud Bay, British Columbia, is situated at the mouth of the Nikomekl and Serpentine River estuaries on the western side of the Strait of Georgia (49°N). The climate is wetter and cooler, but still has alternating wet and dry seasons. Boundary Bay is said to support some of the most extensive expanses of mud and sand tidal flats, salt marsh habitat, and eel grass beds in Canada (Dale 1997). This embayment experiences semidiurnal tidal flushing and is exposed to significant stream flow from the Serpentine and Nikomekl rivers. Boundary and Mud Bays are certainly not free of human impact, as evidenced by a toxic chemical spill in 1984 (Burd et al. 1987) and the presence of agricultural, forestry, and marine non-point source pollution (British Columbia, Ministry of Environment, Lands and Parks 1999). However, this coastal system is almost certainly less environmentally stressed by pollution and development than Southern Californian waters. Although no directly comparable bottom temperatures were available for this embayment, the 130 year regional mean sea surface temperatures (1857-1985, mean ± standard deviation) ranged from 7° ± 2.5° C in February to 12° ± 2° C in September (Brown et al. 1986), seemingly too cold for successful spawning. Specific microclimate temperature effects cannot be ascertained from these data.

Given *Mercenaria mercenaria's* tolerance of extreme environmental conditions, it is perplexing that this species has been unable to colonize other embayments along the Pacific coast where it has been introduced both intentionally and with eastern oysters. High survivorship between New York and Europe on board steamer ships (de Broca 1876) and the ability to withstand desiccation for weeks (Greene and Becker 1977) suggest that *Mercenaria mercenaria* would have survived the cross-country train ride before introduction. While it is unclear what has prevented *Mercenaria mercenaria* from colonizing other Pacific coastal embayments, temperature may play a critical role in Europe. European populations of *Mercenaria mercenaria* are confined to warmer waters, e.g., power plant cooling effluent plumes in the English Channel and the Atlantic coast of France to the south of Brittany (Eno et al. 1997, Goulletquer and Heral 1997).

Mya arenaria

The soft-shell clam (*Mya arenaria)* is distributed from Arcachon, France along the Atlantic and North Sea coasts to the White Sea of Russia, as well as the Faroe Islands and all coasts of Ireland and the United Kingdom (Tebble 1966, Seaward 1990). *Mya arenaria* is also reported as one of the most common bivalves in the Baltic Sea (Leppäkoski 1984) but is not numerically dominant in northern regions of the Bothnian Sea (Olenin and Leppäkoski 1999). *Mya arenaria* populations exist in the Black Sea (Shadrin 1998) and the Mediterranean (CIESM 1999).

In 1862 Lieutenant de Broca, the Director of the Port of Havre, France traveled to the United States to review the oyster industry and to ascertain the feasibility of culturing oysters (*Crassostrea virginica*), quahogs (*Mercenaria mercenaria*), and soft-shell clams (*Mya arenaria*) in French waters. At that time de Broca indicated *Mya arenaria* was not found in France except at Dunkirk (de Broca 1876). Based on the limited supply of suitable bait materials found along the French coast and the common use of salted *Mya arenaria* for fish bait in the United States by mackerel fisherman, de Broca stated:

> The importance of the fact that the soft clam of North America lives in the latitude of Dunkirk is evident, as it shows the possibility, I may say the certainty, of realizing Professor Agassiz's programme. Once propagated in several localities on the coast, this mollusk will furnish a bait without rival for the coast fisheries; and when salted, it might be used for the cod-fishery of Iceland and Newfoundland. We know that at certain periods of the year the fishermen along the coast find it difficult to obtain bait; for instance, the fisherman of Havre, who, at the season of fishing for "gross-yeux," sometimes pay five centimes apiece for small cuttle-fishes, and cannot always obtain enough even at that price. *Mya arenaria* would supply this want.

If accurate, de Broca's assessment indicates that French *Mya arenaria* populations are probably more recently introduced than more northern populations.

Interestingly, de Broca (1876) observed much higher in-transit mortality rates during trans-Atlantic voyage (approximately 12 days aboard steamer ship from New York to

Havre plus time for ground transport) for *Mya arenaria* than for either *Crassostrea virginica* or *Mercenaria mercenaria*. Being a gaping bivalve, *Mya arenaria* is unable to retract its large siphon far enough to close its shell completely, making it more prone to desiccation than non-gaping bivalves (Yonge 1949). When *Mya arenaria* were specially packed in containers with a bed of sand and re-supplied with sea water several times daily, de Broca still found mortality to be 50%.

Strasser (1999) provides an extensive global invasion history of *Mya arenaria*, tracing its natural invasion pathways from the Pacific to the Atlantic Ocean during the Miocene and Pliocene epochs as well as its anthropogenic movement from western to northeastern Atlantic during the last several hundred years. Peterson et al. (1992) dated *Mya arenaria* shell material to the 13th century in Denmark, and suggested that introductions from the New to the Old World were possible, but noted that *Mya's* date of European invasion is, as yet, undetermined. Strasser (1999) acknowledges Viking transport of live clams in the bilge of their vessels as a possible mechanism of European introduction.

Given the difficulty of transporting live soft-shell clams across the Atlantic by steamship over the course of days, the probability of introducing viable *Mya arenaria* after many weeks in the hold of a Viking sailboat seems remote. A Viking transit from Iceland to continental Europe is a voyage of over 1000 miles. In reviewing *Mya* specimens from arctic regions, Laursen (1966) reassigned all specimens from Iceland to *Mya truncata.* These findings cast further doubt on the likelihood of a stepwise invasion pattern of *Mya arenaria* from Newfoundland to Greenland to Iceland, and then Europe.

An alternative explanation is that Vikings consumed soft-shell clams or used them for bait en route. Upon arrival to Denmark, leftover shell materials could well have been discarded. With increased direct traffic from Europe to the New World and back beginning in the 16th century, the likelihood for live shipboard introductions increased. Carlton (1999) also lists members of the Myidae as potential colonizers of crevices or shipworm cavities on the hulls of wooden vessels, providing another possible mode of introduction to Europe. It is important to note that since stochastic elements certainly play a role in the invasion process, even an unlikely invasion pathway is impossible to dismiss entirely. Without further evidence, it is impossible to know with certainty how long *Mya arenaria* has inhabited European waters.

Having invaded as far north as the Arctic Ocean (the White Sea), *Mya arenaria* has exercised the greatest capacity to colonize high latitudes of any of the five northwest Atlantic molluscan invaders of Europe (Figure 4.1e). This distribution likely reflects the soft-shell clam's extraordinary capacity to withstand cold waters. According to de Broca's account (1876), Louis Agassiz frequently observed ice formation inside living *Mya arenaria* shells with no apparent adverse effects to the viability of the clam.

Mya arenaria is among six bivalve oyster associates whose native distributions reach as far north as Labrador: *Mya arenaria, Macoma balthica, Mytilus edulis, Hiatella arctica, Cerastoderma pinnulatum,* and *Zirfaea crispata.* Of these bivalves, only *Mya arenaria* and the Northern dwarf cockle *Cerastoderma pinnulatum* do not have amphi-Atlantic distributions. Although the rest of these species might have been moved back and forth trans-Atlantically, successful introductions from west to east would not be detectable without genetic analyses. In the case of *Cerastoderma pinnulatum*, the abundantly common edible cockle, *Cardium edule*, in northwestern Europe could have competitively influenced the western Atlantic species' ability to invade, but this interaction remains unstudied. Anecdotally, in describing a sandy shore in Wales, Yonge (1949) stated "In suitable areas this [*Cardium edule*] occurs in almost astronomical numbers…." Given extensive enough niche overlap in a recipient area, competitive exclusion is theoretically possible, but experiments are necessary to test such a hypothesis. The inoculation rate or propagule pressure of *Cerastoderma pinnulatum* was probably less than that of many other oyster associated mollusks since its abundance in the New York Bight/Long Island Sound was relatively low in the 19th century (see Chapter 3).

Of the five northwest Atlantic mollusks that have successfully invaded Europe, only *Mya arenaria* has penetrated deeply into the Baltic Sea, where surface salt concentrations are diminished and range from 6-8 ppt. The salinity gradient between the Atlantic Ocean and Baltic Sea is an important ecological barrier to natural dispersal and likely precludes invasions by anything but euryhaline and brackish water species (Olenin and Leppäkoski 1999). Based on typical lower salinity distribution limits in their native regions {*Mercenaria mercenaria* (10 ppt), *Petricolaria pholadiformis* (15 ppt), *Crepidula fornicata* (10 ppt), *Urosalpinx cinerea* (10 ppt)}, these four European invaders are incapable of thriving in the low salinity of the Baltic Sea. This low salinity exclusion is apparent in the Chesapeake Bay where only *Mya arenaria* penetrates into the upper bay where salinities fall below 10 ppt (Lippson and Lippson 1997).

The most striking similarity between *Mya's* invasions of Europe and the Pacific coast is the near continuous colonization of available embayments along the broad distributional ranges in which it has become established. *Mya arenaria's* ability to colonize sites rapidly along the northeastern Pacific from Elkhorn Slough to Prince William Sound, Alaska, (Hines and Ruiz 2000) in a span of just 125 years or less, suggests that the species need not have been present in Europe since the 13th century to attain its current distribution there.

Patterns of Oyster-Mediated Molluscan Invasions of the Northeast Atlantic and Northeast Pacific

Biological Differences Among Successful and Failed Invaders

When overall eastern oyster-mediated molluscan invasions to the northeastern Atlantic and northeastern Pacific are compared, aside from species identity, there is little similarity. Table 4.2 summarizes the results from the comparison of two aspects of invasion: 1) invasion incidence as estimated by the number of successful invasion locations along a coast and 2) geographic range of invasion. With the exception of *Mya arenaria*, which has invaded both coastal systems at very high incidence and over a very wide geographic range, there is little consistency among invasion patterns in these regions. On the whole, the average invasion incidence is higher in the northeastern Atlantic than the northeastern Pacific. The pattern is mixed for geographic range of invasion with neither coastal region having consistently higher or lower ranges of invasion. These results suggest that molluscan invasions have proceeded differently in these two regions, but identifying the underlying reasons is difficult.

Comparisons of hard shell clam (*Mercenaria mercenaria*) invasions illustrate both differences and complexities of interpreting such invasion patterns. The wide invasion range of *Mercenaria mercenaria* in the northeastern Pacific is based on just two populations, one in Colorado Lagoon in Southern California and another in Boundary Bay, British Columbia. The Boundary Bay population is reported as an oyster-mediated invasion (Turgeon et al. 1998), but the population in Colorado Lagoon is the result of an intentional introduction (Carlton 1992). *Mercenaria mercenaria* did not naturally expand its range from one location to the other, but was instead the product of two separate introductions. Consequently, while a broad geographic distribution potentially reflects an ability to withstand diverse environmental conditions of widely separated locations, it does not necessarily connote an initial invasion with dispersal from one site to another. In contrast, *Mercenaria mercenaria* populations in the United Kingdom, at least, are thought to have expanded their range by natural dispersal (Eno et al. 1997). Thus, patterns of invasion can be reflections of anthropogenic introduction and movement, as well as post-colonization dispersal. In the case of *Mercenaria mercenaria*, records of first introduction and subsequent surveys appear reasonably complete, but this is not true for most species (e.g., *Petricolaria pholadiformis*). Invasion patterns and mechanisms must therefore be interpreted cautiously.

Differences in Oyster Introductions to Europe and the West Coast

A likely difference between oyster introductions to these two regions is that intensive planting and bedding was more evenly distributed in Europe than along the Pacific coast of North America. In Great Britain and other European countries, coastal cities and towns were long established and the demand for imported oysters broader than on the West Coast of the United States. Imported *Crassostrea virginica* was seen as a potential replacement for the crashing populations of native flat oyster (*Ostrea edulis*) that had supported 120,000 oystermen and supplied 700,000,000 bushels to London alone in the 1860s (Philpots 1890).

By contrast, during the middle of the 19th century, easterners flocked to the Sierra Nevada for the gold rush, and the population of San Francisco exploded. For the most part, live eastern oysters were shipped to San Francisco to fulfill the demand of new Californians desiring a familiar flavor from home (Barrett 1963). Although eastern oysters were introduced in smaller numbers to several other Pacific coast locations (e.g., Washington: Puget Sound, Willapa Bay, Grays Harbor; Oregon: Yaquina Bay; California: Humboldt Bay, Tomales Bay, Drakes Estero, Morro Bay), the quantities paled in comparison with those sent to San Francisco (Carlton 1979). West Coast sites of oyster introduction were widely separated, with little oyster habitat available in between. These differences in human and physical geography almost certainly influenced the inoculation patterns of oysters and their associates and perhaps account partly for the differences in invasion incidence observed in the two coastal regions.

Given the close proximity in time of commercial introductions of eastern oysters to the northeast Pacific and the northeast Atlantic, the oyster associates introduced to each location were likely the same. It is unclear why the Pacific coast of North America supports so many more nonindigenous species. The question remains whether differences in invasion numbers of these two coasts indicate fundamental differences in the receiving environments or if the invasion patterns observed are better explained by separate historical inoculation patterns.

DISCUSSION

When molluscan invaders of the northeastern Pacific and northeastern Atlantic are compared, all 5 northwestern Atlantic invaders are also found in the northeastern Pacific. Repeated invasion success in multiple locations suggests that invasions are not simply chance events. A probabilistic analysis of these patterns indicates that invasion is far from random. These results suggest strongly that species may instead vary in their abilities to invade new regions. If invasion was truly a random process (i.e., all species introduced to a new geographic location had an equal chance of invasion success), then a greater diversity of invading species should be observed. Instead, many of the same species invade repeatedly in geographically far-flung regions. This conclusion does not deny that invasions involve stochastic characteristics, only that chance does not appear to be the most important component of invasion success.

In spite of commonality in the species invading the northeast Pacific and the northeast Atlantic, the outcome of the invasions differ. Among the invaders common to the northeastern Pacific and northeastern Atlantic, only *Mya arenaria* shows similar invasion patterns in both regions. Other invaders are not consistent with respect to their incidence of invasion (frequency of reported successful invasions within a coastal system) or geographic ranges of invasion. This conclusion highlights the notion that, even among successful invaders, invasions can proceed differently in separate geographic areas. While past invasions may help predict whether a species is likely to succeed in a new location, it is still not possible to know the nature of a new invasion.

The number of successful oyster-mediated molluscan invaders to the northeast Atlantic is only one third that of the northeast Pacific (5 versus 15 species). Despite massive transport of eastern oysters to the northeastern Atlantic and northeastern Pacific over the same time period (Ingersoll 1881, Barrett 1963, Kochiss 1974), the molluscan invasion rate was lower on European coasts. The reasons underlying this difference in invasion success are unknown, but could include the following: 1) Differential in-route survivorship of biota as oysters were sent by train or steam ship to their respective destinations; 2) Differences in the recipient habitats to which oysters were introduced.

It is well established that oysters moved on trains were barreled and placed in refrigerator rail cars for fast freight service (reports vary from 8-21 days) to the West Coast (Ingersoll 1881, Collins 1892, Barrett 1963). Oysters bound for Europe were also barreled and placed in the coolest holds located near the extreme bow of the vessel for a 12-day voyage (Ingersoll 1881). Oyster survivorship was said to be good for both modes of transport (Ingersoll 1881, Barrett 1963). Clearly, survivorship must have been good enough to continue the practice for nearly 70 years. Transport conditions that produced low oyster mortality likely meant low mortality for accompanying biota as well, but there are no data to consult on this matter. Since the goal of the oyster export business was to keep the oysters as fresh as possible, it is hard to imagine a vector more conducive to the favorable, albeit accidental, transport of mollusks to new geographic regions.

Perhaps the most elusive and difficult aspect of invasion biology concerns the concept of habitat matching between a species' source and recipient regions. The nature of the recipient habitat must allow an introduced species to survive, colonize, and spread if an invasion is to be successful. It is intuitive that physical differences among source and recipient habitats can pose significant impediment to invasion (e.g., differences in salinity, temperature, available substrate, wave exposure). Indeed, this physical mismatch currently lies at the heart of ballast water management for the reduction of marine invasions in the United States (NRC 1996) and in many other parts of the world where open-ocean ballast water exchange is the ballast water management technique of choice. The assumption is that by exchanging ballast water of coastal origin with open-ocean water before deballasting in a subsequent coastal port, the rate of invasion will be reduced. Open-ocean organisms living under full marine conditions (~35 ppt salinity) are, presumably, less likely to survive in reduced salinity coastal waters than organisms originating in other, similar coastal systems (NRC 1996). Introducing organisms into physical habitats that differ greatly from the conditions they evolved in will likely result in many failed invasions, but to date, little is known concerning the degree of dissimilarity necessary to prevent invasions. Nevertheless, there are many examples of invaders that have been wildly successful in mismatched habitats.

The characterization of oyster-mediated invasions to the northeast Atlantic and northeast Pacific coasts demonstrates three main points. 1) Invasions are non-random events. 2) Invasions by the same species tend to proceed differently in different recipient regions. 3) Despite similar massive introductions of oysters, the northwest Pacific has three times as many molluscan invaders from the northwest Atlantic than does the northeastern Atlantic. This chapter also highlights the need for more detailed future study of invader/habitat interactions and the relationship between inoculation patterns and invasion patterns.

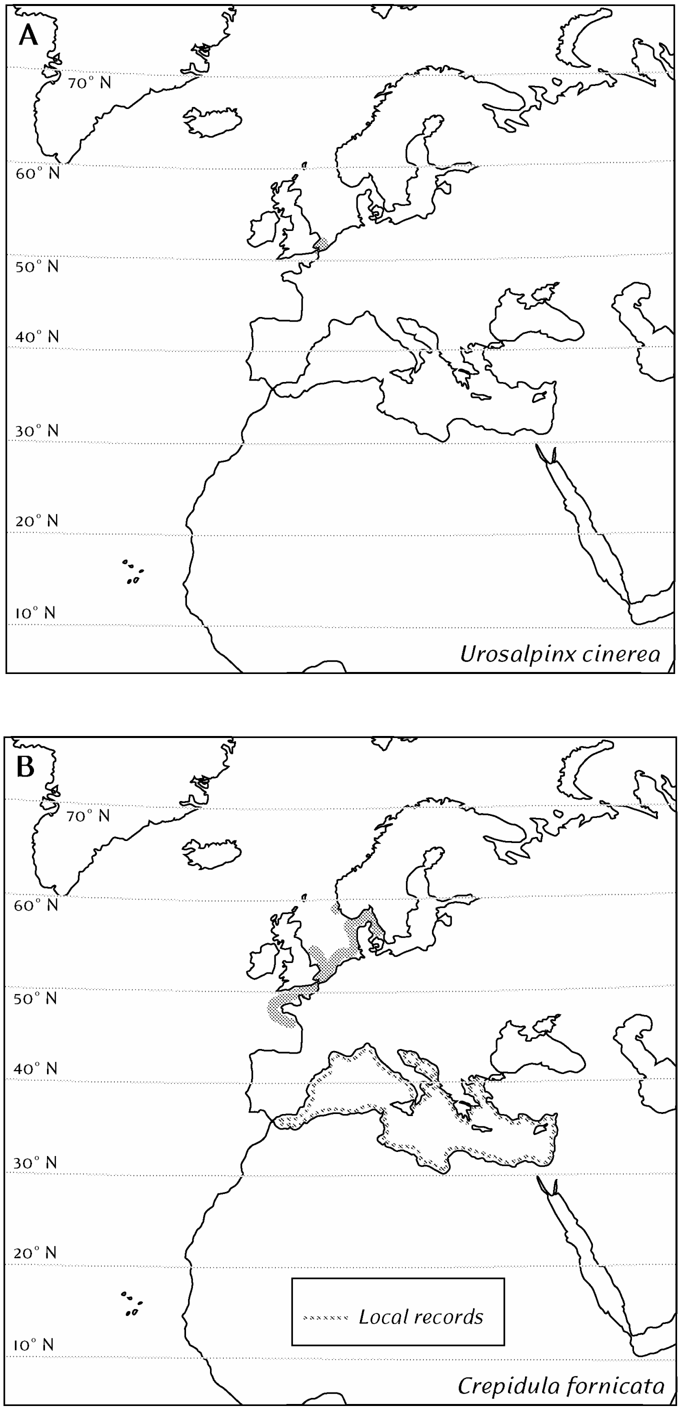


Figure 4.1. Invasion ranges of western Atlantic mollusks in eastern Atlantic coastal systems, (A) *Urosalpinx cinerea*, (B) *Crepidula fornicata*. Dashed line indicates local, but geographically unspecified, records.

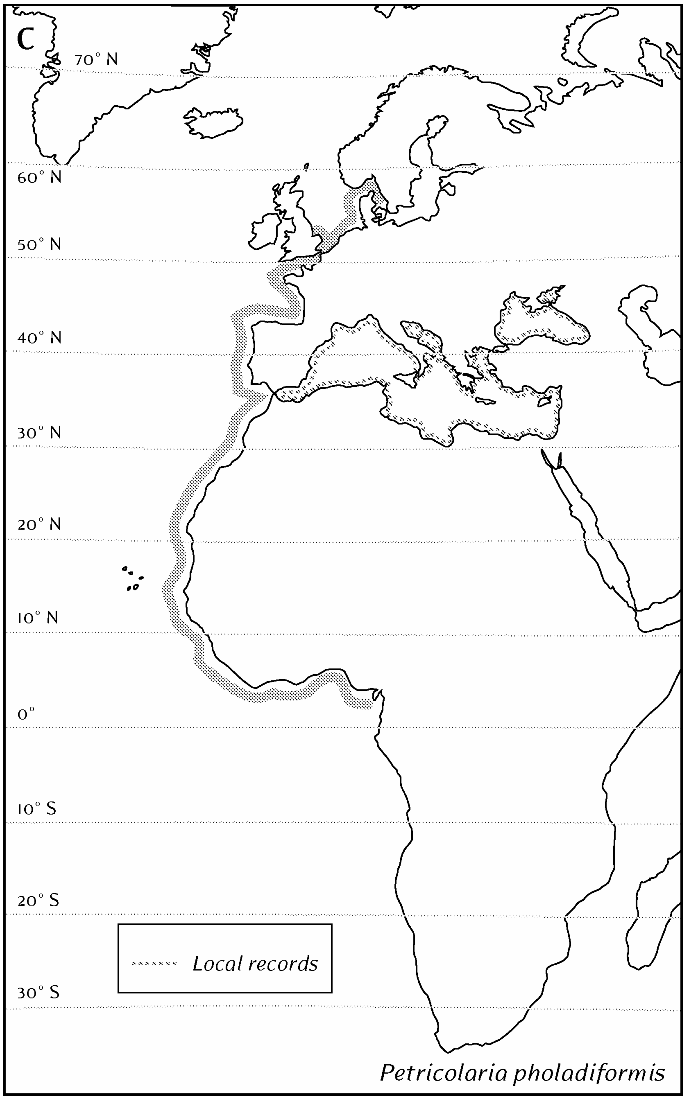


Figure 4.1 cont. Invasion ranges of western Atlantic mollusks in eastern Atlantic coastal systems, (C) *Petricolaria pholadiformis*. Dashed line indicates local, but geographically unspecified, records.

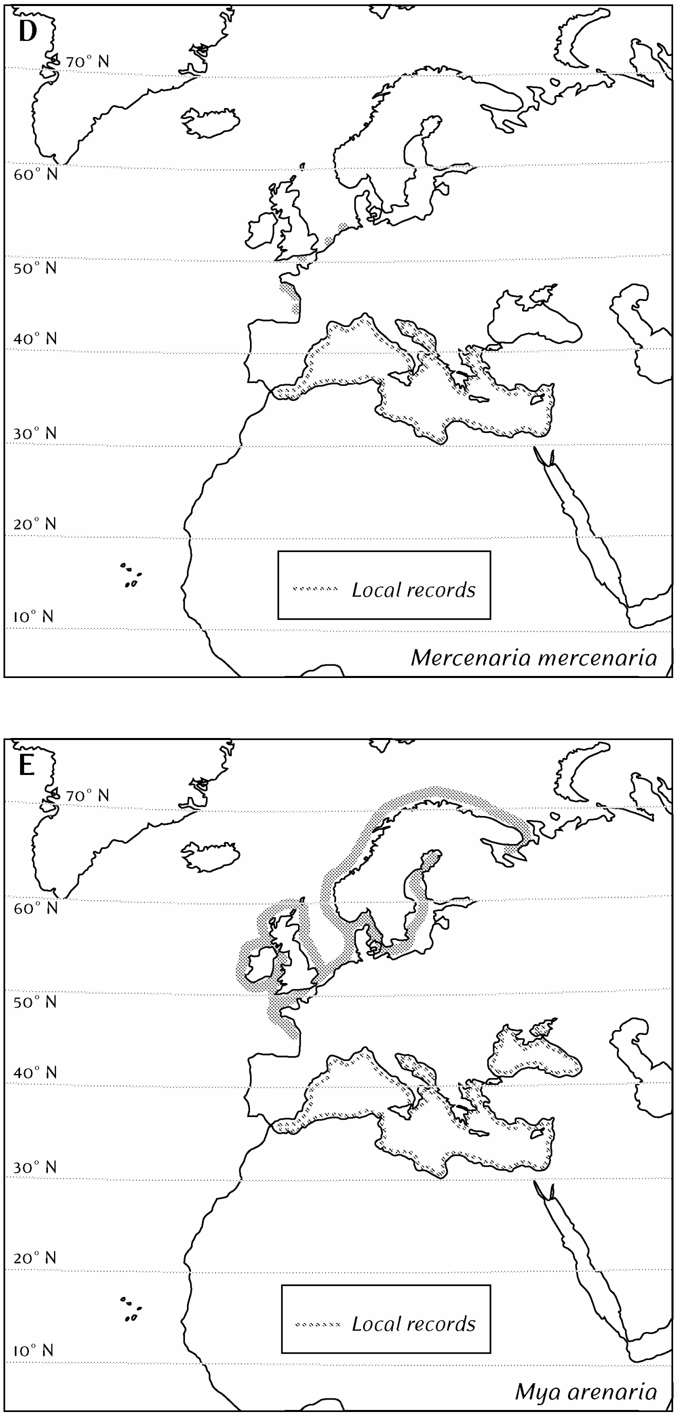


Figure 4.1. Invasion ranges of western Atlantic mollusks in eastern Atlantic coastal systems, (D) *Mercenaria mercenaria*, (E) *Mya arenaria*. Dashed line indicates local, but geographically unspecified, records.

Table 4.1. Earliest reported dates of detection of oyster-mediated molluscan invaders of the Eastern Pacific and Eastern Atlantic. Dates in parentheses are reported in the literature as suspected, but unconfirmed, dates of introduction.

	Northeastern Pacific Coastal Systems		**Northeastern Atlantic Coastal Systems**	
Species	**Date**	**Ref.**	**Date**	**Ref.**
Urosalpinx cinerea	1890	1,2	(1900)	3
Crepidula fornicata	(1905)	1,2	1872	3
Petricolaria pholadiformis	1927	1,2	1890	3
Mercenaria mercenaria	>1967	1,2	1864	3
Mya arenaria	1874	1,2	(1200s)	3

Notes: 1. Carlton (1979) and citations therein; 2. Carlton (1992) and citations therein; 3. Eno et al. (1997) and citations therein.

Table 4.2. Incidence and geographic range of oyster-mediated molluscan invasions of the Eastern Pacific and Eastern Atlantic coastal systems.

	Northeastern Pacific		**Northeastern Atlantic**	
Species	**Incidence**	**Range**	**Incidence**	**Range**
Urosalpinx cinerea	Low	Wide	Low	Very Narrow
Crepidula fornicata	Low	Narrow	High	Wide
Petricolaria pholadiformis	Low	Wide	High	Extremely Wide
Mercenaria mercenaria	Very Low	Wide	Medium	Medium
Mya arenaria	Very High	Very Wide	Very High	Very Wide

APPENDIX 4.1. MATHEMATICAL COMBINATIONS

Mathematical combinations are same-sized groups with unique membership. The general formula for calculating a combination number is *C(n,k)=n!/k!(n-k)!*. The formula calculates the number of unique ways that groups of *k* elements can be taken from a set containing *n* elements (Cohen 1990). The following example demonstrates their use when a pool consisting of 5 letters from the alphabet is used ($n = 5$).

Question: If 5 letters (A, B, C, D, E) are placed in a box, what is the probability that a random grab of 4 letters will contain the 2 letter combination AB?

The following is a comprehensive list of 4 letter combinations that can be pulled from the pool of 5 letters: ABCD, ABCE, ABDE, ACDE, and BCDE. By inspection, one can see that AB is included in 3 of 5 combinations. Thus, AB could be expected to occur in 4 letter combinations 60% of the time.

Solving the problem using combinatorial mathematics requires three steps. 1) Calculating the total number of 4 letter combinations that can be taken from a 5 letter set. 2) Calculating the subset of these 4 letter combinations that would contain 2 particular letters (AB). 3) Dividing step 2 by step 1.

Step 1:

The total number of 4 letter combinations chosen from 5 letters is:

$$C(5,4) = \frac{[5!]}{[4!(5-4)!]} = 5$$

Step 2:

Since the combinations of interest must include the 2 letter combination AB, these letters can be subtracted from the pool of 5 letters (A,B,C,D,E becomes C,D,E (*n*=3)). Likewise, the set size chosen from the new pool will also decrease by 2 letters (*k*=4 becomes *k*=2). The goal is to calculate the number of 2 letter combinations that can be taken from a pool of 3 letters (C,D,E) such that when the 2 letter combination AB is added to each, the resulting list represents the total number of 4 letter combinations that include AB. This can be represented in the following equation.

$$C(5-2,4-2)=C(3,2)=\frac{[3!]}{[2!(3-2)!]}=3$$

Therefore, there are three 2 letter combinations, that when linked to the AB combination, represent the total number of 4 letter combinations containing AB. These combinations are CD, CE, DE, and become ABCD, ABCE, and ABDE when AB is added. By inspection, these are the same combinations as found above.

Step 3:

The probability of choosing a combination of 4 letters that contains AB from a pool of 5 letters is:

$$\frac{C(5-2,4-2)}{C(5,4)} = \frac{\frac{3!}{2!(3-2)!}}{\frac{5!}{4!(5-4)!}} = 0.6.$$

LITERATURE CITED

Abbott, R. T. 1974. American Seashells, second edition. Van Nostrand Reinhold Company, New York, 663 p.

AquaSense 1998. Ballast water Overview of available data and estimation of possible risks – Ordered by the Ministry of Transport, Public Works and Water Management, North Sea Directorate. Rapportnummber: 98.1162.

Barrett, E. M. 1963. The California oyster industry. Department of Fish and Game Fish Bulletin 123: 1-103.

Brown, R. D., Balaskas, L. D, Mortsch, L. D., Saulesleja, A., and V. R. Swail 1986. Marine Climatological Atlas – Canadian West Coast. Canadian Climate Centre Report No. 86-10, 372 p.

Burd, B. J., Moore, D., and R. O. Brinkhurst 1987. Distribution and abundance of macrobenthic infauna from Boundary and Mud Bays near the British Columbia/ U.S. border. Can. Tech. Rep. Hydrogr. Ocean Sci. 84.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. dissertation. University of California, Davis. 904 p.

Carlton, J. T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research 11: 489-505.

Carlton, J. T. 1999. Molluscan invasions in marine and estuarine communities. Malacologia 41:439-454.

Carlton, J. T. and R. Mann 1996. Transfers and world-wide introductions. In: V. S. Kennedy, R. E. I. Newell, and A. F. Eble (eds.), The eastern oyster, *Crassostrea virginica*, p 691-706. Maryland Sea Grant Program, College Park.

Carriker, M. L. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Fish Wildlife Serv. Spec. Sci. Rep. Fish. No. 148, 150 p.

Chew, K. K. 1990. Global bivalve shellfish introductions. World Aquaculture 21: 9-22.

Chipperfield, P. N. J. 1951. The breeding of *Crepidula fornicata* (L.) in the River Blackwater, Essex. Journ. Mar. Biol. Assoc. 30:49-71.

CIESM (Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée) 1999. Atlas of exotic molluscs in the Mediterranean. CIESM online database (http://www.ciesm.org/atlas/appendix3.html).

Cohen, D 1990. Precalculus with Unit-circle Trigonometry. West Publishing Company, New York, 744 p.

Cole, H. A. 1942. The American whelk tingle, Urosalpinx cinerea (Say), on British oyster beds. The Journal of Experimental Biology 19:477-508.

Collins, J. W. 1892. Report on the fisheries of the Pacific Coast of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1892, 267 p. Government Printing Office, Washington, D. C.

Dale, N.G. 1997. An overview and strategic assessment of key conservation, recreation and cultural heritage values in British Columbia's marine environment. Prepared by ESSA Technologies Ltd., Vancouver, BC for BC Land Use Coordination Office, Victoria, BC 104 p.

De Broca, P. 1876. On the oyster industries of the United States. Rep. of U. S. Comm. Fish and Fisheries, 1873-1875, 49 p. Government Printing Office, Washington, D. C.

De Montaudouin, X., C. Audemard, P. Labourg 1999. Does the slipper limpet (Crepidula fornicata, L.) impair oyster growth and zoobenthos biodiversity? A revisited hypothesis. Journal of Experimental Marine Biology and Ecology 235:105-124.

De Montaudouin, X. and P. G. Sauriau 1999. The proliferating Gastropoda *Crepidula fornicata* may stimulate macrozoobenthic diversity. Journal of Marine Biological Association of the United Kingdom 99:1069-1079.

Duggan, C. B. 1979. Man's role in the spreading of oyster pests and diseases. In: Kernan, R. P., Mooney, O. V., and A. E. J. Went (eds.), The introduction of exotic species. Advantages and problems, Dublin, Royal Irish Academy, p 51-56.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, England. 181 p.

Eno, N. C. 1996. Non-native marine species in British waters: effects and controls. Aquatic Conservation: Marine and Freshwater Ecosystems 6:215-228.

Eno, N. C., Clark, R. A., and W. G. Sanderson 1997. Non-native marine species in British waters: a review and directory. Joint Nature Conservation Committee, Peterborough, United Kingdom. 152 p.

Epifanio, C. E. and R. F. Srna 1975. Toxicity of ammonia, nitrite ion, nitrate ion, and orthophosphate to *Mercenaria mercenaria* and *Crassostrea virginica*. Marine Biology 33:241-246.

Greene, G. T. and D. S. Becker 1977. Winterkill of hard clams in Great South Bay, New York 1976-1977. Special Report 9. Marine Science Research Center, Stony Brook, New York.

Gosner, K. L. 1971. Guide to identification of marine and estuarine invertebrates – Cape Hatteras to the Bay of Fundy. John Wiley & Sons, New York, 693 p.

Goulletquer, P. and M. Heral 1997. Marine molluscan production trends in France: from fisheries to aquaculture. In: MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.), The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 3. U. S. Dept. of Commer., NOAA Tech. Rep. 129, p 137-164.

Hines, A. H. and G. M. Ruiz 2000. Biological invasions of cold-water coastal ecosystems: ballast-mediated introductions in Port Valdez/Prince William Sound, Alaska. Final Report presented to Regional Citizens' Advisory Council of Prince William Sound, Alaska.

Hopkins, D. R. 1986. Atlas of the distribution and abundance of common benthic species in San Francisco Bay, California. U. S. Geological Survey Waters Resources Investigations Report 86-4003.

ICES (International Council for the Exploration of the Sea) 1972. Report of the Working Group on Introduction of nonindigenous Marine Organisms. Unpublished, International Council for the Exploration of the Sea. (Cooperative Research Report No. 32).

Ingersoll, E. 1881. The oyster-industry of the United States. In: G. B. Goode (ed.), The history and present condition of the fishery industries, 1879-1880, 251 p. Government Printing Office, Washington, D. C.

Kochiss, J. M. 1974. Oystering from New York to Boston. Mystic Seaport, Inc., Middletown, Connecticut, 251 p.

Kornicker , L. S. 1975. Spread of ostracodes to exotic environs on transplanted oysters. Bulletins of American Paleontology. 65:129-139.

Korringa, P. 1951. Crepidula fornicata as an oyster pest. Cons. Int. Explor. Mer., Rapp. Et Proc. Verb. 128 Part 2, 55-59.

Laursen, D. 1966. The genus *Mya* in the Arctic region. Malacologia 3:399-418.

Leppäkoski, E. 1984. Introduced species in the Baltic Sea and its coastal ecosystems. Ophelia, Suppl. 3:123-135.

Lippson, A. J. and R. L. Lippson 1997. Life in the Chesapeake Bay, second edition. The Johns Hopkins University Press, Baltimore, Maryland, 304 p.

MacKenzie, C. L. Jr., Burrell, V. G. Jr., Rosenfield, A., and W. L. Hobart (eds.) 1997. The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vols. 1-3. U. S. Dept. of Commer., NOAA Tech. Rep. 127,128,129.

Mistakidis, M. N. 1951. Quantitative studies of the bottom fauna of Essex oyster grounds. Fish. Invest. 17:1-47.

Murphy, R. C. 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon – The importance of bioturbation. Journal of Marine Research 43:673-692.

Murphy, R. C. 1983. The introduced bivalve, *Mercenaria mercenaria,* in a shallow coastal ecosystem: 1) Factors affecting its distribution, 2) Contribution to the benthic community metabolism. Ph.D. thesis, University of Southern California.

Nelson, T. C. 1922. The oyster drill: a brief account of their life history and possible means of combating them. Appendix Rept. Biol., N. J. Sta. Bd. Shellf.

NRC (National Research Council) 1996. Stemming the tide: controlling introductions of nonindigenous species by ships' ballast water / Committee on Ship's Ballast Operations, Marine Board, Commission on Engineering and Technical Systems. National Academy Press, Washington, D. C., 154 p.

Olenin, S. and E. Leppäkoski 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia 393:233-243.

Orton, J. H. and R. Winckworth 1928. The occurrence of the American oyster pest *Urosalpinx cinerea* (Say) on English oyster beds. Nature 122:241.

Peterson, K. S., Rasmussen, K. L., Helnemeler, J. and N. Rud 1992. Clams before Columbus? Nature 359:679.

Philpots, J. R. 1890. Oysters and all about them. John Richardson and Co., London, 241 p.

Quayle, D. B. 1964. Distribution of introduced marine mollusca in British Columbia waters. J. Fish. Res. Bd. Can. 21:1155-1181.

Seaward, D. R. 1990. Distribution of the marine molluscs of north west Europe. Peterborough, Nature Conservancy Council, for Conchological Society of Great Britain and Ireland.

Shadrin, N. 1998. List of exotic introduced species in the Black Sea. Report on Workshop on non-native species in the Baltic and Black Seas, ZIN RAS, St. Petersburg, Russia, December 1-4, 1998.

Sjøtun, K. 1997. A new observation of *Crepidula fornicata* (Prosobranchia, Calyptraeidae) in western Norway. Sarsia 82:275-276.

Stauber, L. A. 1943. Ecological studies on the oyster drill, *Urosalpinx cinerea*, in Delaware Bay, with notes on the associated drill, *Eupleura caudata*, and with practical consideration of control methods. Unpub. Rept., Oyster Res. Lab., N.J.

Strasser, M. 1999. M*ya arenaria* – an ancient invader of the North Sea coast. Helgoländer Meeresunters 52:309-324.

Tebble, N. 1966. British bivalve seashells: a handbook for identification. The British Museum (Natural History), London, 212 p.

Turgeon, D. D., Quinn, J. F. Jr., Bogan, A. E., Coan, E. V., Hochberg, F. G., Lyons, W. G., Mikkelsen, P. M., Neves, R. J., Roper, C. F. E., Rosenberg, G., Roth, B., Scheltema, A., Thompson, F. G., Vecchione, M., and J. D. Williams 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, second edition. American Fisheries Society, Special Publication 26, Bethesda, Maryland. 535 p.

Utting, S. D. and B. E. Spencer 1992. Introductions of marine bivalve molluscs into the United Kingdom for commercial culture – case histories. ICES Mar. Sci. Symp. 194:84-91.

Vermeij, G. J. 1989. Invasion and extinction: the last three million years of North Sea pelecypod history. Conservation Biology 3: 274-281.

Yonge, C. M. 1949. The sea shore. Collins Clear-Type Press, London, 350 p.

CHAPTER 5

Biological Invasions: The Challenges Ahead

The study of invasion biology has only recently truly captured the widespread attention of ecological researchers. One can now find an article relating to invasion biology in almost any current ecological journal volume. This situation was not the case 3-5 years ago. Conservation scientists and natural resource managers are beginning to recognize the serious threats to the environment that marine and aquatic nonindigenous species pose. Much of this interest has only come about as a result of well publicized, large-scale invasions (e.g., the alga species *Caulerpa taxifolia* in the Mediterranean Sea, the comb jelly *Mnemiopsis leidyi* in the Black Sea, and the zebra mussel *Dreissena polymorpha* and *Dreissena bugensis*, in the Great Lakes and inner waterways of the United States). Such invasions have inflicted devastating ecological and economic damage to recipient ecosystems. However, despite tremendous environmental damage from marine invasive species, recognition and funding for research and management of marine invasions still lags far behind efforts in terrestrial systems.

Despite the passage of millions of years, and tens of thousands of years of human history, Earth's biological regions have remained distinct. But this condition has changed dramatically during the last 500 years as humans have found more efficient ways to cross the seas and breach the natural barriers that have separated near-shore marine and estuarine regions through evolutionary time. While threats to the economy and physical infrastructure are generally the concerns of legislators and the public, these threats are usually mere symptoms of larger biological diversity and ecological integrity losses that can be inflicted by biological invasions. The Earth's natural assets are, quite literally, in jeopardy. What has accrued over millions of years of evolutionary history can be easily and quickly destroyed. The arrival of the western Atlantic comb jelly, *Mnemiopsis leidyi*, to the Black Sea illustrates this point. *Mnemiopsis leidy*i was accidentally introduced there in the early 1980s, likely in the ballast water of a commercial vessel. Between 1984 and 1990 the anchovy fishery underwent a near total collapse, largely the result of the comb jelly's predation on the anchovy's planktonic food resources (Vinogradov et al. 1993, Travis 1993). Although the Black Sea was far from a pristine environment prior to the arrival of *Mnemiopsis leidyi*, the addition of this single nonindigenous species produced an unprecedented ecological disaster. Had the invasion of *Mnemiopsis leidyi* not wiped out the Black Sea's most important fishery, estimated at $250 million dollars of damage to fisheries (Travis 1993), the news may never have surfaced. This is a dramatic example of what may be occurring every day. The homogenizing of Earth's ecosystems and loss of co-evolved communities can never be reversed, despite the rate of this loss.

Increasing concern for biological invasions, inside and outside the scientific community, is encouraging. Indeed, the recent introduction of a new journal from Kluwer Academic Publishers, entitled *Biological Invasions*, is dedicated to the advancement of ecological and evolutionary understanding of the invasion process. Additionally, this journal provides a forum for discussion and exploration of management and policy issues associated with biological invasions. A greater awareness of biological invasions, brought about through increased scholarly research and public outreach, is apt to better our chances for curbing new introductions. However, if the scientific community does not choose to take a lead and earnestly address the fundamental questions regarding how invasions occur, an important opportunity will be lost.

Although the landscape in invasion science does appear to be changing, the field is still dominated by qualitative approaches. And while it must be emphasized that the compilation and maintenance of nonindigenous species lists is extremely important, further steps must also be taken. Species lists must not become an end in and of themselves, but instead should be gathered in a way that promotes fuller analytical and synthetic treatment. Without greater quantitative rigor, it will be difficult, if not impossible, to truly understand how and why invasions take place. Scientists must be innovative in their approaches toward collecting and analyzing new data, but should also be cognizant of the reservoir of data that already exists, even though it may have been collected for a different purpose. Conservation biologists must step up quantitative and experimental efforts to address the biological and ecological underpinnings of invasions. Such efforts will be important for combating this environmental challenge.

A MODEST BEGINNING

This dissertation has examined characteristics of invading species. To this end, the retrospective approach employed was successful at identifying the greater historical abundance of successful invaders and tolerance of low salinity as two important attributes of successful molluscan invaders. When historical abundance is taken as a proxy for propagule pressure, the results agree with the findings of recent studies that identify propagule pressure as a critical factor for invasion success among plants (Levine 2000) and birds (Pimm 1991, Veltman et al. 1996).

However, the findings of this research also indicate that invasions are dependent on other factors than just those of the potential invading organisms. The results from Chapters 3 and 4 hint at the complex nature of marine invasions. On one hand, perhaps due to specific biological and ecological attributes, invasions by the same species occur repeatedly and are therefore clearly not random events. On the other hand, separate invasion events by the same species are variable across space. What accounts for such differences? At least two explanations seem plausible. First, individual invasions are likely shaped by the recipient ecosystem in which non-natives are introduced. Both the physical and biological environment should affect the way invasions proceed. Second, the patterns of invasion in different ecosystems probably also reflect patterns of initial inoculation. Since multiple anthropogenic inoculations can sometimes be misidentified as a single inoculation followed by natural dispersal, and vice versa, invasion patterns must be interpreted carefully. Ultimately, these two aspects of invasion need to be considered when attempting to characterize invasions fully. Recipient ecosystem's influences on colonization and invasion are perhaps the most complicated and least understood aspects biological invasion and warrant further investigation.

Although the findings presented here are based on data from the literature, and are thus observational rather than experimental, this retrospective approach is critical for pattern recognition of invasions. Until invasion biology develops adequate predictive power, invasions will continue to be studied after the fact. Extracting as much information as possible from past invasions and from existing data, although sometimes difficult, can enhance our understanding of the invasion process (Daehler and Strong 1993). The application of quantitative approaches is vital for the study of invasion biology and is necessary for the effective design of more powerful experimental investigations (Grosholz et al. 2000, Grosholz and Ruiz 1996).

AREAS FOR FUTURE RESEARCH

The challenge posed by retrospective analysis is choosing a system that is not fatally confounded by uncontrolled variables. The approach used here was to choose a well-studied taxonomic group (mollusks) in combination with a well-defined vector (commercial oyster transport) to frame questions concerning past invasion success and failure. Many important invasion vectors lack the spatial and temporal resolution of commercial oyster transport (e.g., shipping vectors such as ballast water and hull fouling have numerous sources and extremely complex delivery patterns), and therefore make the compilation of meaningful species pools impossible. Nevertheless, this approach could be applied to many other vectors and taxonomic groups. For example, manmade canal systems such as the Suez and Welland Canals have been important thoroughfares through which aquatic organisms have moved from one ecosystem to another. The Lessepsian migrations between the Red Sea and the Mediterranean are just a subset of two much larger and historically separate biotas. The Suez Canal system could be evaluated in the same manner that oyster-associated mollusks have been here. For that matter, other taxonomic groups that are associated with oysters or other aquaculture target species are prime candidates for this kind of approach as well.

Although studies of historical invasions obviously cannot undo past events, they can provide insights about how invasions occur and how future invasions by similar vectors might be prevented. There is still much to be learned from the study of past invasions. Existing data sets and information should continue to be synthesized and analyzed.

In Situ Investigations of Invaders and Recipient Environments

To fully understand how invasions occur, and by extension how undesirable invasions might be prevented and managed, research must reach beyond retrospective analyses. Whether invasions are long established or brand new, comparisons between invaded communities and similar non-invaded communities can be made to characterize the ecological effects of invasions as well as critical environmental factors that limit spread. Early detection of new invasions may provide the best opportunity to test for environmental impacts since locating appropriate, non-invaded control sites nearby may be easiest when an invasion is of small scale (e.g., within a single embayment). Early detection also provides the best chance for eradication and possible control measures (see below). For invaders with continually expanding ranges, studies might focus on range edges (expansion fronts) to look for ecological effects of invaders. For invasions that appear to have reached their expansion limits (e.g., the common periwinkle *Littorina littorea* or European green crab *Carcinus maenas* in the western Atlantic), the search for the environmental factors that limit further expansion might be fruitful (i.e., comparing environmental characteristics within and just outside the invaded range).

Invasions provide the opportunity to pursue manipulative field experiments as well as descriptive natural experiments (in areas where invasions have already taken place). Such studies could focus on the population dynamics of invaders, community effects, ecosystem effects, and environmental impacts of invaders (e.g., Crooks 1998, Byers 2000, Suarez et al. 1999, Grosholz et al. 2000, Levine, J. M. 2000, Salt et al. 2000). Field experiments, although more constrained in time and space, have the potential to provide the most robust tests of the actual ecological effects of invaders. Properly designed descriptive investigations such as natural experiments may provide an opportunity to generalize over greater scales of space and time (Diamond 1986). It is suggested that both approaches be pursued to address the issue of biological invasions.

Invasions Research and Management

While there is widespread consensus that invasion prevention is superior to attempted control after the fact (Mack et al. 2000, Myers et al. 2000), the reality is that biological invasions will continue to occur despite the best prevention measures. How are residual invasions to be handled? What approaches should conservation biologists and natural resource managers take to reduce the environmental impacts and minimize the range expansion of invaders? Currently, there are no clear answers to these questions.

One approach is extirpation of invaders following colonization. Although eradication of some exotic marine species has been shown possible (e.g., the black-striped mussel *Mytilopsis sp.* in Australia and the sabellid polychaete *Terebrasabella heterouncinata* in southern California), these invasions were very recent and very localized. Two methods were employed: 1) mechanical removal (*Terebrasabella heterouncinata*) and 2) chemical treatment of the black-striped mussel. In the case of the black-striped mussel, three conditions contributed to the success of the extirpation efforts. 1) A coordinated nonindigenous species monitoring program sponsored by Australia's Centre for Research on Introduced Marine Pests (CRIMP) detected the mussel within six months of its colonization. 2) The invasion occurred inside a portion of the Port of Darwin that could be mechanically closed off from outside waters so that veligers and chemical treatment could be contained. 3) An aggressive eradication response began immediately after mussel discovery (C. Hewitt - CRIMP, pers. comm.). Unfortunately, the chances of eradicating well-established, widespread invaders, marine or otherwise, appears much less practical (Mack et al. 2000, Myers et al. 2000).

Proper environmental monitoring programs increase the likelihood of detecting invasions early. For example, recent localized invasions of southern California embayments by the marine alga, *Caulerpa taxifolia*, were detected in June 2000 and eradication efforts initiated. However, scientists and natural resource managers did not agree fully on how such efforts should proceed (Dalton 2000). Genetic analyses indicate that the strain of *Caulerpa taxifolia* found in California is the same as the invasive strain that has caused widespread ecological environmental damage in the Mediterranean (Jousson et al. 2000). Such results reinforce the necessity for aggressive eradication in California. Time will tell whether these eradication efforts are successful.

Typically, eradication is not possible, and the next line of defense becomes control of nonindigenous species population size. Control programs attempt to prevent rapid expansion of nonindigenous species populations. If populations can be kept in check through continual mechanical, chemical, or biological control methods, the likelihood of harm to native ecosystems is lessened. However, species that are targeted for control are often the ones that have made themselves apparent through rapid growth and invasion.

The magnitude of biological invasions is huge and the extent of our understanding still exceedingly low. A recent review of the aquatic and marine invasion literature of the United States indicates that there is a severe lack of quantitative information and analysis surrounding biological invasions (Ruiz et al. 1999). Given this discrepancy, it is unrealistic to presume that effective and broadly applicable methods for management of marine invasions will be available anytime soon. Perhaps a more conscientious view of marine invasions' management would reconcile our relative lack of knowledge with the extent of the problem. Such a view might aim to amass more fundamental quantitative data on the process of invasion with a focus on identifying information that is relevant and applicable to control measures. To do this will, no doubt, require a major effort on the part of conservation biologists. If a concerted endeavor were to be undertaken, at minimum, it should include: 1) careful environmental monitoring for early detection of new invasions and generation of important ecological baseline data; 2) thoughtfully designed field experiments to measure the dynamics and ecological impacts of invasions - old and new; 3) the application of both these components at multiple spatial and temporal scales; 4) continued data mining of existing information from past invasions.

For better or worse, there is currently no shortage of invaders to be studied. Ruiz et al. (2000) report 298 likely aquatic invaders of marine and estuarine ecosystems in the United States alone. With the exception of just a few, these organisms are not well studied and current understanding of their true ecological impacts is minimal.

Despite the crucial need for more in-depth study of invasions, appropriate caution must be used when attempting to apply specific scientific results to invasive species management. If conclusions are over-generalized, perhaps due to excessively short-term or small-scale experiments, their premature application could be destructive. Invasion biologists must pay close attention to the spatial and temporal contexts of their investigations for this reason.

For example, investigations lacking adequate statistical power can lead to the acceptance of a false null hypothesis (i.e., a type II error). Concluding that an invasion has had no substantial ecological effect, when in fact one actually exists, can lead to a false sense of security, inaction, and ecological damage (Eberhardt and Thomas 1991, Osenberg et al. 1994). As described in Chapter 4, invasions by the same species can vary considerably. Control measures that work in one location may not necessarily work in another. In addition to spatial differences of invasions, temporal differences also exist. Rates of population growth and range expansion can vary tremendously for a single species from the time of initial colonization to later stages of invasion (Mack et al. 2000). Depending on the particular species and the particular environment colonized, the lag time between colonization and maximum rate of spread can be variable. Crooks and Soulé (1999) indicate that lags can arise from 1) inherent dynamics of natural population growth and range expansion, 2) changing environmental conditions at the site of invasion, and 3) genetic lags due to initial lack of genetic fitness of invaders to their new environment. The implication is that control measures must be adaptive and varied to address the particular temporal stages of invasion.

When their temporal variation is combined with their spatial variability, the bewildering nature of invasions becomes fully apparent. Even for a single species, invasion characteristics are clearly sensitive to the spatial and temporal context of the invasion. At present, there is little scientific information on marine invasions to incorporate into control and management plans. Indeed, it is impossible to say whether a deeper scientific understanding of the invasion process will ultimately provide beneficial insight into how invasions should be handled once they are underway. The hope, of course, is that some generality does exist among invaders and that one day such information can be marshaled in a predictive framework to lessen the continuing ecological damage of nonindigenous species. As with most issues in conservation biology, the goal is to take actions that will do more good than harm. When critical information is lacking, this goal is a challenging one.

LITERATURE CITED

Crooks, J. A. and M. E. Soulé 1999. Lag times in population explosions of invasive species: causes and implications. In: (eds. O. T. Sandlund, P. J. Shei and Å. Viken) Invasive species and biodiversity management. Based on a selection of papers presented at the Norway/UN Conference on Alien Species, Trondheim, Norway. Kluwer Academic Publisher, Dordrech, 444 p.

Dalton, R. 2000. Researchers criticize response to killer algae. Nature 406:447.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. In: Diamond, J. and T. J. Case (eds.) Community Ecology. Harper and Row, New York.

Eberhardt, L. L. and J. M. Thomas 1991. Designing environmental field studies. Ecological Monographs 61:53-73.

Grosholz, E. D., Ruiz, G. M., Dean, C. A., Shirley, K. A., Maron, J. L., and P. G. Connors 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206-1224.

Jousson, O., Pawlowski, J., Zaninetti, L., Zechman, F. W., Dini, F., Di Guiseppe, G., Woodfield, R., Millar, A., and A. Meinesz 2000. Invasive alga reaches California. Nature 408:157-158.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852-854.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and F. A. Bazzaz 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689-710.

Myers, J. H., Simberloff, D, Kuris, A. M., and J. R. Carey 2000. Eradication revisited: dealing with exotic species. Trends in Ecology and Evolution 15:316-321.

Osenberg, C. W., Schmitt, R. J., Holbrook, S. J., Abu-Saba, K. E., and A. R. Flegal 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. Ecological Applications 4:16-30.

Pimm, S. L. 1991. The balance of nature?: ecological issues in the conservation of species and communities. The University of Chicago Press, Chicago, IL, 447 p.

Ruiz, G. M., Fofonoff, P., and A. H. Hines 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography 44:950-972.

Ruiz, G. M., Fofonoff, P., Carlton, J. T., Wonham, M. J., and A.H. Hines 2000. Invasions of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics (in press).

Salt, S. M., Liu, W., Thompson, D. J., Godfry, H. C. J. and M. Begon 2000. Invasion sequence affects predator-prey dynamics in a multi-species interaction. Nature 405:448-450.

Simberloff, D. 1997. Eradication. In (D. Simberloff, D. C. Schmitz, and T. C. Brown, eds.) Strangers in paradise. Island, Washington, D. C.

Travis, J. 1993. Invader threatens Black, Azov Seas. Science 262:1366-1367.

Veltman, C. J., Nee, S., and M. J. Crawley 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist 147:542-557.

Vinogradov, M. E, Shushkina, E. A., and G. G. Nikolaeva 1993. The state of zoocoene in the open areas of the Black Sea during late summer 1992. Okeanologiya 33:382-387.