Marine Bioinvasions

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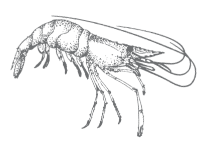
proceedings of a conference

January 24–27, 1999

Edited by
Judith Pederson
MIT Sea Grant College Program



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Preface

As recently as twenty years ago, only a handful of experts was discussing marine bioinvasions or expressing concern about impacts of nonindigenous species on ocean communities or ecosystems. That situation changed around the world with the appearance in the 1980s of the Eurasian zebra mussel (*Dreissena polymorpha*) in the Great Lakes (U.S. and Canada), the American comb jellyfish (*Mnemiopsis leidyi*) in the Black Sea and Japanese dinoflagellates in southern Australia. The resultant ecological and economic impacts ushered in a new era of awareness. National legislation (the National Aquatic Nuisance Species Prevention and Control Act of 1990) was passed and called for action to prevent new invasions. Funding supported new research initiatives and managers explored options for preventing new invasions, especially through ballast water introductions. Scientists, managers and industry representatives began to meet annually to share information, identify ways to manage and control invasive species, and describe technologies designed to prevent future introductions.

With the reauthorization of nonindigenous species legislation (Nonindigenous Species Act of 1996) greater emphasis was placed on marine invasions. The conference on which this volume is based grew from a perceived need by a steering committee to convene a national meeting for those studying marine invasions to share insights into the science of invasion ecology and into managing what is a growing worldwide problem. The first National Conference on Marine Bioinvasions was held January 24–27, 1999 at the Massachusetts Institute of Technology, Cambridge, Massachusetts, USA and attracted approximately 250 national and international participants. The purpose was to bring together scientists, students, and managers to examine patterns of marine bioinvasions, ecological and evolutionary consequences, and ballast water management.

This volume, *Marine Bioinvasions: Proceedings of a Conference*, consists of many of the papers presented at the conference. It covers new and ongoing research, work in progress, current status of management options, and recommendations for new approaches to prevent and better manage biological invasions. Each submitted paper was subjected to peer review by at least two external reviewers and revised by the authors. Over half of the presenters submitted papers; abstracts of the remaining presentations have been included to provide a comprehensive view of the subject matter of the conference.

The volume is organized around three major topics: Patterns of Invasions, Ecological and Evolutionary Consequences, and Ballast Water Management. An additional section on outreach and education highlights the Sea Grant Programs' efforts to inform a broad-based audience. The papers cover a range of topics that are fundamental to understanding marine bioinvasions and their impacts. The distribution and pattern of species in space and time, molecular approaches to identifying sources, management options to prevent introductions, estimation of risk, and technological developments for managing ballast water are addressed by several authors. Together the papers represent a rich assemblage describing what is known about marine invasions and options for managing or preventing introductions.

Not all topics were addressed at the conference and their absence in this volume reflects a lack of response rather than a deliberate omission. Issues relating to aquaculture where alien species are intentionally and unintentionally released are only touched upon. However, the changes to native populations through predation, competition, and genetic alterations may be significant. The more general topic of the effects of aliens species on biodiversity is acknowledged, but not discussed in depth. The role of nonindigenous species in homogenizing communities is poorly documented but may have significant evolutionary consequences. Biological control is a topic that generates passionate debate as to its viability in marine waters, but this topic was poorly represented at the conference.

Some of the more open-ended issues were discussed as part of a panel discussion held at the end of the conference. The panelists were asked to respond to the following statement:

> "*We have no evidence that we can prevent ALL bioinvasions in the long term, and with few exceptions bioinvaders are here to stay*."

The dialogue between the audience and the panelists went beyond the individual studies and highlighted areas for further study. Ballast water management remains as a major topic of discussion with different technologies proposed but few have been field tested on ships. Nor was there consensus that biological control in marine waters is a viable option. The statement implies that all bioinvaders are unwanted, but in some regions the invasive species has become a source of income—a new resource. The proponents of "black lists" argue that risk assessments can be used to identify species most likely to become invasive, others argue that we cannot predict which species will become invaders and we should assume that all species are potential problems. There was much discussion about early detection and rapid responses to invaders that are likely to cause problems, and examples were given illustrating successes and failures of responding and not responding to early sightings. There was agreement that prevention, early detection, and eradication were more cost effective than management and control efforts once a species was established. It is anticipated that the unresolved issues will serve to focus the next conference.

This volume should be of use to marine biologists, environmental scientists, managers, students, industries that may introduce or be impacted by marine invasions, and those with an abiding interest in the sea and how humans impact it. The challenges are clear: How do we, as a society, do a better job of preventing new invasions? What is needed to more realistically document ecosystem impacts and to translate these for managers and policy makers? What are the socio-economic costs to individuals who lose their livelihoods and to society, which pays for control of marine invasions? Through sharing ideas and exchanging information, the many facets of marine bioinvasions will become more understood and lead to new insights. Collectively, this volume of papers and abstracts offers insights beyond the individual discussions and offers a holistic view that is greater than the sum of the individual parts.

Judith Pederson
Editor

First National Conference on Marine Bioinvasions

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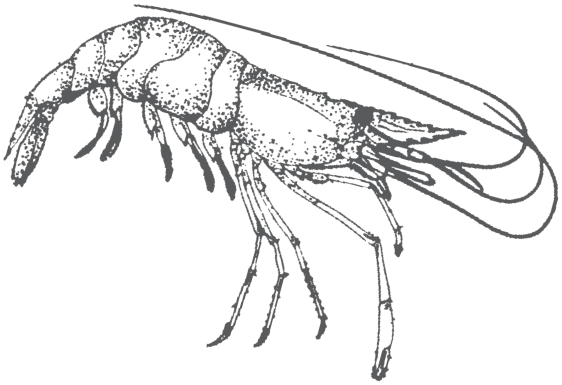
In Memoriam

We mourn the passing of Neil Richmond, Oregon Department of Fish and Wildlife, who took great interest in and concern about the impact of invasions on aquatic resources.

Index of Acronyms

AAPMA	Australian Association of Ports and Marine Authorities
ABWMAC	Australian Ballast Water Management Advisory Council
ANOVA	analysis of variance
ANS	aquatic nuisance species
APEC	Asian Pacific Economic Co-operation
APHIS	Animal and Plant Health Inspection Service (in U.S. Department of Agriculture)
AQIS	Australian Quarantine and Inspection Service
ARCO	Atlantic Richfield Company (oil company)
ASP	amnesiac shellfish poisoning
AW	abdominal width
BACI	before-after-control-impact
BAH	Biologische Anstalt Helgaland
BAT	best available technology
BFU	Baltic Floating University
BT	biological treatment
BW	ballast water
BWE	ballast water exchange
BWR	Ballast Water Reporting (Forms)
Cal-Sag Channel	Channel between Calumet River and Saganeshkee Slough, IL, U.S.
cfs	cubic feet per second
CL	carapace length
COTP	Captain of the Port (U.S. Coast Guard)
CRC	Cooperative Research Centres (Australia)
CRIMP	Centre for Research on Introduced Marine Pests (Australia)
CSIRO	Commonwealth Scientific Industrial Research Organisation (Australia)
CW	carapace width
CWA	Clean Water Act (U.S.)
DAF	dissolved air filtration
DNA	deoxyribonucleic acid
DSP	diarrhetic shellfish poisoning
DSS	decision support system
DSTO	Defense Science and Technology Organisation
DWT	dead weight metric tons (or dwt)
EEC	European Economic Community
EEZ	Economic Exclusive Zone
EGM	extragenomic markers
EMECS	Environmental Management of Enclosed Coastal Seas
EPA	U.S. Environmental Protection Agency (*see also* USEPA)
ETI	Environmental Technical Institute (Singapore)
EUCA	European Union of Concerted Action
EUMAST	European Union Marine Science and Technology Program
EXCH.	exchange
FAO	Food and Agricultural Organizations (United Nations)
Forum	1998 Forum on Ecological Surveys of Aquatic Nuisance Species
FY	Fiscal Year
GESAMP	Group of Experts on the Scientific Aspects of Marine Pollution
GLBTDP	Great Lakes Ballast Technology Demonstration Project
HAZOP	hazard and operability
HIMB	Hawaiian Institute of Marine Biology
HMSC	Hatfield Marine Science Center (OR, U.S.)
HSD	Tukey multiple range test
ICES	International Council for the Exploration of the Sea
ILTA	invasions lag-time analysis
IM Canal	Illinois Michigan Canal
IMA	ideal mechanical advantage
IMO	International Maritime Organization (United Nations)
IPM	integrated Pest Management
ITS	internal transcribed spacer
IUCN	International Union for the Conservation of Nature
LPOC	last port of call
MAF	Ministry of Agriculture and Fisheries (New Zealand)
MAFF	Ministry of Agriculture, Fisheries and Food (United Kingdom)
MANOVA	Multivariate analysis of variance

MARAD	Maritime Administration (U.S. Department of Transportation)
MARFI	Marine and Freshwater Resources Institute (Australia)
MARPOL	Convention for the Prevention of Pollution from Ships
MassGIS	Massachusetts Geographic Information System
MBL	Marine Biological Laboratory (Woods Hole, MA, U.S.)
MDH	malate dehydrogenase
MEPC	Marine Environmental Protection Committee (IMO, United Nations)
MFish	Ministry of Fisheries (New Zealand)
MIST	Marine Invasive Species Team
MITSG	Massachusetts Institute of Technology Sea Grant College Program
MLLW	mean low, low water
MLW	mean low water
MPA	Maritime and Port Authority (Singapore)
MS	motorship
MSA	mixed stock analysis
MT	motor transport (also as M.T.)
MV	motor vessel (also as M/V)
NABS	National Ballast Survey
NANPCA	Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990
NAS	National Academy of Science (U.S.)
NEMO	Nonindigenous Estuarine and Marine Organisms
NE-MWI	Northeast-Midwest Institute
NIS	nonindigenous species
NISA	National Invasive Species Act of 1996 (U.S.)
NIWA	National Institution of Water and Atmospheric Research
NMFS	National Marine Fisheries Service (U.S.)
NOAA	National Oceanic and Atmospheric Administration (U.S.)
NOBOB	no exchangeable ballast on board
NPDES	National Pollution Discharge Elimination System (issued as a permit)
NRC	National Research Council (U.S.)
NSF	National Science Foundation (U.S.)
NTIS	National Technical Information Service (U.S.)
NTU	nephelometric turbidity unit
NUS	National University of Singapore
PCR	polymerase chain reaction
P.L.	Public Law (enacted by U.S. Congress)
PGI	phosphoglucose isomerase
PGM	phosphoglucose mutase
PPB	Port Philip Bay (Australia)
ppt	parts per thousand (refers to salinity; *see also* psu, ‰)
PSP	paralytic shellfish poisoning
psu	practicality salinity unit
PVA	population viability analysis
QRA	quantitative risk assessment
R&D	research and development
RAPD	randomly amplified polymorphic DNA
RCAC	Regional Citizens Advisory Council (Prince William Sound, AL, U.S.)
RFLP	restriction length polymorphisms
RFP	request for proposal
RI	retention index
RNA	ribonucleic acid
RSHMU	Russian State Hydrometerological University
San-Ship Canal	Chicago Sanitary and Ship Canal
SCOPE	Scientific Committee on Problems of the Environment
SERC	Smithsonian Environmental Research Center (U.S.)
sp.	unknown, but assumed, single species
spp.	several species, genus not identified to individual species
ssp.	subspecies
SST	sea surface temperature
Task Force	generally refers to the ANS Task Force (U.S.)
TBT	tributlyltin
TEMA	Training Education and Mutual Assistance
TEP	transposable element polymorphism
UN	United Nations
UNEP	United Nations Environmental Programme
UNESCO	United Nations Environmental and Cultural Organization
-IOC	-International Oceanographic Commission
U.S.	United States
USA	United States of America (also U.S.)
USACE	U.S. Army Corps of Engineers
USCG	U.S. Coast Guard
USDA	U.S. Drug and Agriculture
USEPA	U.S. Environmental Protection Agency (also EPA)
USFWS	U.S. Fish and Wildlife Service (also called Service)
UV	ultraviolet
UW	University of Washington (U.S.)
VLCC	very large crude carrier
WHO	World Health Organization
wwt	wet weight
WWU	Western Washington State University (U.S.)
y.o.y.	young of the year



Plenary Lectures

'In 1962… it was beyond imagination that we would close this century with a higher level of national and international awareness of bioinvasions in the seas than ever before.'

PLENARY LECTURES

Launching a Counterattack Against the Pathogens of Global Commerce

Secretary of the Interior Bruce Babbitt
U.S. Department of the Interior
1849 C. Street NW
Washington, DC 20240 USA

At the outset, let me congratulate the conference sponsors. You are taking the initiative in a much neglected field. Marine bioinvasions have large consequences for our food supply, our economy, our fishing industry, and human health. These invasions also threaten to degrade and homogenize coastal waters in every corner of the seven seas.

Ten years ago, just after midnight on March 24, the Exxon Valdez crashed into a reef in Prince William Sound. Eleven million gallons of crude oil poured into the pristine waters, casting a shroud over hundreds of miles of shoreline. Television crews on the scene broadcast images of seabirds, otters, and sea lions, slicked black with oil. Those images fixated the world on the dangers of oil spills and led to many new laws and regulations designed to prevent another such tragedy.

Yet the biological spills taking place in Prince William Sound from oil tankers go virtually unnoticed. Just over a year ago the U.S. Fish and Wildlife Service discovered four new species of zooplankton spreading through the Sound, released from ballast water brought by tankers from Southeast Asia via San Francisco Bay. In the long run, these zooplankton, feeding on phytoplankton utilized by the Dungeness crab, may change the Sound more extensively and permanently than any oil spill. And no one has a clue—or a dime—to contribute toward a massive clean up. Were that even possible.

With just four small bioinvasive species, Prince William Sound is relatively lucky, so far. But look farther south, where a prolific and hungry European stowaway has disembarked. The green crab has begun to infest Pacific coastal waters, devouring anything from commercially valuable oysters and clams to barnacles, algae, and snails. And it's not alone: in the northwest nearly forty percent of all aquatic species are exotic, including the *Spartina alterniflora* that has choked Willapa Bay, Washington, and decimated the shellfish industry. This particular invader came from our own Atlantic coastal estuaries.

It gets worse inside the Golden Gate. There, as Interior Secretary, I have worked with environmentalists, irrigation farmers, and cities to get more freshwater down California's main rivers into the Delta and San Francisco Bay. Our goal is to help restore endangered native fish like Chinook salmon and Delta smelt. Only now I know that it is not enough to ensure healthy flows downstream; our real threats may be coming upstream.

Specifically, some 30 species of exotic fish—Asian goby, Atlantic shad, Mississippi catfish, carp, bass, perch, sunfish, goldfish—are swarming the Bay, a veritable marine zoo. An additional 200 bioinvasive species are suffocating native fisheries and helped drive the thicktail chub to extinction. Those are only the documented cases, with new arrivals every ten weeks.

Moving eastward, the Gulf of Mexico is being mugged by the brown mussel, which displaces native mollusks, threatens mangroves, and fouls water intake systems. In the Chesapeake, a hotspot with over 150 documented bioinvasive species, oyster beds now succumb not only to polluted runoff, or overharvest, but to the new arrival of a predatory whelk. I'll let the courageous researchers detail what's happening less than a mile away from here, in North America's oldest coastal port and fishery. It's too depressing for me.

It might be easier if we could simply blame the rest of the world for our troubles. But the truth is that ballast water sloshes both ways. In the early 1980s, a small, luminescent blob called Leidy's comb jelly was pumped aboard ships along our coast, then discharged weeks later into the Black Sea. With no predators, it mushroomed into one of the most intense marine invasions ever recorded, nearly wiping out anchovies and other fisheries.

Zebra mussels exchanged for jellyfish: the maritime law of reciprocity at its darkest.

No place on earth is immune from the twin threats of extinction and alien invaders. In the mid-nineteenth century, when wooden whaling ships crisscrossed the seas in bloody pursuit, Herman Melville pondered "whether Leviathan can long endure so wide a chase and so remorseless a havoc; whether he must not at last be exterminated from the waters." He took note of how we were pushing the buffalo to extinction on the prairies, but dismissed it as impossible on the high seas, rationalizing that, surely, whales could escape to polar regions and thus become "immortal in his species."

Mankind never used to navigate such frozen regions, even though the fouled wooden hulls like Ahab's surely carried a few unwelcome guests. To be sure, bioinvasion from ships is as ancient as the Vikings and the Phoenicians. Even when ballast consisted of stones, dirt, and iron, some exotic bioinvasive species hitchhiked along.

What has changed in the past half-century is the rate of spread, leading to faster, wider, more complex dispersal. We reach remote ports on a weekly, daily, hourly basis—from more diverse trade routes, loaded with much larger volumes of ballast. Discharge of that ballast is nothing more than "point source pollution" and must be treated as such.

Global aquaculture—shrimp farms, public fish hatcheries, commercial oyster beds—also bears responsibility for the spread of epibionts, parasites, predators, and pathogens. So does the aquarium industry: the outbreak of giant African snails in Florida or the *Caulerpa taxifolia* clone, an alga taking over the Mediterranean, originated not in ballast, but from aquarium tanks.

All these sources must be included in our response, both policy and research. But at a more immediate level, we must grasp the root of the problem. That root lies not in isolated incidents, but in scope: the dramatic rate of spread, the increasing vectors of pathogens that carried cholera to Alabama and seem to multiply toxic red tides around the world.

As a very crude rule of thumb, ten percent of invasive species will establish breeding populations; ten percent of those will launch a major invasion. At first, that one percent factor seems negligible. Then, consider how San Francisco Bay is approaching 300 exotics.

Consider also that ships in this century have grown from 3,000 tons to 300,000 tons, and the volume of ballast water slurry—pumped and sucked at 20,000 cubic meters an hour—has kept apace. Faster crossings let more species survive, reproduce, make connections, and take baggage. The fall of trade walls brings global exposure to once quiet seaside ports, and vice versa. In the ballast water of timber cargo ships traveling between Coos Bay, Oregon, and Japan, researchers found 367 species of living animals and plants.

That's a single route. Consider how larger ports, say Norfolk and Baltimore, receive more than 12 million metric tons of foreign ballast water per year, originating in 48 different foreign ports, and 90 percent of them carried live organisms, including barnacles, clams, mussels, copepods, diatoms, and juvenile fish. Worldwide, it is estimated that tens of thousands of ships carry several thousand species daily.

Let me put this another way: In the time it takes me to deliver this speech, two million gallons of foreign plankton will have been discharged somewhere in American waters. We'd better get busy. And fast.

How? What is our response? So far it has been pitiful. Frankly, in light of the economic and ecological devastation, we have been too timid. We restrain ourselves with voluntary guidelines, a scattered approach, and limited unenforced codes. No longer.

In 1997, President Clinton, responding to concerns of scientists like yourselves, asked the Departments of Interior and Agriculture to draft an executive order for his consideration. That order, which is now before the President, will contain two broad initiatives. First, it will require federal agencies to review their existing authorities and activities to reduce the risk of bioinvaders. Second, it will create an interagency working group to draft a plan—possibly including regulatory and legislative change—necessary for a coordinated response to bioinvaders.

What will this look like in practice? I'll sketch the rough outlines in pencil. For there are existing models, and while there is still much to learn, we do know this: the first and best line of defense against bioinvaders is to keep them out in the first place. Period. Not one marine bioinvasive species, after it has taken hold, has ever been eliminated or effectively contained. There is simply no silver bullet. This is a sobering fact. It means our efforts must be focused primarily on prevention. And that, in turn, means effective regulation and enforcement.

In 1990, in response to the damage caused by the zebra mussel in the Great Lakes, the Congress enacted the Nonindigenous Aquatic Nuisance Prevention and Control Act. Among other provisions, the Act now requires ballast water exchange at sea rather than in the Great Lakes system. We should now move toward mandatory ballast exchange for not just the Great Lakes, but for all shipping in all American ports. In California, water districts whose systems are threatened by invaders working their way upstream out of San Francisco Bay have begun to call for ballast water regulation by federal and state agencies.

We need to mount a coordinated research program to better understand the threats posed by alien invaders including fish, crustaceans, mollusks, and pathogens and to guide programs of prevention and control. Perhaps we can find economical and safe means to decontaminate ballast water and sediments *in situ*. The Agricultural Research Service and APHIS in the Department of Agriculture, the Coast Guard, the National Oceanic and Atmospheric Administration, and the Biological Research Division of the United States Geological Service should mount a coordinated effort to understand agricultural threats, threats to natural ecosystems, and new methods of prevention and control.

Does this mean our agency budgets must catch up to, and keep pace with, the ecological devastation they target? Yes, because that devastation is economic as well. Vast as they are, the Great Lakes are easy to manage compared to the task ahead, and but offer few unqualified success stories. Yet, the results there make a strong case for why an aggressive, well-funded public response to bioinvasion is well worth the expense and effort.

We spend several million dollars a year sterilizing, catching, poisoning, and putting up barriers to suppress the sea lamprey. Well, it's still there and it may never go away. But for every dollar we invest, the Great Lakes earn $30.25 in increased fisheries revenue. Your stock portfolio should perform as well.

Global cooperation is an imperative. Our joint efforts with Canada on the Great Lakes provides an example. Two global entities—the Convention on Biological Diversity and the World Trade Organization—should play a major role in international cooperation. The Convention on Biological Diversity is the place to begin, and indeed preliminary discussions pursuant to Section 8 of the Biological Diversity Treaty are underway. Those discussions underline the need for Senate ratification of the Biodiversity Treaty. The World Trade Organization must also take an active role in the movement to develop and harmonize regulations in this area.

Let me conclude on a cautious note of hope. You've all heard that the flip side of crisis is opportunity? Well, the Exxon Valdez crash gave us such an opportunity. It led Congress to require double-hulled tankers and stiffen training, navigation, and technology within the shipping industry. It prompted state, federal, and private agencies to establish habitat restoration programs and undertake comprehensive research on the North Pacific ecosystem.

We face an even greater opportunity now. The time is at hand for scientists, policy makers, industry, and the public to join together for an intensive coordinated counterattack on the threat of bioinvasions. You have initiated that process, and we in the public sector must now respond in kind.

PLENARY LECTURE

Quo Vadimus Exotica Oceanica? Marine Bioinvasion Ecology in the Twenty-First Century[1]

James T. Carlton[2]
Maritime Studies Program
Williams College, Mystic Seaport
P. O. Box 6000
75 Greenmanville Avenue
Mystic, CT 06355 USA

Key words: invasion ecology; historical perspective, evolutionary consequence

These are heady times in the world of marine bioinvasions, as witnessed by the gathering of over 200 persons here this morning. In January 1989, such a congregation would have been inconceivable. A new journal, *Biological Invasions*, is being launched this fall[3] that will serve as a platform for invasion science. And as we will hear tomorrow morning, a Presidential Executive Order on exotic species will be released 10 days from now.[4]

Despite this remarkable blossoming of interest, marine invasion science is a young science and challenges abound. The depth and breadth of the profound alteration to marine communities by invasions in the oceans remain, in large part, unknown and thus vastly underestimated. Invasions have occurred not only in estuaries and harbors but also in exposed rocky intertidal shores, coral reefs, mangrove communities, open continental shelves, and the deep sea. Indeed, it may be that, at the least, no shallow-water temperate or tropical marine community in the world now remains untouched by human-mediated bioinvasions, but that hypothesis remains to be tested. This morning I will suggest ways in which we need to be more rigorous, more refined, and more aggressive in our grasp of the temporal and spatial scales of the ecology of invasions in the seas.

We need to be clearer and less hesitant about the *scale* of invasions that must have occurred prior to the 19th century. We need to wash away the salty cloud of antiquity that obscures the modern history of marine communities. It is impossible to overemphasize the poor picture that we have of the nature of the ocean's biota only 100 or 200 years ago. Ships with organisms on and in their hulls and in their rock and sand ballast have moved species around the world since at least the 14th century. But we too often think of invasions as beginning, more or less, in the 19th century. If in the 300-year period between 1500 and 1800, only three species a year were spread around the world (the number, of course, may be much greater), then nearly 1000 coastal species of marine organisms that are now regarded as naturally cosmopolitan are in fact "simply" early introductions.

This estimation is not a mere historical curiosity: an understanding of the number and identity of pre-19th century invaders would profoundly impact both our understanding of modern marine community ecology and our basic assumptions about and interpretation of the natural diversity, biogeography, and rate of evolution in the seas. In terms of invasion biology itself, we can ill afford to seek patterns such as the relative susceptibility or resistance of different regions to invasions, or attempt to define guilds or clades of invaders that may be more or less likely to invade, if we persist in ignoring more than 75% of the modern invasion history in the ocean. It follows that at least some of the hundreds of

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[1]This paper is the conference opening Plenary Lecture, with modifications, as presented on January 25, 1999. As such the lecture format is retained here and no references are cited in the text. However, an extensive and partially annotated bibliography of marine bioinvasions literature is presented at the end.

[2]Corresponding author; telephone: 860-572-5359; fax: 860-572-5329; email: jcarlton@williams.edu

[3]The first issue of *Biological Invasions* was published in October 1999.

[4]Secretary of the Interior Bruce Babbitt spoke on Tuesday morning, January 26, 1999. President William Clinton's Executive Order was released in Washington, D.C. on Wednesday, February 3, 1999.

pre-1800 invasions are likely to be the common, if not abundant, species where they were introduced long ago, and thus perhaps some of the most important organisms regulating community structure.

But which ones are they? How startled would we be if we could look back at some of our "best known" shallow marine communities—kelp beds, rocky shores, and coral reefs—and find that keystone species were absent in 1599 or 1699 or 1799? Why is it that we cannot tell if a species has been present for 100 years or 100,000 years, or are we not paying attention to what evolution is telling us? Should not the presence of certain clades or lineages in certain marine communities that appear to have evolutionary roots elsewhere—such as mussels of the northern genus *Mytilus* in the southern hemisphere—not surprise us? By using morphological, genetic, historical, paleontological, archeological, and other evidence we may be able to begin to look below this cryptic invasion iceberg:

- The ship-boring isopod, *Sphaeroma terebrans*, possibly native to the Indian Ocean, appeared in the Caribbean Sea or northwestern South American coast sometime in the 19th century. It bores into and destroys the seaward root tips of mangroves. It may have reset the lower intertidal limit, and thus the history of outward propagation, of the mangrove ecosystems of the tropical western Atlantic Ocean. It passes without notice in the literature of invasions.
- The Asian seasquirt, *Styela plicata*, was carried to the North American Atlantic coast perhaps two or more centuries ago and became one of the hallmark species in the concept of multiple stable state communities. The species falls outside of our general view of marine invasions.
- And, as hinted at above, the northern hemisphere mussels, *Mytilus galloprovincialis* and *Mytilus edulis*, were carried as fouling organisms by ships to the southern hemisphere for centuries, and there given a plethora of local names.

These are merely a few examples. We need iconoclastic invasion ecology. We need to question the "assumption of naturalness." In fact, the modern historical geography of thousands of coastal species of planktonic and benthic organisms remains unknown. Thus, such species must be removed from the category of "native until shown otherwise", and instead be placed in the rapidly growing category of cryptogenic species. Did the giant kelp, *Macrocystis pyrifera*, for example, now found in both the southern and northern hemispheres, and taken to be a classic textbook example of natural bipolarity, of necessity naturally occur in both hemispheres? Or could *Macrocystis* have been carried on the hulls of Spanish ships—since it can be a fouling organism—from the North Pacific Ocean as early as the 1500s? The early footprints of human activities across the oceans became the ship-prints of the world and yet we have largely fallen virtually silent about the potential for such early invasions.

Why be concerned about earlier invasions? Why should we care about invasions of 100 or 200 or 300 years ago? There is the potential value to a greater resolution of global invasion patterns as noted earlier, but beyond that, are not such early invasions "naturalized"? Aren't they "integrated" into the community? Isn't the community "in equilibrium" by now? That we should invoke naturalization, integration, and equilibrial processes underscores another arena of ambiguity in our thinking in invasion ecology. The word "naturalized" was introduced in 19th century botanical literature to mean "reproducing in the wild"—not to mean a remarkably rapid conversion over a few decades or centuries to mirror the integration that native species achieve over tens or hundreds of thousands of years. The answer is that we cannot pronounce invasions of past decades or centuries as being well integrated: there are by and large no data to support such concepts. Simply becoming abundant and widespread is not ecological integration. Simply eating or being eaten is not ecological integration. Integration implies a vast suite of interrelated functions, rather than a functional response along one or a few axes, such as predation, space utilization, or competition. We know little about the rate of these integrative processes in invasion ecology. It may be that in terms of evolutionary processes and community integration, the European periwinkle, *Littorina littorea*, which arrived on the shores of Atlantic North America in the early 19th century, arrived only "yesterday."

Several other famous myths in invasion science are worth noting. One is that "everything that could have been introduced would have been introduced by now." This is not simply an image in the mind of a ship's captain who is contemplating 100 years of ballast water movement, nor is it the imagination of the hopeful commercial entrepreneur. Rather, we learn that grant proposals to investigate dispersal vectors are turned down even today by a hand-wave of such statements. That everything has not been introduced by now is demonstrated every day. Were it so, all the ship fouling organisms of Europe that could survive and reproduce in American waters would be here by now.

Another myth is the following: "Invasions are part of nature. They always happen. Human-mediated invasions are only speeding up what would happen eventually." This statement is, of course, also not true. Most—perhaps all?—of the invasions now occurring would not only *not* happen sooner or later, they would *never* happen. Species are not "eventually" exchanged by natural processes between San Francisco Bay and the Black Sea, species do not "eventually" find their way in ecological time between Australia and England, and species do not "eventually" move between Argentina and Puget Sound. The fact that over geological time there is a predictable natural ebb and flow of biota along coastlines and within or between ocean basins, as barriers dissolve or are created, has little to do with the past several centuries of human-mediated alterations to the oceans.

Another myth is that phytoplankton have been and are, with a few exceptions, not part of the modern invasion story. Since just the reverse may be true, the existence of this illusion may have had profound impacts on our ability to understand the scale of invasions and invasion processes—and indeed may have caused us to be several to many decades behind in ballast management, relative to one major reason why harmful algal (toxic phytoplankton) blooms may have mushroomed in the past quarter century.

This sense of size-mediated invasion is a huge bias in our science. We recognize introductions most often among the charismatic megainvasions—clams, crabs, seastars, large seaweeds. We recognize some invasions among smaller organisms—copepods, amphipods, bryozoans, hydrozoans, and so forth. But when we get to very small organisms—the diatoms, the dinoflagellates, the pfiesterias, the brown tides (aureococuses)—we simply say, with rare exception, "no invasions here." The transparency of recognizing invasions only by size could not be clearer: not one professional phytoplankton ecologist, biogeographer, or systematist is speaking at or attending this meeting, although we will hear again and again about phytoplankton and ballast water from other workers. Ironically, one of the very first invasions to be recognized as being due to ballast water was the appearance of an Asian diatom in Europe in the early 1900s. We presume that such invasions have continued steadily, if largely unreported, around the world since.

We need, then, to increase the rigor of our overall thinking about invasions. And this rigor needs to be applied to every aspect of our science.

We need to pay more attention to the many biases in making "species lists" of marine invasions if we are to do more sophisticated comparisons. Our lists tend to be extraordinarily sensitive to the history of local taxonomic interest or current local available expertise, generating lists of very different emphases.

We must be more rigorous and focused in our thinking about whether introduced species have an "impact" or not. In terms of ecological and evolutionary science *every* invasion has an impact. The definition—the nature and extent—of impact is the question, not whether an impact did, did not or will occur. The extent to which invasions alter the diversity, abundance, distribution or phenology of previously existing species can be a measure of impact. *Who* is concerned—ecologists, the public, or politicians—about the type and scale of impact is a different question, but perhaps the question more often meant. *Why* we are concerned—for example, whether the invasion changes the ability of humans to use the oceans as a resource—is yet another question still. Because impact is a long sliding scale we would do better to abandon the concepts of the "Top 10 Invaders" or "Worst 100 Invaders." Rather, under the assumption that all invasions alter *some* aspect of the community mesh in which they find themselves embedded, we should focus on the *types and scales* of impacts that invasions have, rather than implying that only some small percent of invasions actually lead to impacts or cause "problems."

Perhaps there is no more important arena where we need to refine our thinking than in the field of prediction. The interface between the public and science insists on prediction, whether it is hours after an oil spill or hours after the discovery of a new introduced species. We are also interested in prediction in our science in and of itself, whether or not there are sociopolitical pressures, or questions from the press. We are thus now engaged in a great search—we seek the Predictive Invasion Grail. We desire more than ever before to be able to predict who will invade, when invasions will occur, and what the impacts of the invasion will be. Thousands of invasions have occurred and yet, like the weather, it appears that we cannot predict the next invasion.

Is it all too stochastic? Can we evolve more rigorous models that better resolve the invasions sweepstakes—the roulette nature of invasions? In predicting who will invade is it ever possible to point to some species that will forever be unsuccessful invaders? Or is the match between an invading species' biology and the new prospective environment, in fact, a shapeshifter model of invasion
ecology, where at times it appears to be a matter of try-

ing to fit a round invasion into a square environment—but at other times the round invasion slips smoothly in?

Where do we look to unlock some of these questions? I suggest that we look more closely at those invasive species which, despite numerous apparent opportunities for dispersal, inoculation, and establishment, and which for centuries have failed to become introduced, suddenly become successful colonists. Rather than focusing on those species that *appear* to have permanently failed to invade, we should look more carefully at species that have failed to invade for centuries and then do so. These are the *delayed invaders*. Is it in these species that we can find answers to some of the long-term mysteries of those processes that regulate invasions?

An example is the five-centimeter-long European seasquirt, *Ascidiella aspersa*, a translucent, recumbent filter feeder in shallow fouling communities. This ascidian, common on hard bottoms throughout western and northern Europe was, we may speculate, on the bottoms of hundreds or thousands of vessels coming to America for 500 or more years. It first appeared in fouling communities about 1985 between Cape Cod (Massachusetts) and Long Island Sound, in southern New England, long after such communities would appeared to have been "filled" by previous ascidian invaders such as *Styela clava, Molgula manhattensis, Ciona intestinalis, Botrylloides* sp. and *Botryllus schlosseri*, which combined formed 100 percent cover in fouling communities prior to the arrival of *Ascidiella*.

Up until 1985, we might have chosen *Ascidiella* as an example of a permanently unsuccessful invader, and sought compelling reasons as to why it had failed to become established in North America after half-a-millennium of presumed transport. Why then did it invade in the 1980s and not the 1880s or 1780s or 1680s? Invasion lag-time analysis (ILTA) remains virtually untouched as a field of investigation, and yet may be a singularly important key to unlocking invasion processes.[5] This then is the *Paradox of Ascidiella,* a puzzle that must be solved. If we were to pay more attention to these creatures—the ascidiellas of the world—invasion science may move forward all that much faster.

We know—or we think that we know—some of the roads that we must explore when considering ILTA: were there changes in the donor region or changes in the recipient region? Did invasion windows open or were there unusual inoculation episodes? Did the dispersal vector change in some way? These are complicated phenomena, but complicated is not the same as unknowable or unpredictable. The answers to each question have striking implications relative to the ecology, biology, and evolutionary history of invaders; each question also opens the door to many more questions. We have to pursue interactive pathways and *integrative invasion ecology* much more robustly. Why do we not find, in invasion biology, more examples of subtle webs such as the one that links spirochete bacteria, acorn production, white-footed mice, black-legged ticks, white-tailed deer and climatic models all in one intricate mesh to predict the potential for Lyme disease? Are we not looking? The European marine fauna continues to dribble and leak into and invade North America over a long blue line that fades vaguely into the past 500 years and yet we are surprised at every new invasion. Is this because we rarely seek out the vast arrays of physical and chemical and oceanographic and biological data now available for coastal waters in order to detect a web of environmental change—and then combine such webs with detailed vector data and our knowledge of species' biology and ecology—that would anticipate new invasion opportunities?

For management purposes, predictive marine invasion science is now of only limited value. It may of course improve considerably. As an example, we cannot, today, look at what is inside the ballast water of a ship and imply that the contents are of little or no concern if a few recognized pests on a short list are absent from that tank or from the region from which the ballast water was drawn. Noting the absence of a few target species does not make the ship "safe" or "certified" or "clean." It may remain full of dozens or scores of species, like the ascidiellas of Europe or the potamocorbulas of China or the hemigrapsuses of Asia, of which we can predict little about whether they can become established outside their native regions, or, if they do, what impacts they may have.

Despite this, we must clearly get more serious about our regulatory framework. Whether it is ballast water, whose scale is so profound that perhaps it is not 3000 species a day being carried around the world but five times that, or whether it is ships' sea chests, or whether it is the live Mediterranean mussels, Chilean mussels, and New Zealand mussels that can be purchased globally in seafood stores, or whether it is the now web-based purveyors of marine life—such as one company whose website claims it to be the "World's Largest Marine Livestock Retailer: 1000s of species [of] fish, corals, clams, [and other] invertebrates. We ship to 65 coun-

5. ILTA is distinct from lag times in population "explosion" (Crooks and Soule 1999).

tries."—whichever vector it may be, we remain with fundamental regulatory vacuums. We need to invest in prevention far more than we have, following the same philosophy that drives us to close the windows in a rainstorm before we start mopping—or at least while we are mopping—up the floor.

In closing, a common question is that if the vectors that we see today are indeed so fluid and so effective in transporting species, why do we not see more invasions? In part, we have already answered this: if we see invaders, they tend to be the larger species, and thus we tend to ignore the greater number of smaller taxa. But even more important is that despite the surge in interest in invasions, there are in fact fewer workers every passing year who are exploring the shore and fewer still who can identify what is found. There is a profound demise in the sheer pride of knowing about the natural world and about being able to identify its contents—as if such knowledge was mutually exclusive with being an experimental ecologist or a molecular geneticist or a cell biologist. With the exception of a relatively few sites around the world, our best eyes are not those of marine ecologists but those of the interested public who seek out experts to report novelties—and that puts most of the shores of the world outside our view. Bait fishermen called our attention to the Asian shore crab (*Hemigrapsus sanguineus*) in Long Island Sound, it took an amateur naturalist to alert the scientific world to the invasion of an abundant Caribbean barnacle (*Chthamalus proteus*) to the Pacific Islands, and another to discover the Japanese shore crab (*Pachygrapsus fakaravensis*) in Hawaii, and the public knew about zebra mussels (*Dreissena polymorpha*) in the Great Lakes at least a year before scientists found them. The answer to the question of "why are there not more invasions?" is that there are without doubt many more invasions than we have been recording. The demise in the knowledge of systematic biology and natural history is a critical hole to patch if we are to gain a more accurate picture of the scale and rate of change in coastal ecosystems.

In September 1962, I was introduced to the world of exotic marine organisms by unceremoniously stepping on what I was to learn, a few days later, was a small colony of exotic tubeworms in a lagoon off San Francisco Bay.[6] It was beyond imagination at that time that we would close this century with a higher level of national and international awareness of bioinvasions in the seas than ever before. This first conference on marine bioinvasions is very appropriately set on the edge of the 21st century. We are witnessing a vastly changing paradigm.

6. The southern hemisphere serpulid polychaete worm *Ficopomatus enigmaticus,* then known as *Mercierella enigmatica*, on the small beach on Adams Point, in Lake Merritt, in Oakland, California.

Annotated References on Marine Bioinvasions: A Highly Selective Bibliography

The following papers, and the papers they cite in turn, provide an entrée to the literature on marine introduced species. About 1,600 additional references are found in Carlton (1979). I use the hedgpethian method (Ricketts et al. 1968) of annotation here; thus, annotations are often telegraphic, not full sentences, leave out verbs and the occasional noun, and are often only understood as juxtapositions to the title of the paper itself.

Agard, J., R. Kishore, and B. Bayne. 1992. *Perna viridis* (Linnaeus, 1758): first record of the Indo-Pacific green mussel (Mollusca: Bivalvia) in the Caribbean. *Caribbean Marine Studies* 3:59-60.
See Hicks and Tunnel 1993.

Aguirremacedo, M.L. and C.R. Kennedy. 1999. Diversity of metazoan parasites of the introduced oyster species *Crassostrea gigas* in the Exe Estuary. *Journal of the Marine Biological Association of the United Kingdom* 79:57-63.

Allen, F.E. 1953. Distribution of marine invertebrates by ships. *Australian Journal of Marine and Freshwater Research* 4:307-316.
A classic paper outlining the principles of the subject.

Alpine, A.E. and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946-955. *The Asian clam, Potamocorbula amurensis, plays an important role, along with other introduced bivalves, in controlling water column productivity in San Francisco Bay.*

Asakura, A. 1992. Recent introductions of marine benthos into Tokyo Bay (review): process of invasion into an urban ecosystem with discussion on the factors inducing their successful introduction. *Journal of the Natural History Museum and Institute (Chiba, Japan)* 2:1-14 (English abstract, pp. 13-14).
A useful discussion of the introduction into Japan of the polychaetes Hydroides elegans and Ficopomatus enigmaticus, the bryozoans Zoobotryon pellucidum and Bugula californica, the bivalves Limnoperna fortunei, Perna viridis, Mytilopsis sallei, and Mytilus galloprovincialis, the slipper limpet snail Crepidula onyx, the barnacles Balanus improvisus and B. eburneus, the crabs Carcinus aestuarii (as C. mediterraneus) and Pyromaia tuberculata, and the ascidians (sea squirts) Molgula manhattensis and Ciona intestinalis.

Bastrop, R., K. Jürss, and C. Sturmbauer. 1998. Cryptic species in a marine polychaete and their independent introduction from North American to Europe. *Molecular Biology and Evolution* 15:97-103.
Two species of the American worm, Marenzelleria, have been introduced to northern Europe; see Essink and Schottler (1997).

Bellan-Santini D., P.M. Arnaud, G. Bellan, and M. Verlaque. 1996. The influence of the introduced tropical alga *Caulerpa taxifolia* on the biodiversity of the Mediterranean marine biota. *Journal of the Marine Biological Association of the United Kingdom* 76:235-237.

Benech, S.V. 1978. Ocean transport of a community of the grapsid crab *Plagusia dentipes* (de Haan, 1833). *Crustaceana* 35:104.
A rare contribution to the role of semisubmersible self-propelled exploratory platforms in the transoceanic dispersal of marine life.

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.
The players are the native snails, Assiminea californica and Littorina subrotundata, and the introduced Atlantic snail, Ovatella myosotis: "the successful establishment of this Atlantic snail in the Pacific Northwest did not arise at the expense of native species."

Berman, J., L. Harris, W. Lambert, M. Buttrick, and M. Dufresne. 1992. Recent invasions of the Gulf of Maine: three contrasting ecological histories. *Conservation Biology* 6:435-441.
The insertion into marine communities in the Gulf of Maine (that body of water between Cape Cod in Massachusetts and Canada) of three recent invaders is considered: the seasquirts (ascidians), Styela clava and Botrylloides diegensis, and the bryozoan, Membranipora membranacea.

Bertness, MD. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* 65:370-381.
An experimental demonstration of the impact of the introduced European snail, Littorina littorea, on low energy habitats of the southern New England coast: the outward growth of the Spartina marsh is compromised by Littorina eating the shoots and rhizomes of the marsh grass, while at the same time the grazing activities of the snail foreword of the marsh prevented the accumulation of soft sediments creating more exposed hard substrate (onto which the marsh cannot grow).

Bertness, MD., P.O. Yund, and A.F. Brown. 1983. Snail grazing and the abundance of algal crusts on a sheltered New England rocky beach. *Journal of Experimental Marine Ecology and Biology* 71:147-164.
More experiments on the ecological effects of the introduced European snail, Littorina littorea.

Beukema, J.J. and R. Dekker. 1995. Dynamics and growth of a recent invader into European coastal waters: the American razorclam, *Ensis directus*. *Journal of the Marine Biological Association of the United Kingdom* 75:351-362.

Boalch, G.T. 1994. The introduction of non-indigenous marine species to Europe: planktonic species. pp. 25-27 In: Boudouresque *et al*. 1994 (see below).
Professor Boalch has been one of the very few phytoplankton workers to recognize the introduction of diatoms and dinoflagellates by

ballast water.
Boudouresque, C.F., F. Briand, and C. Nolan (eds.). 1994. Introduced species in European Coastal Waters. *European Commission (Luxembourg), Ecosystems Research Report* 8:1-111 (EUR 15309) (ISBN 92-826-6727-8).
A collection of 13 papers in English and French, originating from a symposium held in Monaco in early March 1993; nine papers provide histories of introductions. The color cover appears to show the spread of the Japanese brown seaweed, Sargassum muticum, across all of the European waters into the Mediterranean in compelling yellow, green, purple, and red colors, in 1966 (first report in France), 1977 (north and south of the English channel), 1988 (much of the rest of western and northern Europe), and 1992 (Portugal, southern Spain, and into the Mediterranean)— that is, every ten years, except for the last date, when the picture was produced for the symposium. No explanation of the cover appears in the book: in fact, it is solely a computer-based projection of the spread of Sargassum, and has no bearing upon actual records! (Inger Wallentinus, pers. comm.).
Blackstone, N.W. 1986. Variation of cheliped allometry in a hermit crab: the role of introduced periwinkle shells. *Biological Bulletin* 171:379-390.
The introduced periwinkle Littorina littorea in New England and its utilization by the native hermit crab Pagurus longicarpus (see also Blackstone and Joslyn 1984).
Blackstone, N.W. and A.R. Joslyn. 1984. Utilization and preference for the introduced gastropod *Littorina littorea* (L.) by the hermit crab *Pagurus longicarpus* (Say) at Guilford, Connecticut. *Journal of Experimental Marine Ecology and Biology* 80:1-9.
Bouchain, J., E. Pradier, and M.T. L'Hardy-Halos. 1999. The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St. Malo area: Morphology and growth of the sporophyte. *Botanica Marina* 42:71-82.
This seaweed was intentionally planted on the Atlantic coast of France for mariculture purposes under the initial proclamation that it could not reproduce or spread. It did and it did.
Brenchley, G.A. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Marine Ecology Progress Series* 9:255-262.
The introduced species are the European periwinkle snail Littorina littorea and the European shore crab Carcinus maenas.
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.
Of native Ilyanassa obsoleta by introduced Littorina littorea. See also the work of Whitlatch and Obrebski (1980) and Race (1982).
Buttermore, R.E., E. Turner, and M.G. Morrice. 1994. The introduced northern Pacific seastar *Asterias amurensis* in Tasmania. *Memoirs of the Queensland Museum* 36:21-25.
There is little doubt that this seastar invasion finds its roots in Japan; the common name reflects political necessities. Millions upon millions of this omnivorous seastar have become established in the Derwent estuary of southern Tasmania, Australia. It has since spread to mainland Australia.
Calvo-Ugarteburu, G. and C.D. McQuaid. 1998. Parasitism and introduced species: epidemiology of trematodes in the intertidal mussels *Perna perna* and *Mytilus galloprovincialis*. *Journal of Experimental Marine Biology and Ecology* 220:47-65.
Calvo-Ugarteburu, G. and C.D. McQuaid. 1998. Parasitism and invasive species: effects of digenetic trematodes on mussels. *Marine Ecology Progress Series* 169:149-163.
The native mussel, Perna perna, in South Africa is commonly infected by digenetic trematodes while the introduced Mediterranean mussel, Mytilus galloprovincialis, lacks trematodes; this may lend Mytilus a competitive advantage.
Carlton, J.T. 1965. Lake Merritt fauna. *News of the Western Association of Shell Clubs (Northern California Malacozoological Club)* 6(1):N25-N26.
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 pp.
A species index was prepared by Todd Miller and John Chapman in 1999 and posted at the following site: http://www.hmsc.orst.edu/library/carlton.html
Carlton, J.T. 1982. The historical biogeography of *Littorina littorea* on the Atlantic coast of North America, and implications for the interpretation of the structure of New England intertidal communities. *Malacological Review* 15:146.
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.
A monographic review of ballast water prior to most of the world's studies on ballast water.
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.
The title of this paper plays off the famous monumental mid-20th century tome, "Man's Role in Changing the Face of the Earth", although a double entendre may have been intended, as few women are responsible for the current state of the oceans.
Carlton, J.T. 1992. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. pp.13-45 In: Rosenfield, A. and R. Mann (eds.). *Dispersal of Living Organisms into Aquatic Ecosystems.* Maryland Sea Grant Publication, College Park, Maryland. 471 pp.

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. 1994. Biological invasions and biodiversity in the sea: the ecological and human impacts of nonindigenous marine and estuarine organisms. Keynote Address. pp.5-11 In: *Nonindigenous Estuarine and Marine Organisms (NEMO). Proceedings of the Conference and Workshop, Seattle, Washington, April 1993.* U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of the Chief Scientist. (September 1994). Government Document No. C55.2:N73, Government Printing Office No. 0208-C-04. 125 pp.

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

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

Carlton, J.T. 1996. Pattern, process, and prediction in marine invasion ecology. *Biological Conservation* 78:97-106.
A table herein presents a series of six hypotheses as to why invasions occur when they do.

Carlton, J.T. (ed.). 1998. *Ballast Water: Ecological and Fisheries Implications.* International Council for the Exploration of the Sea (ICES) Cooperative Research Report No. 224. 146 pp.
From a September 1995 symposium in Aalborg, Denmark.

Carlton, J.T. 1999. The scale and ecological consequences of biological invasions in the world's oceans. pp. 195-212 In: Sandlund, O.T., P.J. Schei, and Å. Viken (eds.). *Invasive Species and Biodiversity Management.* Kluwer Academic Publishers, Dordrecht, Netherlands. 431 pp.
The giant kelp (brown seaweed) Macrocystis pyrifera is used as an example of a possible southern hemisphere invasion of centuries ago, what might have occurred on the bottoms of 18th-century ships is further explored, and estimates are made of the potential number of invasions that could have occurred between 1500 and 1800. The entire book, less than 20 mm thick, costs US$255, making it largely unavailable to most workers.

Carlton, James T. 1999. Molluscan invasions in marine and estuarine communities. *Malacologia* 41: 439-454.
Includes a summary of the names in the southern hemisphere by which the northern hemisphere fouling mussels, Mytilus edulis and Mytilus galloprovincialis, go, as well as an argument that more than a few shipworms may owe their modern distribution to the history of wooden shipping.

Carlton, J.T. and J.B. Geller. 1993. Ecological roulette: The global transport of nonindigenous marine organisms. *Science* 261:78-82.
The results of sampling the ballast water in 159 ships arriving in Coos Bay, Oregon, from Japan: 367 species of animals, plants, and protists are reported, thus having implications for the global history, biogeography, systematics, and ecology of many phyla. In Table 1 of this paper, the number of species shown for Urochordata should be 6, not 10 (however, the total of 367 remains correct). Professor Les Watling of the University of Maine (pers. comm.) has identified 4 additional species of cumaceans from these samples, and Pierce et al. (1997) report an additional 31 species of tintinnids (in addition to the 2 previously reported), making 402 species recorded to date from these samples.

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.
What survived on experimental fouling panels attached to a replica of Sir Francis Drake's Golden Hinde as it sailed down the American Pacific coast. The vessel sailed between four bays at slow (3.5-4 knots) speeds, resided in each bay for about 30 days, and spent one to three days in the open ocean between ports. All common fouling species survived the open sea voyages; in one port, the vessel settled onto the harbor floor, and several entrained benthic organisms were transported almost 400 km to the next port.

Carlton, J.T. and K. Richardson. 1995. *International Council for the Exploration of the Sea Code of Practice on the Introductions and Transfers of Marine Organisms, 1994. Preamble and a Brief Outline of the ICES Code of Practice, 1994.* International Council for the Exploration of the Sea, Copenhagen, Denmark. iii+5 pp.
A bilingual edition of the famous ICES Code of Practice, which sets forth principles to be followed when contemplating the intentional movement of aquatic organisms. Available by writing to the International Council for the Exploration of the Sea (ICES), Palaegade 2-4, 1261 Copenhagen K, Denmark.

Carlton, J.T. and M.H. Ruckelshaus. 1997. Nonindigenous marine invertebrates and algae. pp. 187-201 In: Simberloff, D., D.C. Schmitz, and T.C. Brown (eds.) *Strangers in Paradise. Impact and Management of Non-Indigenous Species in Florida.* Island Press, Washington, D.C. and Covelo CA. 467 pp.
Wherein the argument is developed that the boring isopod Sphaeroma terebrans (= S. destructor) is native to the Indian Ocean.

Carlton, J.T., D.P. Cheney, and G.J. Vermeij (eds.). 1982. A minisymposium and workshop. Ecological effects and biogeography of an introduced marine species: the periwinkle, *Littorina littorea*. Abstracts of papers presented at the *Littorina* Minisymposium and Workshop. First North American Symposium on *Littorina*, 28-30 August 1981, Nahant. *Malacological Review* 15:143-150.

Carlton, J.T., D.M. Reid, and H. vanLeeuwen. 1995. *Shipping Study. The Role of Shipping in the Introduction of Non-indigenous Aquatic Organisms to the Coastal Waters of the United States (other than the Great Lakes) and an Analysis of Control Options.* The National Sea Grant College Program/Connecticut Sea Grant Project R/ES-6. Department of Transportation, United States Coast Guard, Washington, D.C. and Groton, Connecticut. Report Number CG-D-11-95. Government Accession

Number AD-A294809. xxviii + 213 pp. and Appendices A-I (122 pp.).
The cover bears the date April 1995, but the report contains no new information after April 1993, when it was first submitted to the United States Coast Guard.

Carlton, J.T., J.K. Thompson, L.E. Schemel, and F.H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Marine Ecology Progress Series* 66:81-94.

Castric-Fey, A., C. Beaupoil, J. Bouchain, E. Pradier, and M.T. L'Hardy-Halos. 1999. The introduced alga *Undaria pinnatifida* (Laminariales, Aliraceae) in the rocky shore ecosystem of the St Malo area: morphology and growth of the sporophyte. *Botanica Marina* 42:71-82.
See the comments under Bouchain et al. 1999.

Castric-Fey, A., C. Beaupoil, J. Bouchain, E. Pradier, and M.T. L'Hardy-Halos. 1999. The introduced alga *Undaria pinnatifida* (Laminariales, Aliraceae) in the rocky shore ecosystem of the St Malo area: growth rate and longevity of the sporophyte. *Botanica Marina* 42:83-96.

Chapman, J.W. 1988. Invasions of the northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. *Journal of Crustacean Biology* 8:364-382.
A new species of amphipod, Corophium alienense, is described from San Francisco Bay; on the basis of morphology it is regarded as native to southeast Asia, where it remains unknown.

Chapman, J.W. and J.T. Carlton. 1991. A test of criteria for introduced species: the global invasion of the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 11:386-400.
A Japanese isopod redescribed in the late 19th century from San Francisco Bay as Synidotea laticauda.

Chapman, J.W. and J.T. Carlton. 1994. Predicted discoveries of the introduced isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 14:700-714.

Chew, K.K. 1990. Global bivalve introductions. *Journal of the World Aquaculture Society* 21:9-22.

Chu, K.H., P.F. Tam, C.H. Fung, and Q.C. Chen. 1997. A biological survey of ballast water in container ships entering Hong Kong. *Hydrobiologia* 352:201-206.

Clark, P.F., P.S. Rainbow, R.S. Robbins, B. Smith, W.E. Yeomans, M. Thomas, and G. Dobson. 1998. The alien Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura), in the Thames catchment. *Journal of the Marine Biological Association of the United Kingdom* 78:1215-1221.
The neoestablishment of Eriocheir in England, perhaps related to drought patterns.

Cohen, A.N. and J.T. Carlton. 1995. *Biological Study. Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of the San Francisco Bay and Delta.* A Report for the United States Fish and Wildlife Service, Washington, D.C., and The National Sea Grant College Program, Connecticut Sea Grant, NTIS Report Number PB96-166525. 246 pp.+Appendices.
A monographic account of the introduced species of the fresh, brackish, and marine waters of the San Francisco Bay and Delta in central California. Available at the following web sites: http://elib.cs.berkeley.edu/TR/ELIB:701 and http://www.nfrcg.gov/nas/sfinvade.htm (missing Figures 1 and 8 and Tables 1 and 9).

Cohen, A.N. and J.T. Carlton. 1997. Transoceanic transport mechanisms: the introduction of the Chinese mitten crab, *Eriocheir sinensis,* to California. *Pacific Science* 51:1-11.
As with the European shore crab, Carcinus maenas, a plethora of dispersal mechanisms are available to Eriocheir.

Cohen, A.N. and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555-558.
An average of one new invasion occurred in San Francisco Bay, California, every 14 weeks between 1961 and 1995; a total of 234 non-native species are reported. There are more there now.

Cohen, A.N., J.T. Carlton, and M.C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab, *Carcinus maenas,* in San Francisco Bay, California. *Marine Biology* 122:225-237.
Carcinus can move around the world in the 1990s by an embarrassing variety of human-mediated mechanisms, hampering the ability to decrease the probability of such invasions.

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

Cordell, J.R.R. and S.M. Morrison. 1996. The invasive Asian copepod *Pseudodiaptomus inopinus* in Oregon, Washington, and British Columbia estuaries. *Estuaries* 19:629-638.

Cory, R.L. 1967. Epifauna of the Patuxent River estuary, Maryland, for 1963 and 1964. *Chesapeake Science* 8:71-89.
Three of the seven "most productive" species are introduced (the hydroid Cordylophora lacustris and the bryozoan Bimeria franciscana) or cryptogenic (the seasquirt Molgula manhattensis).

Critchley, A.T. 1983. *Sargassum muticum*: a taxonomic history including world-wide and western Pacific distributions. *Journal of the Marine Biological Association of the United Kingdom* 63:617-625.

Crooks, J.A. 1998. Habitat alteration and community level effects of an exotic mussel, *Musculista senhousia*. *Marine Ecology Progress Series* 162:137-152.
An Asian mussel introduced to California.

Crooks, J.A. and H.S. Khim. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology* 240:53-75.

Crooks, J.A. and M.E. Soule. 1999. Lag times in population explosion of invasive species: causes and implications. pp.103-125 In: Sandlund, O.T., P.J. Schei, and Å. Viken (eds.) *Invasive Species and Biodiversity Management*. Kluwer

Academic Publishers, Dordrecht, The Netherlands. 431 pp.
Includes discussion of several marine species; this is not ILTA per se (see the main body of the present paper), but rather lag times of species blooms after they have become established.

Daehler, C.C. and D.R. Strong. 1997. Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110:99-108.

Daehler, C.C. and D.R. Strong. 1997. Hybridization between introduced smooth cordgrass (*Spartina alterniflora*; Poaceae) and native California cordgrass (*Spartina foliosa*) in San Francisco Bay, California, USA. *American Journal of Botany* 84:607-611.

Den Hartog, C., F.W.B. Van den Brink, and G. Van der Velde. 1992. Why was the invasion of the river Rhine by *Corophium curvispinum* and *Corbicula* species so successful? *Journal of Natural History* 26:1121-1129.
Examines several hypotheses (biological, ecological, and temporal) to address the question. The amphipod Corophium curvispinum is a fresh- to brackish-water species to be expected in North America at any time; the clam Corbicula is a well-known bivalve invader of both Europe and North America.

De Wreede, R.E. 1983. *Sargassum muticum* (Fucales, Phaeophyta): regrowth and interaction with *Rhodomela larix* (Ceramiales, Rhodophyta). *Phycologia* 22:153-160.

De Wreede, R.E. 1988. *Lithothrix aspergillum* (Rhodophyta): regrowth and interaction with *Sargassum muticum* (Phaeophyta) and *Neorhodomela larix* (Rhodophyta). *Phycologia* 27:469-476.
This and the previous paper present quantitative studies on the Asian seaweed Sargassum in British Columbia. "One probable effect of the introduction of Sargassum has been a reduction in cover of Rhodomela."

Duda, T.F. 1994. Genetic population structure of the recently introduced Asian clam, *Potamocorbula amurensis*, in San Francisco Bay. *Marine Biology* 119:235-241.

Edwards, C. 1976. A study in erratic distribution: the occurrence of the medusa *Gonionemus* in relation to the distribution of oysters. *Advances in Marine Biology* 14:251-284.
An elegant analysis.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London. 181 pp.
This famous book includes a chapter, "Changes in the Sea." See Carlton (1989) for background comments by Elton.

Eno, N.C. 1996. Non-native marine species in British waters: effects and controls. *Aquatic Conservation: Marine and Freshwater Ecosystems* 4:215-228.

Eno, N.C., R.A. Clark, and W.G. Sanderson. 1997. *A Review and Directory of Non-native Marine Species in British Waters.* Joint Nature Conservation Committee, Peterborough, UK. 153 pp.
The first monographic review of marine bioinvasions in the U.K.

Essink, K. and H.L. Kleef. 1993. Distribution and life cycle of the North American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. *Netherlands Journal of Aquatic Ecology* 27:237-246.

Essink, K. and U. Schottler (eds.) 1997. Studies on *Marenzelleria* spp. (Polychaeta: Spionidae). *Aquatic Ecology* 31(2):117-258.
A collection of 10 papers on the invasion of northern Europe by two species of this North American worm, one in the North Sea and one in the Baltic (see Bastrop et al. 1998).

Farnham, W.F. 1994. Introduction of marine benthic algae into Atlantic European waters. pp.28-36 In: Boudouresque, C.F., F. Briand, and C. Nolan (eds.) 1994. Introduced species in European Coastal Waters. European Commission (Luxembourg), *Ecosystems Research Report* 8:1-111 (EUR 15309) (ISBN 92-826-6727-8).

Fitzhugh, K. and G.W. Rouse. 1999. A remarkable new genus and species of fan worm (Polychaeta: Sabellidae: Sabellinae) associated with marine gastropods. *Invertebrate Biology* 118:357-390.
See Kuris and Culver (1999). This is Terebrasabella heterouncinata, a name easier to pronounce than it looks, native to South Africa but first discovered in California.

Ford, S.E. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *Journal of Shellfish Research* 15:45-56.

Galil, B.S. and N. Huelsmann. 1997. Protist transport via ballast water—biological classification of ballast tanks by food web interactions. *European Journal of Protistology* 33:244-253.

Galil, B.S. and J. Lützen. 1998. Jeopardy: host and parasite lessepsian migrants from the Mediterranean coast of Israel. *Journal of Natural History* 32:1549-1551.
Although the southern crab Charybdis longicollis came through the Suez Canal into the eastern Mediterranean in the 1950s, its parasite, the Gulf of Suez parasitic castrating sacculinid barnacle Heterosaccus dollfusi did not follow until the 1990s: "it is possible that (the crab) populations ... will suffer drastic perturbations" as a result. "In this case, a game of Jeopardy is played out between host and parasite."

Garbary, D.J., H. Vandermeulen, and K.Y. Kim. 1997. *Codium fragile* ssp. *tomentosoides* (Chlorophyta) invades the Gulf of St Lawrence, Atlantic Canada. *Botanica Marina* 40:537-540.
Forty years after being first detected on Long Island, this Asian kelp is reported from the Gulf of St. Lawrence.

Geller, J.B. 1996. Molecular approaches to the study of marine biological invasions. pp.119-132 In: Ferris, J.D. and S.R. Palumbi (eds.) *Molecular Zoology. Advances, Strategies, and Protocols*. Wiley-Liss, A John Wiley & Sons, Inc., Publication, New York. 580 pp.

Geller, J.B. 1999. Decline of a native mussel masked by sibling species invasion. *Conservation Biology* 13:661-664.
With the invasion of the Mediterranean mussel, Mytilus gallo-

provincialis, the native mussel, Mytilus trossulus, disappeared from southern California, but as the two are externally nearly identical, the passage of the latter went without notice.

Geller, J.B., J.T. Carlton, and D.A. Powers. 1994. PCR-based detection of mtDNA haplotypes of native and invading mussels on the northeastern Pacific coast: latitudinal pattern of invasion. *Marine Biology* 119:243-249.

Geller, J.B., E.D. Walton, E.D. Grosholz, and G. M. Ruiz. 1997. Cryptic invasions of the crab *Carcinus* detected by molecular phylogeography. *Molecular Ecology* 6:901-906.

Gerard, V.A., R.M. Cerrato, and A.A. Larson. 2000. Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. *Biological Invasions* 1:353-361.
The Asian shore crab, Hemigrapsus sanguineus, invades New England shores.

Gollasch, S. and E. Leppäkoski. 1999. *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*. Nord 1999: 8. Nordic Council of Ministers, Copenhagen. 244 pp.

Gosliner, T.M. 1995. Introduction and spread of *Philine auriformis* (Gastropod: Opisthobranchia) from New Zealand to San Francisco Bay and Bodega Harbor. *Marine Biology* 122:249-255.
A ballast-water-mediated introduction of this intertidal mudflat seaslug which preys on small bivalves.

Gray, P.W.G. and E.B.G. Jones. 1977. The attempted clearance of *Sargassum muticum* from Britain. *Environmental Conservation* 4:303-308.
An accounting of the famous attempts to remove this invading brown seaweed from English shores by hand picking. Sargassum remains a common British seaweed.

Greenberg, N., R.L. Garthwaite, and D.C. Potts. 1996. Allozyme and morphological evidence for a newly introduced species of *Aurelia* in San Francisco Bay, California. *Marine Biology* 125:401-440.
The authors propose that a San Francisco Bay population of this jellyfish is introduced from Japan by ballast water.

Griffiths, C.L., P.A.R. Hockey, C. Van Erkom Shurink, and P.J. Le Roux. 1992. Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *South African Journal of Marine Science* 12:713-722.
Including the Mediterranean mussel, Mytilus galloprovincialis, and the European shore crab, Carcinus maenas. Mytilus has displaced the native mussel, Aulacomya ater, in many areas.

Grizel, H. and M. Heral. 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *Journal du Conseil* 47:399-403.

Grosholz, E.D. and G.M. Ruiz. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Marine Biology* 122:239-248.

Grosholz, E.D. and G.M. Ruiz. 1995. Does spatial heterogeneity and genetic variation in populations of the xanthid crab *Rhithropanopeus harrisii* (Gould) influence the prevalence of an introduced parasitic castrator? *Journal of Experimental Marine Biology and Ecology* 187:129-145.
Spatial heterogeneity yes, genetic variation, no; the introduced castrator here in Chesapeake Bay is the Gulf of Mexico sacculinid barnacle Loxothylacus panopaei.

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.

Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99.

Hallegraeff, G.M. 1998. Transport of toxic dinoflagellates via ship's ballast water: bioeconomic risk assessment and efficacy of possible ballast water management strategies. *Marine Ecology Progress Series* 168:297-309.

Hallegraeff, G.M. and C.J. Bolch. 1991. Transport of toxic dinoflagellate cysts via ships' ballast water. *Marine Pollution Bulletin* 22:27-30.

Hallegraeff, G.M. and C.J. Bolch. 1992. Transport of diatom and dinoflagellate resting spores in ships' ballast water: implications for plankton biogeography and aquaculture. *Journal of Plankton Research* 14:1067-1084.

Hallegraeff, G.M., C.J. Bolch, J. Bryan, and B. Koerbin. 1990. Microalgal spores in ships' ballast water: a danger to aquaculture. pp. 475-480 In: Graneli, E. (ed.) *Toxic Marine Phytoplankton*. Elsevier, New York.
Professor Hallegraeff and colleagues have thoroughly documented the arrival of Japanese dinoflagellates in Australian waters.

Harding, J.M. and R. Mann. 1999. Observations on the biology of the veined rapa whelk, *Rapana venosa* (Valenciennes, 1846) in the Chesapeake Bay. *Journal of Shellfish Research* 18:9-17.
This large (15 cm tall) heavy molluscivorous Asian whelk arrives on North American shores, possibly from the Black Sea or the Mediterranean, whose populations arose from intentional releases many years ago.

Hayes, K.R. 1998. Ecological risk assessment for ballast water introductions: a suggested approach. *ICES Journal of Marine Science* 55:201-212.

Hayward, B.W. 1997. Introduced marine organisms in New Zealand and their impact in the Waitemata Harbour, Auckland. *Tane* 36:197-223.
Figure 3 of this summary paper shows ten of the most common introduced species in Waitemata Harbour. All but two bivalves (the file shell Limaria orientalis and the oyster Crassostrea gigas) are also found in San Francisco Bay.

Healy, J.M. and K.L. Lamprell. 1996. The Atlantic-Mediterranean bivalve, *Corbula gibba* (Olivi) (Corbulidae: Myoidea) in Port Philip Bay, Victoria. *Memoirs of the Queensland Museum* 39:315-318.
Another possible ballast water introduction into southern Australia; can such clams also survive long-distance transport in ships' sea chests?

Hicks, D.W. and J.W. Tunnell, Jr. 1993. Invasion of the south Texas coast by the edible brown mussel *Perna perna* (Linnaeus, 1758). *Veliger* 36:92-94.
See Agard et al. (1992).

Hines, A.H., F. Alvarez, and S.A. Reed. 1997. Introduced and native populations of a marine parasitic castrator: variation in prevalence of the rhizocephalan *Loxothylacus panopaei* in xanthid crabs. *Bulletin of Marine Science* 61:197-214.

Hirakawa, K. 1986. A new record of the planktonic copepod *Centropages abdominalis* (Copepoda, Calanoida) from Patagonian waters, southern Chile. *Crustaceana* 51:296-299.
Introduced copepods should be watched for everywhere: this Japanese species now occurs in Chilean fjords.

Jamieson, G.S., E.D. Grosholz, D.A. Armstrong, and R.W. Elner. 1998. Potential ecological implications from the introduction of the European green crab, *Carcinus maenas* (Linnaeus), to British Columbia, Canada, and Washington, USA. *Journal of Natural History* 32:1587-1598.
Carcinus maenas was discovered in British Columbia in June 1999.

Jousson O., J. Pawlowski, L. Zaninetti, A. Meinesz, and C. Boudouresque. 1998. Molecular evidence for the aquarium origin of the green alga *Caulerpa taxifolia* introduced to the Mediterranean Sea. *Marine Ecology Progress Series* 172:275-280.
See Meinesz's book.

Kelly, J.M. 1993. Ballast water and sediments as mechanisms for unwanted species introductions into Washington state. *Journal of Shellfish Research* 12:405-410.

Kimmerer, W.J., E. Gartside, and J.J. Orsi. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. *Marine Ecology Progress Series* 113:81-93.
The Asian clam, Potamocorbula amurensis (see Carlton et al. 1990 and Nichols et al.1990) consumes the copepod, Eurytemora affinis.

Kinzie, R.A. III. 1984. Aloha also means goodbye: a cryptogenic stomatopod in Hawaii. *Pacific Science* 38:298-311.
The mantis shrimp (stomatopod) Gonodactylus aloha, although described as a new species from Hawaii, and although treated in this paper as cryptogenic, was introduced from the Indo-Pacific after World War II to the Hawaiian Islands. The native mantis shrimp Pseudosquilla ciliata was displaced wherever Gonodactylus was abundant.

Kittelson, P.M. and M.J. Boyd. 1997. Mechanisms of expansion for an introduced species of cordgrass, *Spartina densiflora*, in Humboldt Bay, California. *Estuaries* 20:770-778.
A Chilean species introduced many years ago to North America.

Krapp, F. and R. Sconfietti. 1983. *Ammothea hilgendorfi* (Böhm, 1879), an adventitious pycnogonid new for the Mediterranean Sea. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli* 4:123-132.
Sea spiders are underreported as ship-mediated invasions in most community invasion studies.

Kube, J., M.L. Zettler, F. Gosselck, S. Ossig, and M. Powilleit. 1996. Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the southwestern Baltic Sea in 1993/94—ten years after introduction. *Sarsia* 81:131-142.

Kuris, A.M. and C.S. Culver. 1999. An introduced sabellid polychaete pest infesting cultured abalones and its potential spread to other California gastropods. *Invertebrate Biology* 118:391-403.
See Fitzhugh and Rouse, 1999. An elegant and masterful study of a South African worm making its way on the other side and other half of the world.

Lambert, C. and G. Lambert. 1998. Non-indigenous ascidians in southern California harbors and marinas. *Marine Biology* 130:675-688.
A wave of exotic seasquirts has inundated southern California at the close of the 20th century.

Kuzman, S., S. Olsen, and O. Gerasimova. 1996. Barents Sea King Crab (*Paralithodes camtschaticus*): transplantation experiments were successful. pp. 649-663 In: *High Latitude Crabs: Biology, Management, and Economics*. Alaska Sea Grant College Program, Anchorage, Alaska. Number AK-SG-96-02.
Intentional plantings in the 1960s of this edible crab from the Sea of Japan to the Arctic Ocean (Barents Sea) led to the successful establishment of this crab, a rare invader of the deep sea: "large males have been caught in fair numbers down to 330 meters."

Laruelle, F., J. Guillou, and Y.M. Paulet. 1994. Reproductive pattern of the clams, *Ruditapes decussatus* and *R. philippinarum*, on intertidal flats in Brittany. *Journal of the Marine Biological Association of the United Kingdom* 74:351-366.
"In British Columbia," says the text, this clam was "introduced from Japan in the 1930s, and then spread rapidly... In the same way, this species was introduced twenty years ago to (France) for aquaculture purposes." This is not exactly so: this clam was introduced by accident to British Columbia whereas this clam was introduced intentionally into France in the 1970s, with apparently no prior studies as to what its ecological impact might be. The authors find that the exotic clam had a more extended reproductive season and a greater number of spawning events than the native congener, R. decussatus, reminiscent of the advantages that a number of introduced species have over natives (and which eventually causes the native to become somewhat less abundant).

Lee, C.E. 1999. Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution* 53:1423-1434.

Lee, C.E. 1999. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends in Ecology and Evolution* 14:284-288.

Lohrer, A.M. and R.W. Whitlatch. 1997. Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*) in Eastern Long Island Sound. pp. 49-60 In: Balcom, N. (ed.) *Proceedings of the Second*

Northeast Conference on Nonindigenous Aquatic Nuisance Species. Publication Number CTSG-95-02, Connecticut Sea Grant College Program, University of Connecticut, Groton CT.

The first detailed published ecological information on this crab. For a copy of the whole proceedings, which is not in most libraries, write to: Connecticut Sea Grant Extension Program, University of Connecticut, 1084 Shennecossett Road, Groton , Connecticut 06340 USA.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23-39.

The role of the introduced European periwinkle, Littorina littorea, in regulating the intertidal flora of New England.

Malyshev, V.I. and A.G. Arkhipov. 1992. The ctenophore *Mnemiopsis leidyi* in the western Black Sea. *Hydrobiological Journal* 28:33-39.

A comb jelly introduced from the Americas.

Mann, R. (ed.). 1979. *Exotic Species in Mariculture*. The MIT Press, Cambridge, Massachusetts.

A symposium (and book) published 20 years before the 1999 popularity of this subject.

McCarthy, S.A. and F.M. Khambaty. 1994. International dissemination of epidemic *Vibrio cholerae* by cargo ship ballast and other nonpotable waters. *Applied Environmental Microbiology* 60:2597-2601.

McDermott, J.J. 1998. The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. *ICES Journal of Marine Science* 55:289-298.

First discovered in New Jersey in 1988, by the late 1990s the crab occurred from north of Cape Cod to North Carolina. It may have been introduced by ballast water, although other ship-related mechanisms (such as sea chests or external hull fouling, with small crabs in empty barnacles in the fouling matrix, for example) are possible.

McDermott, J.J. 1998. The western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: reproduction. *Journal of Crustacean Biology* 18:308-316.

McDermott, J.J. 1999. The Western Pacific brachyuran *Hemigrapsus sanguineus* (Grapsidae) in its new habitat along the Atlantic coast of the United States: feeding, cheliped morphology and growth. pp. 425-444 In: Shram, F.R. and J. C. Von Vaupel Klein (eds.) *Crustaceans and the Biodiversity Crisis. Proceedings of the 4th International Crustacean Congress.* Koninklijke Brill NV, Leiden.

Meinesz, A. 1999. *Killer Algae*. University of Chicago Press. 376 pp.

The English translation (by Daniel Simberloff) of the remarkable, emotional, political story of how the aquarium seaweed Caulerpa taxifolia was released into the Mediterranean at the foot of the Monaco Aquarium and the sordid events of denial and obfuscation that followed. The title, "Killer Algae", is a partial translation of that of the original French book, "Le roman noir de l'algue tueuse" (The Black Novel of the Killer Alga), and refers to the erroneous name—applied by the French press—by which the French public knows of this invasion; it means nothing outside of France, and the alga doesn't kill anything.

Although the advertising website produced by the publisher in advance of the book proclaims several times the alga doesn't kill, the publisher persisted with the title, evidently for sales purposes, doing little good to improve an understanding of invasions by the public or political world.

Meng, L. and J.J. Orsi. 1991. Selective predation by larval striped bass on native and introduced copepods. *Transactions of the American Fisheries Society* 120:187-192.

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

Minchin, D. 1996. Management of the introduction and transfer of marine molluscs. *Aquatic Conservation: Marine and Freshwater Ecosystems* 6:229-244.

Monniot, C., F. Monniot, and P. Laboute. 1985. Ascidies du port de Papeete (Polynesie francaise): relations avec le milieu naturel et apports intercontinentaux par la navigation. *Bulletin du Museum National d'Histoire Naturelle (4)* 7:481-495.

The Monniots have produced numerous papers demonstrating the role of ships in moving seasquirts as fouling organisms around the world. Many of these species have now become the aspect dominant organisms in many shallow-water communities.

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

Includes brackish water invasions, particularly those in California's Sacramento-San Joaquin estuary.

National Research Council. 1996. *Stemming the Tide. Controlling Introductions of Nonindigenous Species by Ships' Ballast Water.* National Academy Press, Washington, D.C., 141 pp.

The committee nature of this book inevitably bubbles up occasionally.

Nehring, S. 1998. Establishment of thermophilic phytoplankton species in the North Sea: biological indicators of climatic changes? *ICES Journal of Marine Science* 55:818-823.

Newman, W.A. 1967. On physiology and behaviour of estuarine barnacles. pp. 1038-1066 In: *Proceedings of the Symposium on Crustacea held at Ernakulam from January 12 to 15, 1965*. Symposium Series 2, Part III. Marine Biological Association of India.

The distributional ecology and physiology of the introduced barnacles, Balanus improvisus and Balanus amphitrite, in San Francisco

Bay, California.

Nichols, F.H. and J.K. Thompson. 1985. Persistence of an introduced mudflat community in South San Francisco Bay, California. *Marine Ecology Progress Series* 24:83-97. *Of more than 20 introductions, the Atlantic clam, Gemma gemma, the Atlantic amphipod, Ampelisca abdita, and the Atlantic worm, Streblospio benedicti, are the most abundant.*

Nichols, F.H., J.K. Thompson, and L.E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Marine Ecology Progress Series* 66:95-101.

Noël, P., E. Tardy, and C. D'Ukem D'Acoz. 1997. Will the crab *Hemigrapsus penicillatus* invade the coasts of Europe?. *Comptes rendus de l'academie des sciences de la vie* 320:741-745. *Yes.*

Ofoighil, D., P.M. Gaffney, A.E. Wilbur, and T.J. Hilbish. 1998. Mitochondrial cytochrome oxidase I gene sequences support an Asian origin for the Portuguese oyster *Crassostrea angulata. Marine Biology* 131:497-503. *The Japanese oyster Crassostrea gigas was introduced by the Portuguese from Japan to southern Europe probably in the 16th century; it was described as a species native to Europe in the 18th century, where even now it continues to most often be referred to by the synonymous name Crassostrea angulata, under the guise of being a native species! Ofoighil put a final nail into the junior synonymy of angulata, a matter nicely discussed by Edwards in 1976.*

Olenin, S. and E. Leppakoski. 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. *Hydrobiologia* 393:233-243. *Introduced species "have significantly altered ecosystems of the southeastern Baltic coastal lagoons": one of these is Vistula Lagoon, whose modern-day dominance by invasions bears comparison to similar environments elsewhere around the world, such as the l'etang de Thau (Thau Lagoon) in Sete, on the south coast of France; the Ala Wai Canal in Waikiki, Honolulu, on the south coast of Oahu, Hawaii; and Lake Merritt in Oakland, California, on the east shore of San Francisco Bay.*

Orsi, J.J. and T.C. Walter. 1991. *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest copepod immigrants to California's Sacramento-San Joaquin estuary. *Proceedings of the Fourth International Conference on Copepoda. Bulletin of the Plankton Society of Japan Special Volume* (1991):553-562.

Paula, E.J. and V.R. Eston. 1987. Are there other *Sargassum* species potentially as invasive as *S. muticum*? *Botanica Marina* 30:405-410. *Yes there are.*

Petersen, K.S., K.L. Rasmussen, J. Heinemeler, and N. Rud. 1992. Clams before Columbus? *Nature* 359:679. *Extends the arrival of the North American clam, Mya arenaria, in Europe back to the 1200s, and thus within the realm of Viking transport.*

Petraitis, P.S. 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. *Ecology* 64:522-533. *The impacts of the European periwinkle Littorina littorea in New England.*

Petraitis, P.S. 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. *Journal of Experimental Marine Biology and Ecology* 109:117-136.

Petraitis, P.S. 1989. Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinalis* (Muller). *Journal of Experimental Marine Biology and Ecology* 125:99-115. *The removal of the introduced European snail Littorina littorea in lower intertidal areas in sheltered bays enhanced the growth, weight gain, and survival of the native limpet Tectura testudinalis.*

Pierce, R.W., J.T. Carlton, D.A. Carlton, and J.B. Geller. 1997. Ballast water as a vector for tintinnid transport. *Marine Ecology Progress Series* 149:295-297. *Identifies 33 species of tintinnids in ballast water arriving in Coos Bay from Japan; as Carlton and Geller (1993) had already reported 2 tintinnid species, this adds 31 to the total number of ballast species reported in Carlton and Geller.*

Por, F.D. 1978. *Lessepsian Migration: The Influx of Red Sea Biota into the Mediterranean Sea by Way of the Suez Canal.* Berlin: Springer-Verlag. *This is the classic summary up to the mid 1970s; see Spanier and Galil (1991).*

Posey, M.H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69:974-983. *The Japanese eelgrass in Oregon: experimental manipulations demonstrate that the plant has changed the physical habitat (mean sediment grain size declined with Z. japonica patches as compared to unvegetated areas) and the richness and density of resident invertebrate infauna (higher in than outside of the patch).*

Planes, S. and G. Lecaillon. 1998. Consequences of the founder effect in the genetic structure of introduced island coral reef fish populations. *Biological Journal of the Linnean Society* 63:537-552. *Allozyme studies on what it takes in terms of minimum population size inoculation to make for a successful planting of non-native fish into the Hawaiian Islands. In the case in hand, only 3 of 11 fish from French Polynesia purposefully released between 1955 and 1961 in Hawaii became established; of the three successful species, even though "only a few individuals bequeathed their characteristics to subsequent generations, no significant change in genetic diversity was observed."*

Prince, J. and W. LeBlanc. 1992. Comparative feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for the invasive green seaweed, *Codium fragile* ssp. *tomentosoides* (Chlorophyceae) and four other seaweeds. *Marine Biology*

113:159-163.

Race, M.S. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologia* 54:337-347.
The players are the introduced Atlantic mudsnail, Ilyanassa obsoleta, and the native California mudsnail, Cerithidea californica. The former eats the eggs of the latter and otherwise eliminates Cerithidea from the lower shore. See also the work of Whitlatch and Obrebski (1980) and Brenchley and Carlton (1983).

Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47:393-407.
Although not mentioned by the author, virtually all of the prey of these native birds are species introduced to San Francisco Bay .

Reise, K. 1999. Exotic invaders of the North Sea shore. Preface. Proceedings of a workshop held on the island of Sylt, 19-22 February 1998. *Helgolander Meeresuntersuchungen* 52 (3/4):217-218.
A symposium of 16 papers:

- *Introduced marine species of the North Sea coasts*
- *Exotic flagellates of coastal North Sea waters*
- *Red algal exotics on North Sea coasts*
- *Introduced brown algae in the North East Atlantic, with particular respect to Undaria pinnatifida (Harvey) Suringar*
- *From introduced species to invader: what determines variation in the success of Codium fragile ssp. tomentosoides (Chlorophyta) in the North Atlantic Ocean?*
- *On the population development of the introduced razor clam Ensis americanus near the island of Sylt (North Sea)*
- *Introductions and developments of oysters in the North Sea area: a review*
- *Mya arenaria - an ancient invader of the North Sea coast (see Strasser, 1998)*
- *Rapid colonization of new habitats in the Wadden Sea by the ovoviviparous Littorina saxatilis (Olivi)*
- *The neozoan Elminius modestus Darwin (Crustacea, Cirripedia): Possible explanations for its successful invasion in European water*
- *The recent arrival of the oceanic isopod Idotea metallica Bosc off Helgoland (German Eight, North Sea): an indication of a warming trend in the North Sea?*
- *The Asian decapod Hemigrapsus penicillatus (de Haan, 1835) (Grapsidae, Decapoda) introduced in European waters: status quo and future perspective*
- *Dispersal and development of Marenzelleria spp. (Polychaeta, Spionidae) populations in NW Europe and the Netherlands*
- *Ecophysiological capability of Marenzelleria populations inhabiting North Sea estuaries: an overview*
- *Styela clava Herdman (Urochordata, Ascidiacea), a successful immigrant to North West Europe: ecology, propagation and chronology of spread*
- *Exotic invaders of the meso-oligohaline zone of estuaries in the Netherlands: why are there so many?*

Reusch, T.B.H. and S.L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. *Oecologia* 113:428-441.
The introduced Japanese mussel, Musculista, when experimentally added to Zostera beds, causes eelgrass rhizomes to grow 40% less than controls.

Ribera, M.A. and C.F. Boudouresque. 1995. Introduced marine plants, with special reference to macroalgae: mechanisms and impact. pp. 188-268 In: Round, F.E. and D.J. Chapman (eds.) *Progress in Phycological Research 11*.
The first thorough global review of introduced marine algae.

Ricciardi, A. and H.J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution* 15:62-65.
Species from the Black and Caspian Seas are often euryhaline and have formed a conspicuous global element in the invasions picture.

Ricketts, E.F., J. Calvin, and J.W. Hedgpeth. 1968. *Between Pacific Tides*. Fourth Edition. Stanford University Press, Stanford, CA. 614 pp.

Rosenfield, A. and R. Mann (eds.). 1992. *Dispersal of Living Organisms into Aquatic Ecosystems*. University of Maryland and Maryland Sea Grant College Program, College Park, Maryland. 436 pp.

Rueness, J. 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. *Marine Pollution Bulletin* 20:173-176.

Russell, D.J. and G.H. Balazs. 1994. Colonization by the alien marine alga *Hypnea musciformis* (Wulfen) J. Ag.(Rhodophyta: Gigartinales) in the Hawaiian Islands and its utilization by the green turtle, *Chelonia mydas* L. *Aquatic Botany* 47:53-60.

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

Ruiz, G.M., P. Fofonoff, 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.
Uses Chesapeake Bay as a model system, with 196 introduced and cryptogenic taxa used for analysis: while 39 (20 %) of these species were believed to have had "some significant impact", the authors could find quantitative data on impacts for only 12 of the 39, representing only 6% of the 196 species surveyed!

Sheath, R.G. 1987. Invasions into the Laurentian Great Lakes by marine algae. *Archive fur Hydrobiologie Beiheft Ergebnisse der Limnologie* 25:165-186.
An all-too-rarely cited paper; with rare exception usually cited as Arch. Hydrobiol. Beih. Ergebn. Limnol., *a mysterious set of abbreviations to most English-speaking workers.*

Shushkina, E.A., G.G. Nikolaeva, and T.A. Lukasheva. 1990. Changes in the structure of the Black Sea planktonic community at mass reproduction of sea gooseberries *Mnemiopsis leidyi* (Agassiz). *Oceanology* 51:54-60.
An early paper on the invasion of this comb jellyfish (ctenophore) from the Americas to the Black Sea.

Sindermann, C.J. 1993. Disease risks associated with importation of nonindigenous marine animals. *Marine Fisheries Review* 54:1-10.

Skerman, T.M. 1959. Marine fouling at the Port of Auckland. *New Zealand Journal of Science* 2:57-94.
A mid-century look at a fauna dominated by introduced species.

Smith, L.D., M.J. Wonham, L.D. McCann, G.M. Ruiz, A.H. Hines, and J.T. Carlton. 1999. Invasion pressure to a ballast-flooded estuary and an assessment of inoculant survival. *Biological Invasions* 1:67-87.

Southward, A.J., R.S. Burton, S.L. Coles, P.R. Dando, R. De Felice, J. Hoover, P.E. Parnell, T. Yamaguchi, and W.A. Newman. 1998. Invasion of Hawaiian waters by an Atlantic barnacle. *Marine Ecology Progress Series* 165:119-126.
The Caribbean barnacle, Chthamalus proteus Dando and Southward, 1980, invades the Hawaiian archipelago, but exactly when it did so in the previous 20 years is surprisingly unclear.

Spanier, E. and B.S. Galil. 1991. Lessepsian migration: a continuous biogeographical process. *Endeavour* 15:102-106.
…through the Suez Canal; see Por 1978.

Stachowicz, J.J., R.B. Whitlatch, and R.W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577-1579.
"In experimental communities of sessile marine invertebrates, increased species richness significantly decreased invasion success, apparently because species-rich communities more completely and efficiently used available space, the limiting resource in this system." Species contributing to this richness and said to be native in this Long Island Sound, Connecticut, fouling community were the blue mussel Mytilus edulis, the ascidian seasquirts Molgula manhattensis, Ciona intestinalis and Botryllus schlosseri, and the bryozoan Cryptosula pallasiana: with the exception of the mussel, all of these species, however, are either cryptogenic or introduced from Europe.

Stigzelius, J., A. Laine, J. Rissanen, A.B. Andersin, and E. Ilus. 1997. The introduction of *Marenzelleria viridis* (Polychaeta, Spionidae) into the Gulf of Finland and the Gulf of Bothnia (northern Baltic Sea). *Annales Zoologi Fennici* 34:205-212.

Strasser, M. 1999. *Mya arenaria*—an ancient invader of the North Sea coast. *Helgolander Meeresuntersuchungen* 52:309-324.
A clam that was once widespread through the cold waters of the Northern Hemisphere until the Pleistocene glaciers wiped it out from the Eastern Pacific and the Eastern Atlantic, only to be introduced (not reintroduced!) to the Eastern Pacific and the Eastern Atlantic by humans so that its modern distribution parallels its ancient distribution. American readers will note that the author's reference to the "Pacific west coast" means Asia.

Sutherland, J.P. 1974. Multiple stable points in natural communities. *American Naturalist* 108:859-873.
A major controlling species focused upon in this foundation paper is the stalked seasquirt (ascidian), Styela plicata, which forms one of the stable points in the fouling community at Beaufort, North Carolina, and directly and indirectly impacts many other species in the community. Unbeknownst to the author, this is an Asian species introduced in the 18th or 19th centuries to Atlantic North America.

Sutherland, J.P. 1981. The fouling community at Beaufort, North Carolina: a study in stability. *American Naturalist* 118:499-519.
See Sutherland 1974. Introduced or cryptogenic species (not so noted by the author) included among the fouling community's "foundation species" include the seasquirts (ascidians) Styela plicata, Molgula manhattensis, and Botryllus schlosseri, the barnacle Balanus amphitrite and Balanus reticulatus (identified as Balanus tintinnabulum), and the bryozoan Anguinella palmata.

Swennen, C. and R. Dekker. 1995. *Corambe batava* Kerbert, 1886 (Gastropoda: Opisthobranchia), an immigrant in the Netherlands, with a revision of the family Corambidae. *Journal of Molluscan Studies* 61:97-107.
An interesting case wherein the "endemic" brackish water Zuiderzee seaslug (once listed in the endangered species Red Book) is found to be the introduced North American species Doridella obscura.

Trowbridge, C.D. 1996. Introduced versus native subspecies of *Codium fragile*: how distinctive is the invasive subspecies *tomentosoides*. *Marine Biology* 126:193-204.

Trowbridge, C.D. 1998. Ecology of the green macroalga *Codium fragile* (Suringar) Hariot 1889: invasive and non-invasive subspecies. *Oceanography and Marine Biology: An Annual Review* 36:1-64.

Utting, S.D. and B.E. Spencer. 1992. Introductions of marine bivalve molluscs into the United Kingdom for commercial culture - case histories. *ICES Marine Science Symposia* 194:84-91.

Vadas, R.L. 1992. Littorinid grazing and algal patch dynamics. pp. 197-209 In: Grahame, J., P.J. Mill, and D.G. Reid (eds.). *Proceedings of the Third International Symposium on Littorinid Biology*. Malacological Society of London, London, 324 pp.
A thorough demonstration of the control that the European periwinkle, Littorina littorea, exerts on upper and mid intertidal algal patches.

Vallarino, E.A. and R. Elias. 1997. The dynamics of an introduced *Balanus glandula* population in the southwestern Atlantic rocky shores. The consequences on the intertidal community. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli* 18:319-335.
An experimental study in this winter-recruiting species in Argentina. The authors argue that a combination of reproductive phenology, the absence of predators, the neutral or positive interaction with algae, and "spatial and temporal partitioning of the substrate allow this barnacle to successfully outcompete intertidal mussels and other barnacles species of both sheltered and exposed" sites. Remarkable too is the very presence of this barnacle in east-

ern South America: Balanus glandula finds it original home in the Eastern Pacific (from Alaska to Mexico), and is one of the very few native western North American species to ever leave home.

Verlaque, M. 1994. Inventaire des plantes introduites en Méditerranée: origines et répercussions sur l'environnement et les activités humaines. *Oceanologica Acta* 17:1-23.

Verlaque, M. 1996. L'etang de Thau (France), un site majeur d'introduction d'especes en Mediterrannee—relations avec l'ostreiculture. pp. 423-430 In: Ribera, M.A., E. Ballasteros, C.F. Boudouresque, A. Gomez, and V. Gravez (eds.) *Second International Workshop on Caulerpa taxifolia*. Publicacions Universitat. Barcelona, Spain.
A few French ecologists are steadily documenting the many Asian species that came in with massive inoculations of Japanese oysters commencing in the 1970s.

Villalard-Bohnsack, M. and M.M. Harlin. 1997. The appearance of *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) on the northeast coast of North America. *Phycologia* 36:324-328.
A large red seaweed established in Narragansett Bay, Rhode Island, south of Cape Cod; first record July 1996.

Wasson, K. 1997. Systematic revision of colonial kamptozoans (entoprocts) of the Pacific coast of North America. *Zoological Journal of the Linnean Society* 121:1-63.
Includes a detailed review of the fouling kamptozoan, Barentsia benedeni, widely spread by ships and perhaps oysters.

Werner, I. and J.T. Hollibaugh. 1993. *Potamocorbula amurensis*: comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. *Limnology and Oceanography* 38:949-964.
In San Francisco Bay; see Carlton et al. 1990 and Nichols et al. 1990.

Whitlatch, R.B. and S. Obrebski. 1980. Feeding selectivity and coexistence in two deposit-feeding gastropods. *Marine Biology* 58:219-225.
The interactions between the native California mudsnail Cerithidea californica and the introduced Japanese mudsnail Batillaria attramentaria: small Batillaria are absent in the presence of Cerithidea, a species more specialized for feeding on small particulate material. See also the work of Race (1982) and Brenchley and Carlton (1983).

Williams, R.J., F.B. Griffiths, E.J. Van der Wal, and J. Kelly. 1988. Cargo vessel ballast water as a vector for the transport of non-indigenous marine species. *Estuarine and Coastal Shelf Science* 26:409-420.
One of the first studies on the biology of ballast water.

Wolff, T. 1977. The horseshoe crab (*Limulus polyphemus*) in north European waters. *Videnskabelige meddelelser fra Dansk naturhistorisk forening i Kjobehavn* 140:39-52.
A multicentury record of the appearance of this North American horseshoe crab in European ports.

Woods Hole Oceanographic Institution. 1952. Marine fouling and its prevention. United States Naval Institute, Annapolis, Maryland. 388 pp.
A sine qua non for those interested in the role of ships in dispersing marine life around the world.

Yamada, S.B. and R.A. Mansour. 1987. Growth inhibition of native *Littorina saxatilis* (Olivi) by introduced *L. littorea* (L.). *Journal of Experimental Marine Biology and Ecology* 105:187-196.
On Cape Cod in New England, USA; exactly how the introduced snail inhibits the growth of the native snail is not clear.

Zettler, M.L. 1996. Successful establishment of the spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Darss-Zingst estuary (southern Baltic) and its influence on the indigenous macrozoobenthos. Archives of Fishery and Marine Research 43:273-284.

Zhang, F.Z. and M. Dickman. 1999. Mid-ocean exchange of container vessel ballast water. 1: Seasonal factors affecting the transport of harmful diatoms and dinoflagellates. *Marine Ecology Progress Series* 176:243-251.

Zhang, F.Z. and M. Dickman. 1999. Mid-ocean exchange of container vessel ballast water. 2: Effects of vessel type in the transport of diatoms and dinoflagellates from Manzanillo, Mexico, to Hong Kong, China. *Marine Ecology Progress Series* 176:253-262.

Zibrowius, H. 1974. *Oculina patagonica*, scleractiniaire hermatypique introduit en Mediterranee. *Helgoländer wissenschaftliche Meeresuntersuchungen* 26:153-173.
A remarkable and unusual story: this coral remains known only from the fossil record in South America, with living populations known only from the Mediterranean Sea, where it is introduced. Professor Zibrowius reports (pers. comm.) that he should not have used the term hermatypic: the coral in question has zooxanthellae but is not a reef-builder; see Zibrowius and Ramos (1983).

Zibrowius, H. 1992. Ongoing modification of the Mediterranean fauna and flora by the establishment of exotic species. *Mesogee [Bulletin du Museum d'histoire naturelle de Marseille]* 51:83-107.
The most thorough summary to date of Mediterranean invasions. Not 1991 as often cited.

Zibrowius, H. and A.A. Ramos. 1983. *Oculina patagonica*, Scleractinia ire exotique en Mediterranee - nouvelles observations dans le Sud-Est de l'Espagne. *Rapports Commission internationale de la Mer Mediterranee* 28:297-301.
See Zibrowius (1974).

Zibrowius, H. and C.H. Thorp. 1990. A review of the alien serpulid and spirorbid polychaetes in the British Isles. *Cahiers de Biologie Marine* 30:271-285.

Zolotarev, V. 1996. The Black Sea ecosystem changes related to the introduction of new mollusc species. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli* 17:227-236.
The Japanese snail, Rapana venosa (here called Rapana thomasiana), the North American clam, Mya arenaria, and the Indo-Pacific clam, Scapharca inaequivalvis, were detected in the Black Sea in 1947, 1966, and 1968 respectively: "The resulting

changes in the structure of the bottom biocoenoses after these introductions are in many cases comparable with or exceed the consequences of other episodic environmental events and other kinds of anthropogenic activity."

INVITED LECTURE

Key Threats from Marine Bioinvasions: A Review of Current and Future Issues

Ronald E. Thresher[1]
Head, Centre for Research on Introduced Marine Pests
CSIRO Marine Research
GPO Box 1538
Hobart Tasmania 7001, Australia

Abstract: Australia has been actively researching and developing management strategies for invasive marine species since the mid-1980s, following the discovery that several species of toxic dinoflagellates were likely of foreign origin. While the problem of introduced marine pests is far from solved, an evaluation of the results of efforts to date suggest four key points. First, exotic species have been, and continue to be, introduced by a range of vectors; priorities for management action need to be based on a critical evaluation of the real risks posed by each vector, and encompass an understanding that even major effort directed at a few vectors will not prevent new incursions of major pest species. Second, eradication of new incursions is achievable, but is uncommon and limited to those situations where the pest was either detected quickly or otherwise still had a limited distribution. For most species, practical options for rapid eradication still need to be developed. Third, long-term options for pest management have to take into account social and cultural issues that make some options unfeasible. And fourth, groups likely to pose major threats in the future include pathogens, marine macroalgae, and genetically enhanced production lines developed for use in mariculture. The development of options to deal with these issues will rely heavily on an integration of techniques for management strategy evaluation, fundamental marine ecology, and the emerging science of marine bioinvasions.

Key words: Australia, ballast water, eradication, hull fouling, introduced marine pest, pathogen, pest management

Introduction

For the last decade, Australia has had a national program explicitly to deal with ballast water introductions and their management. Australian government agencies (and particularly the Australian Quarantine and Inspection Service—AQIS) have long recognized the threat posed by exotic marine organisms introduced by shipping, and have led the agenda at the International Maritime Organization to do something about the problem (Paterson 1994). Domestically, Australia has had a continuous program of research and management into ballast water and other potential vectors since 1989 and undertook world-first studies on ballast water exchange and heat treatment as partial solutions to the ballast water problem (Manning *et al.* 1996). The recently (1999) released Australian government Oceans Policy emphasizes the country's continued commitment to managing ballast water as a vector, including support for a nationally integrated management regime, the development of practical management tools, and implementation of a national process for identifying and responding rapidly to new pest incursions and outbreaks. This process is an extension of Australia's existing programs to deal with exotic terrestrial pests such as rabbits, cats, and a plethora of weeds.

Some aspects of the Australian situation are unusual to it, such as the strong social commitment to protecting its unique biota, but the vectors for marine invaders (Carlton 1996) and many of the species themselves are shared problems world-wide (*e.g.*, Cohen and Carlton 1997; Clark *et al.* 1998; Trowbridge 1998). In this paper, I review some of the conclusions that we have gleaned from dealing with these vectors and pests over the last decade, presented as an assessment of the critical threats we currently and are likely to face in the near future. The issues covered and ideas presented are idiosyncratic, but also reflect to an extent emerging priorities in Australia.

Invasion mechanisms

Cohen and Carlton (1997) listed ten broad categories

[1]Corresponding author; telephone: (61)362325378; fax (61)362325485; e-mail: thresher@marine.csiro.au

Table 1. Introduced marine species in Australian waters, divided by state and likely mode of introduction, as compiled through January 1998. The table includes some species of uncertain taxonomic status and some cryptogenic species; species are listed independently if they occur in more than one state; and most species are allocated to more than one transport mechanism as they could have been transported in each. Key: WA – Western Australia, SA – South Australia, Vic – Victoria, Tas – Tasmania, NSW – New South Wales, Qld – Queensland, NT – Northern Territory.

State	Number of Species	Hull fouling and boring	Mariculture	Dry Ballast	Ballast Water	Intentional
WA	53	36	23	12	18	3
SA	48	30	24	7	10	2
Vic	104	61	52	13	23	4
Tas	42	23	21	8	19	4
NSW	56	36	23	8	12	2
Qld	21	17	10	0	2	0
NT	2	0	0	0	0	2

of mechanisms theoretically available for transoceanic transport, many of which have numerous subcategories (*e.g.*, Cohen and Carlton 1995; Eno *et al.* 1997). The significance of each is debatable, doubtless varies among sites, and has changed over time. For many species, transport could have occurred by any one of several vectors. International shipping simultaneously offers transport opportunities via hull fouling, sea chests, and ballast, and species prone to transport as hull foulers are often also amenable to transport in mariculture shipments. Determining with certainty the vector for a particular unintentional introduction is impossible, and in all cases has to be decided on the basis of probability (although in some instances, the probability approaches 1, *e.g.*, the introduction of *Mnemiopsis leidyi* into the Black Sea in ballast water). Data on the number of larvae in ballast tanks or the number of species attached to hulls or in a mariculture shipment only tell us that a particular transport mechanism is operating, but say little about consequent rates of successful invasion and impacts.

One measure of the relative importance of the different transport vectors is the proportion of invasive species attributed to each by different studies. Cohen and Carlton (1995) estimated that four major vectors were historically of roughly equal importance in San Francisco Bay: ship fouling (26% of introduced species), ballast water (24%), accidental introductions due to mariculture (22%), and deliberate introductions (20%). Their study included a large number of freshwater species, however, which inflated the last category. Eno *et al.* (1997) suggested the largest single identifiable transport mechanism for introduced marine species in Britain (31% of the species) was accidental introduction associated with mariculture. Fouling accounted for about 26% and ballast water for another 18%, with an additional 12% of species equally likely to have been introduced by either of these shipping-related vectors. Deliberate introductions accounted for a further 8% of the introduced species. Cranfield *et al.* (1998) stated that "most (69%) of the adventive species...arrived in New Zealand as part of hull fouling communities, " attributing only 3% to ballast water and 21% to either fouling or ballast water. It is not clear from the report whether vectors other than hull fouling, such as mariculture shipments, were considered in detail. Our evaluation of the introduced species in Australian waters (Table 1) suggests that the dominant modes of introduction to Australia historically are hull fouling and accidental releases associated with mariculture, followed by ballast water, dry ballast, and intentional releases. Ballast water accounts for 15-20% of the invasive marine species we have thus far found in Australia.

From a management perspective, a more useful analysis is the relative importance of transport vectors for pest species, here defined as those species likely to cause significant social, health, economic, or environmental damage. The Australian Joint Ministerial Taskforce on Managing Marine Pest Incursions recently (1999) reviewed the known invasive species in Australian waters and overseas against a set of criteria (Table 2), to produce a list of 12 species against which incursion response plans would be developed. This list excluded freshwater species, and also excluded pest species already widely distributed in Australian waters. The latter include the New Zealand screw shell (*Maoriculpus roseus*), the European shore crab (*Carcinus maenas*), the Mediterranean fan worm (*Sabella spallanzanii*), the Pacific oyster (*Crassostrea gigas*) and three species of toxic dinoflagellates (genera *Gynmodinium* and *Alexandrium*).

Of the established pest taxa, only the toxic dinoflagellates almost certainly arrived in ballast tanks (Hallegraeff and Bolch 1991). Of the remaining species, the Pacific oyster was deliberately introduced, the European crab likely arrived in dry ballast, the screw shell was accidentally introduced in oyster shipments from New Zealand, and the rest were most likely fouling organisms in the broad sense of the term (including, for example, transport in sea chests). Of the "dangerous, but not yet here" species, two (*M. leidyi and Pfiesteria piscicida*) are clearly ballast water species, two (*Rapana thomasina* and *Potamocorbula*

Table 2a. Interim selection criteria developed by the National Taskforce on Managing Marine Pest Incursions

Criteria

Necessary and sufficient information to justify including a species on the trigger list (all four need to be satisfied)

1. Demonstrable invasive history.
2. One or more relevant transport vectors are still operating.
3. Demonstrable impact in native or invaded ranges on:
   - economy
   - environment
   - human health
   - amenity
4. Inferred as likely to have major impacts in Australia based on the overseas data and characteristics of Australian environments and marine communities.

Necessary and sufficient information to justify removing species from the trigger list (any one needs to be satisfied)

1. Scientific, empirical data show that impacts overseas are less than previously thought.
2. Scientific, empirical data show that impacts in Australia are likely to be less than previously thought.
3. Already is or becomes widely distributed in Australia.

Table 2b. Interim trigger list developed by the National Taskforce on Managing Marine Pest Incursions

Species	Common Name	Native Distribution	Introduced Distribution
Interim List			
Caulerpa taxifolia	Marine Algae Aquarium strain	Native strains circumtropical	Invasive"hybrid" in Mediterranean Sea
Eriochir sinensis	Chinese Mitten Crab	North West Pacific	Europe; West Coast North America
Mnemiopsis leidyi	Comb Jelly	Western Atlantic	Black Sea; Mediterranean
Mytilopsis sallei	Black Striped Mussel	Caribbean	Hong Kong; India; Singapore; [Darwin, NT]
Pfiesteria piscicida	Dinoflagellate	North West Atlantic	?? (proposed as introduced to N America)
Potamocorbula amurensis	Asian clam	North West Pacific	NE Pacific (SF Bay)
Rapana thomasina	Gastropod	North West Pacific	Black Sea, East Coast North America
Sargassum muticum	A. Seaweed	North West Pacific;	North West Pacific, England
	In Australia, but not widespread		
Asterias amurensis	Northern Pacific Seastar	Tasmania, Victoria Pacific	North West
Codium fragile ssp. *tomentosoides*	Broccoli weed, Dead man's fingers	North East Pacific	Tasmania, Victoria
Musculista senhousia	Asian Date or Bag mussel	NWTasmania, Victoria, Pacific, SW Australia Asian Seas	
Undaria pinnatifida Undaria	Seaweed	NW Tasmania, Victoria Pacific	

amurensis) are most likely to be introduced in ballast water, one (*Sargassum muticum*) is a fouling species, *Eriochier sinensis* would likely be introduced intentionally or in ballast water (Cohen and Carlton 1997), and the hybrid form of *Caulerpa taxifolia* will most likely be introduced in the aquarium trade, though it is also easily transported fouled in fishing gear, anchors, and the like (Meinesz *et al.* 1998).

This analysis suggests two points. First, no single vector or small subset of vectors accounts for all pest species; targeting any single vector will, therefore, not stop the introduction of species with significant pest potential. But second, by far the single most active transport mechanism historically for pest species is fouling, which accounts for five of the nine established pests. Among threatening species, ballast water is more significant, accounting clearly for two species, the most likely vector for two more, and a potential vector for another.

The distinction between fouling, in a broad sense, as the dominant historical vector and ballast water as a major recent threat is consistent with our analysis of invasion patterns in Port Phillip Bay (Victoria, Australia) (Hewitt *et al.* 1999). Even so, fouling appears to currently be a threat equal or greater to ballast water, in Port Phillip Bay and elsewhere in Australian waters. Two additional observations appear to support this point.

First, Australian scientists have now surveyed 15 ports for exotic species. All ports surveyed had exotic marine species. However, ports receiving very high levels of ballast water are not generally any more invaded than those receiving little ballast water (Hewitt, in prep.). The exotic species found typically have been in Australian waters since prior to the use of ballast water, and appear to have been introduced into the high ballast water ports by domestic transport, rather than international shipping.

Second, the major invasion events in Australia over the last decade can be attributed to fouling, mariculture operations, and natural dispersal. None appear to be unambiguously a consequence of ballast water transport. These events include the introductions to Australia of *Asterias amurensis*, *Undaria pinnatifida*, *Codium fragile* ssp. *tomentosoides*, and *Mytilopsis sallei*; the domestic translocation of *A. amurensis* and *U. pinnatifida* from Tasmania to Victoria; the spread of *Sabella spallanzanii* and *Maoriculpus roseus*; and the invasion of *C. maenas* from the mainland to Tasmania.

Of these, the only invasions debatably mediated by ballast water are those involving *A. amurensis*. Evidence for this is the presence of *A. amurensis* larvae in ballast water of ships (Martin and Sutton, in prep.). However, we have also collected adults in sea chests of these same vessels, have had several apparently reliable reports of deliberate attempts to spread the species, and small juveniles are cryptofauna in fouling communities and hence routinely found in aquaculture equipment and on mussel ropes, which are moved by the aquaculture industry among sites. With regard to the initial introduction into Australia, the probable point of introduction (the Derwent estuary in Tasmania) receives little ballast water from the original source location in Japan (*e.g.*, in 1991, the only year for which hard data are available, there was only one visit to Hobart from Japan that resulted in a ballast water discharge, and that vessel was from well outside the area that genetic analysis indicates as the probable source location; qualitative information for other years indicate a similar picture). Large volumes of Japanese sourced ballast water are discharged at sites near the Derwent, but improbable scenarios are required to explain why the animals are common in the Derwent, but not at these sites (Ward and Andrew 1995). In contrast, each year the Derwent harbors a sizable fleet of Japanese fishing vessels from areas that genetic analysis (Ward and Andrew 1995) suggests as the probable source location for the invaders. These vessels, which historically were often heavily fouled (Hobart Port Authority, pers. comm.), dock in the Derwent for several weeks at a time. We conclude that although most of the media and many scientific reports have reported *A. amurensis* as a ballast water introduction in Australia, the evidence suggests otherwise.

There are several likely reasons why the assumption was made that ballast water was the relevant vector for *A. amurensis*, and why Australia has emphasized managing this vector, despite evidence of the historical and current role of hull fouling, sea chests, and associated vectors as sources of invaders, and pest species in particular.

First, ballast water unambiguously results in the introduction of exotic species, some of which achieve pest status. Several of the more prominent invasions can be linked to ballast water: in Australia, Gustaff Hallegraeff's work on the transport of toxic dinoflagellates in ballast water (see Hallegraeff and Bolch 1991) was a key discovery that stimulated much of the Australian effort. The zebra mussel (*Dreissena polymorpha*) and its likely introduction in freshwater ballast had a similar effect in North America, as did *M. leidyi* in Europe. The predominance of ballast water as a likely vector for the threatening species not yet in Australia at least in part justifies the current emphasis.

Second, ballast water is conspicuous and the scale of the vector sounds threatening. The perceived threat and the conspicuous nature of ballast water as a vector have made it the transport mechanism to which new invasions are often quickly linked in public and political arenas. With regard to the latter, media emphasis and recent high-profile technical publications have alerted both managers and environmentalists to the problem, and prompted an emphatic reaction.

Third, the prospect of a technical/operational solution to the problem for an industry used to dealing with such issues (and that acknowledges a problem that needs to be solved) contrasts with the more complex solutions that are likely to be required to address fouling, intentional introductions, and accidental and casual releases from mariculture operations. National and international processes are being developed and implemented to deal with these other vectors, but they often lack the focus or prominence attached to ballast water.

Uncertainty about the relative importance of different vectors as a source of invasive species is not a viable excuse to do nothing. Societal and political pressure to respond to these invasions forces managers to make decisions in the face of uncertainty about underlying biology or effectiveness of policy settings. In this environment, I suggest we need to deliver three messages.

1. Provide realistic expectations to management agencies attempting to solve the problem. The diversity of vectors means that even a perfect system of sterilizing ballast tanks will not prevent new, damaging, and high-profile invasions. In the Australian context, even if such a system was available, it is debatable whether it would have had any effect on the invasions and recent range expansions by *U. pinnatifida*, *S. spallanzanii*, or possibly even *A. amurensis*.
2. Manage the manageable. If the technology and politi-

cal, social, and industrial will exists to deal with ballast water, but not yet other vectors, then deal with ballast water. But at the same time, we should continue to emphasize the multifaceted nature of the threat, and seek to ensure that a focus on ballast water does not preclude the availability of resources to deal with other vectors.

3. Develop and help implement management structures and strategies that are compatible with, if not also actually effective against, multiple invasion paths. In so doing, we can help ensure that effort invested now will be equally useful in the future, should the evidence cause a shift in the emphasis of response actions.

Reflecting these messages, the Australian Ballast Water Management Advisory Council is likely to shortly be re-configured as the Australian Introduced Marine Pests Advisory Council. The AQIS has developed action plans for the next several years that address a range of vectors, rather than continuing to focus solely on ballast water.

Managing Pest Populations

Responding to established pest populations has three logically distinct components: (1) early detection of and, if possible, eradication of new incursions, (2) containing infections by minimizing the rate of spread of established pest species, and (3) long-term pest management.

Logically, the most effective time to eradicate a new pest is before it is well established and has spread from the point of initial infection. Three recent examples demonstrate the viability of the approach. In 1998, early detection and rapid response by South Australian Fisheries led to the elimination of a patch of about 20 New Zealand greenlip mussels, *Perna canaliculus*, detected by chance during a research survey. This action appears to have eradicated the invader from South Australian waters (J. Gilliland, pers. comm.). Joint action by scientists and industry appears to have recently eradicated an undescribed South African sabellid that infested *Tegula funebralis* and *Haliotis rufescens* in California (Culver and Kuris, in prep.). In 1999, a large-scale, coordinated program led by the Northern Territory government and involving most Australian states, several Commonwealth agencies, and a number of industry and community groups eradicated an incursion of a dreissenid, *Mytilopsis sallei*, from three Darwin marinas (Bax 1999). The incursion response involved closing the infested marinas, a prolonged program of poisoning using chlorine and copper sulphate, and the tracking and checking of every vessel that had left the marinas since the estimated date at which the dreissenid invaded. The eradication program cost A $2.8 million, and has led to a whole-of-government review of incursion response mechanisms.

Such attempts often fail, however. A recent effort to trap out *A. amurensis* from Port Philip Bay, Victoria, proved to be too little, too late, as did earlier attempts to physically eradicate infections of *S. muticum* in England, *C. taxifolia* in Spain, and *U. pinnatifida* in Tasmania. The practicality of an eradication attempt critically depends on the nature of the invader, the scale of the infestation (and hence the rapidity with which it was detected), and the willingness of relevant authorities and the community to invest the often considerable effort required. Our experience has been that expectations regarding the effort involved are typically unrealistic, so that insufficient resources are made available for the eradication attempt to have any real hope of success. In response, we are currently preparing a management-oriented guide to rapid response options (Bax, in prep.), that will review what has and has not been successful in the past, recommend response actions for different groups of organisms, specify the likely costs (human and financial), and outline the theoretical and conceptual underpinnings for the response action.

Detection of new pest incursions also frequently leads to demands for it to be contained until effective countermeasures can be developed. In Australia, public education programs and some management actions have been instituted in an attempt to reduce the rates of spread of *U. pinnatifida*, *C. fragile* spp. *tomentosoides* and *A. amurensis*. A similar program against *U. pinnatifida* is underway in New Zealand. The critical issues clearly relate to potential transport vectors, the extent to which they can be managed, and, again, the willingness of government to act. Our experience has been that marine quarantine zones are difficult politically to establish, are often not maintained once the original flurry of activity has passed, and rarely incorporate a community awareness program sufficiently well designed and coordinated as to generate the level of voluntary compliance typically required. The notable exception was the quarantine erected to contain *M. sallei* in Darwin. The very rapid and strong response by government agencies, which included declaring a state of emergency, impounding vessels, at-sea hull inspections, and a well-coordinated public relations campaign, was effective, but also expensive. Legal action for compensation arising from the quarantine is still pending.

Once a pest species is established, the options for its long-term management are still few. In Australia, two crucial sets of issues emerge almost immediately when control options are discussed. The first is an attitude of defeatism. Most managers have stated implicitly or explicitly that once a pest is established, we have to learn to live with it. The reasoning behind this attitude flows from the second issue: the social milieu in which control needs to be undertaken differs fundamentally from those for land or freshwater-based control programs (Lafferty and Kuris 1996). There are three critical differences. First, the ocean is perceived by much of the public as pristine; this perception is illogical and easily refuted in principle, but difficult to overturn in practice. Because of it, suggestions of releasing a local biocide or an exotic biological control organism sometimes evoke strong, negative reactions, based on a perception that it would degrade the pristine ocean. The second difference is the perceived fenceless ocean, which has two important consequences: because marine organisms are perceived to have unlimited dispersal potential, (1) managers assume that local actions are not likely to have local impacts on the target organism, and (2) a segment of the community assumes that any management action, but particularly biological control, will impact adjacent areas, and more to the point, their adjacent areas (a manifestation of the "not in my backyard" syndrome). The third critical difference is that the ocean is utilized by hunter-gatherers (fishermen) who (1) are suspicious of any perceived threat to their independence or fishing success and (2) harvest dispersed resources, which makes it difficult to assign a dollar value to pest impacts or recover cost of control actions. There are obvious exceptions to the last point, such as mariculture operations and pests that affect industrial operations, but these are a minority. Lafferty and Kuris (1996) also raise the point that the level of control required for a marine pest may often be less than required for terrestrial agricultural pests. This is probably true in principal, but may not be true in practice; conservation groups typically push a strong agenda for complete eradication, even if this is currently impractical with available technology for widely distributed pests.

Norton (1988) provides a useful process to evaluate the conflicting objectives of pest eradication and the pristine ocean syndrome. He suggested that for any pest management program to be successful it must fulfill all of five criteria: it must be (1) technically possible, (2) practically feasible, (3) environmentally acceptable, (4) economically desirable, and (5) politically advantageous.

Table 3. Evalution of potential control options for *Asterias amurensis*, using the criteria proposed by Norton (1988). Based on Goggin (1998). The criterion of economic desirability is assumed to have been answered in the positive before any of these options are applied.

Method	Effective	Environmentally Acceptable	Practical	Politically Advantageous
Physical Control				
Trapping	Small scale only	Yes	Yes	Yes
Hand collection	Small scale only	Yes	Yes	Yes
Dredging	Small/Medium scale	No	Yes	No
Mopping	Small/Medium scale	?	Yes	?
Fencing	Small scale only	Yes	Yes	Yes
Chemical Control				
Broadcast	Medium scale only	No	Yes	No
Injection	Small scale only	Yes	?	Yes
Barriers	Farm scale only	Yes	?	No
Enviromental Remediation				
Rehabilitation	?	Yes	?	Yes
Redulate nutrients	?	Yes	?	?
Biocontrol				
Native predator	?	?	?	Yes
Native parasite	?	?	?	Yes
Exotic predator	?	No	?	No
Exotic parasite	?	Yes	Yes	?
Genetic Control				
Programmed fatality	Yes	Yes	?	?
Inducible fatality	Yes	Yes	?	?
Vectored sterilization	Yes	?	?	?

The last is perhaps the most important and the most often overlooked. The crucial standard is not that a management approach be politically acceptable, but rather that the politicians and/or bureaucrats who ultimately will approve application of a control mechanism must benefit from this decision. A good recent Australian example is the proposed use of ichthyocides to kill carp in rivers. Although it appears to be technically feasible to develop a carp-specific biocide, approving the release of such a "poison" into waters in which children swim and farm stock and human communities draw drinking water would be a "brave" decision by a minister, and hence one that may never be taken.

We have applied Norton's (1988) approach to evaluate possible control options for *A. amurensis* in the Australian cultural context (Table 3) (Goggin 1998). From this and similar exercises we have undertaken for other species, pest management options can be ranked on the basis of political and social likelihood of being supported. In descending order of acceptability, these are:

1. Do nothing; the problem might go away.
2. Rehabilitate the environment, in the belief that pests are only problems in degraded areas.
3. Physically remove pests from important sites (fish farms, marine reserves) and ignore the rest.
4. Utilize the pests commercially.
5. Deploy species-specific biocides, reproductive inhibitors, etc.
6. Encourage native predators.
7. Deploy general biocides, selectively applied.
8. Encourage native diseases and parasites.
9. Apply novel genetic approaches that affect only the pest.
10. Apply classical biocontrol, using exotic parasites.
11. Apply classical biocontrol, using exotic nonviral diseases.
12. Apply novel genetic approaches that involve modification of native species (*i.e.*, to use them as vectors).

On the basis of our discussions, two additional approaches are unlikely to be supported in Australia under any circumstances: biocontrol using an exotic predator and biocontrol using a viral disease (or even worse, a genetically modified virus). I suspect these options would not be supported anywhere.

A key element in this ranking is reversibility. Up to option 8, if things go wrong, no permanent change to the system has been made due to the response action itself. From option 9 onwards, participants in our workshops were very loathe to commit, which is reasonable given uncertainties on the specifics of each application. However, there was very strong resistance to the permanent introduction of "another" exotic species—a disease or parasite—to address a problem caused by the original introduction. This contrasts remarkably with Australia's relatively frequent importation and release of insect biological control agents against terrestrial weeds, and reflects the social considerations discussed above.

This ranking does not reflect the likelihood of success. Options 1 and 2 are largely wishful thinking, though option 2 has benefits in its own right and constitutes a "no-regrets" attempt at pest remediation. Physical removal is only likely to be successful against species early in an invasion, and will be limited to those species that can be easily identified and removed. Application of physical removal on a large scale, *e.g.*, commercial harvesting, can generate strong advocates, but was not supported by fisheries and marine environmental agencies on the basis of institutionalizing a pest and encouraging its translocation to areas not already infested. Biocidal approaches were close to the nervousness threshold, but were generally considered acceptable if suitable safety tests were done, collateral damage was slight, and an effective delivery mechanism could be found; the last requirement was considered a major technological difficulty. Among biocontrol options, the only broadly supported approach was enhancing native species to combat the invader, though it was also agreed this would probably not be effective in the long term. Genetic approaches that only modified the target species was also considered likely to be widely supported. Classical biocontrol were broadly seen as an option of last resort, which would require extensive public consultation before it was approved.

Next Pests: What are the Key Threats

The social, economic, and political factors that define a marine pest species are rarely based on a quantitative assessment of real impacts. More often, pest status is conferred on the basis of perceived impacts in other areas and aspect dominance. The central issue, unexamined for most species, is whether a pest does something substantially different from the endemic species it displaces or co-exists with, and, ultimately, whether it distorts nutrient and energy flows and shifts community composition to the point where the effects are conspicuous and/or local species face extinction. Although any exotic species must have an impact, this statement alone is clearly inadequate to justify the cost of reducing its impacts. Invasive species offer huge opportunities to investigate in a quantitative and robust way the dynamics of marine communities, but the extent to which the impacts of a particular species justify remediation can be difficult to determine.

In that light, what are the real threats? I suggest three groups of organisms that not only have a high likelihood of invading, but also are likely to cause substantial ecological and economic impacts.

1. Marine pathogens, parasites, and fungi—Hallegraeff (1993) noted the apparent recent increase in the frequency of toxic algal blooms, which he attributed to the introduction of exotic species in ship's ballast. Since then, outbreaks of marine pathogens, often unexplainable, have occurred with increasing frequency. Examples range from the pilchard kills off southern Australia and New Zealand (Jones *et al*. 1997), which might be the result of an as-yet-unidentified viral agent,

well-publicized *Pfisteria* outbreaks on the U.S. east coast, toxigenic *Vibrio cholera* in the U.S. Gulf states (McCarthy and Khambaty 1994), lobster kills attributable to *Vibrio fluvialis* off Maine, and seal kills in the Mediterranean, suggested to be the result of blooms of introduced toxic dinoflagellates (Hernandez *et al.* 1998).

Marine pathogens are particularly dangerous in two respects. First, the vectors that can transport them are diverse, defenses against them are difficult to develop, and legislative barriers to minimize risks may be difficult to enforce. Australian efforts to prevent importation of fresh Canadian salmon products, for example, as a means of protecting the current disease-free status of the stocks has been rejected by the World Trade Organization as an unjustified trade barrier. This decision is being appealed. Second, pathogens have the potential to fundamentally alter the dynamics of marine systems, perhaps more so than any other group. The decimation of the Caribbean urchin, *Diadema antellarum*, in the 1980s, due apparently to a marine pathogen of unknown origin (Lessios *et al.* 1984), had a profound effect on algal-coral dynamics throughout the region and fundamentally altered the composition of Caribbean reef communities (Hughes 1994). There are similar reports in other regions. Duncan *et al.* (1982) reported on a mass die-off of a large keystone predator seastar in the Sea of Cortez, attributed to unusually warm temperatures and the action of an as-yet-unidentified pathogen, and suggested major changes in benthic communities as a result. A similar die-off of the seastar, *Asterias rubens*, off the coast of the northeastern United States occurred in the 1990s, again for unknown reasons ("ray rot disease"), but attributed at least in part to stress due to water temperatures. Anthropogenically enhanced dispersal of marine pathogens to naive populations may prove to be one of the major challenges globally to marine industries and ecosystems, and is one that we are particularly poorly prepared to handle.

2. Invasive marine macroalgae—Introduced macroalgae are already common and causing substantial concern: *U. pinnatifida* in Australia, New Zealand, and Europe; *C. fragile* ssp. *tomentosoides* in America, Australia and New Zealand; *S. muticum* in Europe; and a number of species of C*aulerpa* at sites worldwide. As well, there are increasingly more frequent reports of pest macroalgal blooms at both temperate and tropical sites (Raffaelli *et al.* 1998), often involving broadly distributed genera and attributed, possibly incorrectly, to outbreaks by native species (as per arguments in Carlton 1996). Introduced macroalgae have a number of features that facilitate their invasion, most notably an ability to easily transport by a variety of vectors and, in many instances, limited dispersal abilities of motile reproductive stages (facilitating population establishment), as well as vegetative and clonal reproduction. Invasive plants may often do little more than increase local diversity or replace native congenerics (Trowbridge 1998), but in at least some cases they clearly occupy habitats and reach such high densities that they become space dominants and fundamentally change community dynamics. Again, preventative options against such invasions are poorly developed, nor do we have any effective means to combat such species once they have invaded. Physical removal has proven unsuccessful in a number of instances, and herbicidal and biological options are still far from being developed.

3. Genetically enhanced production species—The invasion of the Mediterranean by an artificial hybrid of *C. taxifolia*, selectively bred for increased growth and environmental tolerances (Jousson *et al.* 1998), is likely to be only the first of what may in the long term prove to be one of the major problems facing marine systems. Work is underway worldwide to produce species for marine mariculture that grow faster and are more environmentally tolerant than existing species. At least some of these species, such as Pacific oysters (*C. gigas*), are already considered pests in Australia when feral, a situation likely to only worsen when "super-oysters" are introduced. Unlike terrestrial systems, where production lines are often competitively inferior because they are selected for rigidly controlled farm conditions, mariculture often relies on what are essentially natural and unregulated environments, and, hence, in the short term at least, will seek organisms capable of increased production under natural conditions. When these enhanced plants and animals are introduced, it may well be impossible to stop their spread and consequent impacts on native communities. Although the problem has been recognized and some work to contain such production organisms is underway (*e.g.*, the Australian "sterile ferals" project), it is very unclear that caution, regulations, and technological solutions will be adequate to counter advocates driven by increased profit margins and increasing demand worldwide for seafood products. The vectors associated with the introduction of these super-competitors at first are likely to be quite different from those with which we are currently concerned, but as shown in the Mediterranean, once such a taxon is established, the familiar vectors, such as fouling on anchor chains, rapidly come into play in spreading the pest (Meinesz *et al.* 1998).

The prospects for managing these threats are mixed. Marine pathogens are likely to be manageable by reducing the likelihood of transport and by modifications of mariculture and human health operations post-invasion to minimize impacts. As ballast water appears to be a very suitable vector for pathogens, it is crucial that treatment processes for it are effective against them. Treatments that deal only with metazoans and their larvae not only may be targeting the lesser threat, but may even exacerbate the threat due to pathogens (Desmarchalier 1997). Dealing with marine invasive plants, although technically challenging, is likely to be able to borrow from the Integrated Pest Management (IPM) approaches developed for terrestrial weeds, including topical application of specialized herbicides, physical control, and classical biological control. The information we require to implement IPM for any marine plant is lacking, but the conceptual approaches appear to be in place. This is not likely to be true for genetically enhanced invaders. For these, as is the current situation with *C. taxifolia* in the Mediterranean, problem species will need to be approached on a case-by-case basis.

Conclusions

Australia's decade of concerted and coordinated attempts to manage the problem of introduced marine pests has resulted in some successes, some failures, and a far better understanding of the scope of the problem and the scope for management action. A principle outcome of such knowledge is a much greater public and political appreciation of the problem. But this appreciation has led to demands that scientists and managers solve the problem, which has proven difficult at best.

Australia has structured its approach to introduced marine species around a zonal defense system. The first zone—up-take and transport—is targeted by the Australian Ballast Water Management Advisory Council and the Australian Quarantine and Inspection Service, as well as several states. The Northern Territory, for example, evaluates the risk posed by arriving recreational yachts and fishing vessels, and, when in doubt, requires a hull survey and sterilization of any plumbing open to seawater prior to allowing international vessels into berths.

Zone 1 is permeable. Even assuming we could sterilize ballast tanks and clean hulls, sea chests, and internal plumbing, pests would still arrive. To the extent that we have done none of that, or demonstrated that what management actions we have initiated, such as exchanging ballast at sea, are even effective at reducing the rate of invasions, we have barely slowed the invasion rate, if at all. But the preconception that once a species arrives, you have lost the game is not only unacceptable, but wrong. Several successful eradication attempts have been launched in the last few years, though all combined an element of good luck, good planning, and a suitable, still contained incursion. Australia is formalizing a process to maximize its luck, by establishing a nationally coordinated system to manage its second defense zone—the receiver ports. Action is seen to be primarily a state responsibility and, since the successful eradication of the black-striped mussel in particular, focuses on rapid detection of new pest species, development of tactical control options, and the establishment of an effective system of communication among state and commonwealth agencies that would need to be involved. Public awareness campaigns have been put in place in all Australian states, and several are developing programs for routine surveillance of high-risk environments. As well, work has begun at developing more effective and better targeted biocides than the broad spectrum chemicals employed in Darwin.

The third zone of defense is long-term pest control. We have begun testing commercial harvesting as a means of reducing pest numbers, are assessing the potential of environmental remediation to reduce the numbers of *A. amurensis* and *U. pinnatifida*, and have projects underway looking into both biological control and the development of novel biomolecular techniques for pest control. Which, if any, of these approaches will prove useful is still to be determined.

At times, the biological, bureaucratic, and political complexity of the problem is daunting. But, slowly, management structures are being put in place that encourage (and in some instances) require protocols to lower risks of new introductions; programs have begun to be better integrated nationally, particularly through the actions of the recently established Australian National Taskforce on Managing Marine Pest Incursions; and managers are beginning to appreciate the scale of the resources required to solve the problem. The cost of eradicating the dreissenid, *Mytilopsis sallei*, in Darwin, at just under A $3 million, drove home not only the cost of poor barrier controls, but also the threat that even one particularly bad pest species posed to Australia's biodiversity and marine industries.

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Literature Cited

Australia's Oceans Policy. 1999. Environment Australia, Canberra, Australia.

Bax, N. 1999. Eradicating a dreissenid from Australia. *Dreissena!* 10:1-5.

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

Clark, P.F., P.S. Rainbow, R.S. Robbins, B. Smith, W.E. Yeomans, M. Thomas, and G. Dobson. 1998. The alien Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura), in the Thames Catchment. *Journal of the Marine Biological Association of the U.K.* 78:1215-1221.

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.* Unpublished Report for the U.S. Fish and Wildlife Service, Washington, D.C., and the National Sea Grant College Program, Connecticut Sea Grant, NTIS Report No. PB96-166525. 246 pp. and appendices.

Cohen, A.N. and J.T. Carlton. 1997. Transoceanic transport mechanisms: introduction of the Chinese mitten crab, *Eriocheir sinensis*, to California. *Pacific Science* 51:1-11.

Cranfield, H.J., D.P. Gordon, R.C. Willan, B.A. Marshall, C.N. Battershill, M.P. Francis, W.A. Nelson, C.J. Glasby, and G.B. Read. 1998. *Adventive Marine Species in New Zealand.* NIWA Technical Report # 34, Wellington, N.Z.

Desmarchalier,T. 1997. *The Potential for Vibrio cholerae to Translocate and Establish in Australian Waters*. Report to the Australian Ballast Water Management Advisory Council Research Advisory Group. Australian Quarantine and Inspection Service, Canberra, Australia.

Duncan, M.L., T.E. Miller, and D.A. Thomson. 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. *Science* 216:989-990.

Eno, N.C., R.A. Clark and W.G. Sanderson (eds.). 1997. *Non-native Marine Species in British Waters*. Joint Nature Conservation Commission, Peterborough, U.K.

Goggin, C.L. (ed.). 1998. *Proceedings of a Meeting on the Biology and Management of the Introduced Seastar Asterias amurensis in Australian Waters.* CRIMP Technical Report #15, Hobart, Australia.

Hallegraeff, G. 1993. Review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99.

Hallegraeff, G. and C.J. Bolch. 1991. Transport of toxic dinoflagellate cysts via ship's ballast water. *Marine Pollution Bulletin* 22:27-30.

Hernandez, M., I. Robinson, A. Aguilar, L.M. Gonzalez, L.F. Lopez-Jurado, M.I. Reyero, E. Cacho, J. Franco, V. Lopez-Rodas, and E. Costas. 1998. Did algal toxins cause monk seal mortality? *Nature* 393:28-29.

Hewitt, C.L., M.L. Campbell, R. Thresher, and R.B. Martin (eds.). 1999. *Marine Biological Invasions of Port Phillip Bay, Victoria.* CRIMP Technical Report #20. 344 pp.

Hughes, T.P. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551.

Jones, J.B., A.D. Hyatt, P.M. Hine, R.J. Whittington, D.A. Griffin, and N.J. Bax. 1997. Special topic review: Australasian pilchard mortalities. *World Journal of Microbiology and Biotechnology* 13:383-392.

Jousson, O., J. Pawlowski, L. Zaninetti, A. Meinez, and C.F. Boudouresque. 1998. Molecular evidence for the aquarium origin of the green alga *Caulerpa taxifolia* introduced to the Mediterranean Sea. *Marine Ecology Progress Series* 172:275-280.

Lafferty, K.D. and A.M. Kuris. 1996. Biological control of marine pests. *Ecology* 77:1989–2000.

Lessios, H.A., D.R. Robertson, and J.D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335-337.

Manning, M., S.B. Kerr, and D. Staples. 1996. *Ballast Water—Overview Report by the Scientific Working Group on Introductions of Exotic Organisms through Ship's Ballast Water.* AQIS Ballast Water Research Series, # 9. Canberra, Australia.

McCarthy, S.A. and F.M. Khambaty. 1994. International dissemination of epidemic *Vibrio cholerae* by cargo ship ballast and other non-potable waters. *Applied Environmental Microbiology* 60:2597-2601.

Meinesz, A., J.M. Cottalorda, D. Chiaverini, N.Cassar, and J. de Vaugelas. 1998. *Suivi de L'Invasion de L'Algae tropicale Caulerpa taxifolia en Mediterranee: Situation au 31 Decembre 1997.* Laboratorie Environmental Marin Littoral, Universite Nice-Sophia, Antipolis, France.

Norton, G.A. 1988. Philosophy, concepts and techniques. pp. 1-17 In: Norton, G.A. and R.P. Pech (eds.). *Vertebrate Pest Management in Australia.* CSIRO, Canberra, Australia.

Paterson, D. 1994. Ballast water-an Australian perspective. pp. 23-43 In: *AQIS Ballast Water Symposium Proceedings*, Australian Government Publication Service, Canberra, Australia.

Raffaelli, D.G., J.A. Raven, and L.J. Poole. 1998. Ecological impact of green macroalgal blooms. *Annual Review of Oceanography and Marine Biology* 36:97-125.

Trowbridge, C.D. 1998. Ecology of the green macroalga *Codium fragile* (Suringar) Hariot 1889: invasive and non-invasive subspecies. *Annual Review of Oceanography and Marine Biology* 36:1-64.

Ward, R.D. and J. Andrew. 1995. Population genetics of the northern Pacific seastar *Asterias amurensis* (Echinodermata:Asteriidae): allozyme differentiation among Japanese, Russian, and recently introduced Tasmanian populations. *Marine Biology* 124:99-109.

Sources of Unpublished Material

Bax, N. Final Report in Preparation. *Rapid Response Options for Managing Marine Pest Incursions.* National Heritage Trust Grant. Environment Australia, Canberra, Australia. CRIMP.

Culver, C. and A. Kuris. University of California at Santa Barbara. January 1999.

Gilliland, J. South Australian Department of Primary Industry, April 1998.

Hewitt, C. Manuscript in preparation. Distribution and abundance of introduced marine species in Australian ports. CSIRO Centre for Research on Introduced Marine Pests, Hobart, Tasmania, Australia.

Hobart Port Corporation, Hobart, Tasmania, Australia. July 1999.

Martin, R. and C. Sutton. Final Report in Preparation. *Survivalibility of Target Species in Ballast Water*. Report to the Australian Ballast Water Management Advisory Council Research Advisory Group. AQIS, Canberra, Australia. CRIMP.