



SHELLFISH REEFS **AT RISK**

A Global Analysis of Problems and Solutions

Michael W. Beck, Robert D. Brumbaugh, Laura Airoidi,
Alvar Carranza, Loren D. Coen, Christine Crawford, Omar Defeo,
Graham J. Edgar, Boze Hancock, Matthew Kay, Hunter Lenihan,
Mark W. Luckenbach, Caitlyn L. Toropova, Guofan Zhang

CONTENTS

Acknowledgments.....	1
Executive Summary	2
Introduction	6
Methods	10
Results	14
Condition of Oyster Reefs Globally Across Bays and Ecoregions.....	14
Regional Summaries of the Condition of Shellfish Reefs	15
Overview of Threats and Causes of Decline	28
Recommendations for Conservation, Restoration and Management	30
Conclusions	36
References	38
Appendix 1	42

Michael W. Beck^a, Robert D. Brumbaugh^b, Laura Airoidi^c, Alvar Carranza^d, Loren D. Coen^e, Christine Crawford^f, Omar Defeo^d, Graham J. Edgar^g, Boze Hancock^g, Matthew Kay^h, Hunter Lenihan^h, Mark W. Luckenbachⁱ, Caitlyn L. Toropova^a, Guofan Zhang^j

^a The Nature Conservancy, Institute of Marine Sciences, University of California, Santa Cruz, CA, 95060

^b The Nature Conservancy; PO Box 420237, Summerland Key, FL 33042

^c Dipartimento di Biologia Evoluzionistica Sperimentale, Università di Bologna, Via S. Alberto 163, I-48100 Ravenna, Italy

^d Marine Science Unit, Ecology Department, Faculty of Sciences, Montevideo, Uruguay

^e Sanibel-Captiva Conservation Foundation, 900A Tarpon Bay Road, Sanibel, FL 33957

^f Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Hobart, Tasmania, Australia

^g The Nature Conservancy; University of Rhode Island, Narragansett, RI 02882

^h Bren School, University of California, Santa Barbara, CA 93106-5131

ⁱ Virginia Institute of Marine Science, College of William and Mary, Wachapreague, VA 23480

^j Institute of Oceanology, Chinese Academy of Sciences, Qingdao, Shandong 266071, China



ACKNOWLEDGEMENTS

© Barry Truitt/TNC

Many colleagues contributed to this assessment by providing access to data sets ranging from local to global scales, helping to find important and often obscure references, and offering recommendations based on personal and professional experiences. A pair of expert workshops was convened at which participants offered an array of perspectives from scientific research institutions, management agencies, conservation organizations, and the shellfish aquaculture industry. These workshops were instrumental for crafting recommendations in this report and informing the outcomes.

Some of the many people and participants who provided information and perspectives included Bill Arnold, Anne Birch, Rafael Calderon, Ximing Guo, Li Li, Bill Eichbaum, Colin Brannen, John Caddy, Fei Xu, Aad Smaal, Antonella Fatone, Adriana Gracia, Alex Gamarra, Marcela Pascual, Marcelo Henriques, Melissa Holman, Luis Prado, Luis Leon, César Lodeiros, Michael Savarese, Margaret Spring, Greg Tolley and Aswani Volety

The authors in particular thank Christine Shepard, Zach Ferdaña, Jeff Vincent, Antonella Fatone, Ximing Guo, and Bill Arnold for help with the data, figures and maps.

We also thank our many colleagues in the field who have already been working diligently to conserve and restore shellfish habitats and ecosystems. We have learned so much from them. Lynne Hale, Erica Rychwalski, and Emily Woglom have provided critical support and thinking at many times in the development of the report and recommendations.

Funding for this assessment was provided by The Kabcenell Family Foundation. Financial support through the National Partnership between The Nature Conservancy and NOAA Community-based Restoration Program is also gratefully acknowledged. Support was also provided by the University of Bologna through project Adriabio.

Citation: Beck, M.B., R.D. Brumbaugh, L.Airoidi, A. Carranza, L.D. Coen, C. Crawford, O.Defero, G.J. Edgar, B.Hancock, M. Kay, H. Lenihan, M.W. Luckenbach, C.L. Toropova, G. Zhang. 2009. Shellfish Reefs at Risk: A Global Analysis of Problems and Solutions. The Nature Conservancy, Arlington VA. 52 pp.



EXECUTIVE SUMMARY

© Barry Truitt/TNC

Once dominant features in many temperate estuaries around the world, native oyster reefs are critically important ecologically and economically. Centuries of intensive fisheries extraction exacerbated by more recent coastal degradation have put oyster reefs near or past the point of functional extinction globally, but sensible solutions that could ensure conservation of remaining reefs and even reverse losses to restore ecosystem services are available. These solutions involve wider application of area-based conservation approaches, improvements in fisheries management, enhanced restoration for multiple ecosystem services (e.g., water filtration, nutrient removal, shoreline protection and fish habitat provision), and partnerships to improve water quality.

This is the first global assessment of the distribution and condition of bivalve shellfish reefs that occur in temperate and subtropical estuaries. The assessment is focused primarily on biogenic reefs formed by oysters within their native ranges, but also includes observations about mussels that form beds and provide other ecosystem services. We compiled quantitative and qualitative data about these reef-forming species from published literature as well as expert surveys and direct observations and derived condition estimates for oyster reefs in 144 estuaries and 40 ecoregions around the world. Based on these data, we conclude that shellfish reefs are one of, and likely the most, imperiled marine habitat on earth: oyster reefs are in poor condition, defined as having declined >90% from historic levels, in 70% of bays and 63% of marine ecoregions. Even more troubling, oyster reefs are functionally extinct (>99% loss of reefs) in 37% of estuaries and 28% of ecoregions. Globally, we estimate that 85% of oyster reefs have

been lost—even greater than the losses reported for other important habitats including coral reefs, mangroves, and seagrasses. Although oyster reefs are beginning to receive some conservation attention, they remain an obscure ecosystem component and still are vanishing at sometimes alarming rates.

Many threats that have contributed to the profound loss of reefs around the world continue largely unabated today. Destructive fishing practices that directly alter the physical structure of reefs have been implicated in rapid declines in both fisheries productivity and overall reef condition in many estuaries. Fishing practices involving translocation and introduction of non-native shellfish within and between bays has increased the incidence and severity of disease and parasite outbreaks that have all but eliminated fisheries in many coastal areas. Coastal development activities including filling (“land-reclamation”) and dredging of shipping channels have also taken a toll on reefs. Likewise, activities occurring upstream continue to cause problems as human populations increase in coastal watersheds. Altered river flows, construction of dams, poorly managed agriculture, and urban development can all impact the quality and quantity of water and sediments that affect whether shellfish reefs persist or perish.

There are many things that can and should be done to address this glaring gap in marine conservation. We identify a series of cost-effective strategies that can help turn the tide. No one strategy will be right for each area or threat and it is assumed that multiple strategies will be needed in most places. The strategies are grouped into five themes:

- **Improve Protection** for reefs of native shellfish;
- **Restore and Recover Reefs** back to functioning ecosystems that provide multiple services to humans;
- **Manage Fisheries Sustainably** for ecosystems and livelihoods;
- **Stop the Intentional Introduction and Spread of Non-native Shellfish**; and
- **Improve Water Quality.**

First, Native, wild oyster reefs need to be recognized explicitly as a priority for habitat management and conservation and in the development of protected area policies. They are an imperiled habitat with little protection in place. Because they are typically found nearshore and are relatively static features in the coastal zone, shellfish reefs are conducive to being managed through area-based approaches such as marine protected areas (MPAs) and community concessions.

Second, reef recovery and restoration is needed on a scale commensurate with losses. Existing funds can be used better and new funding streams are possible for rebuilding reefs and their services.

Third, shellfish reefs must be managed with more than just fisheries landings in mind. Other ecosystem services such

as water filtration, nutrient removal, shoreline protection, and provision of fish habitat should receive the same consideration (or greater, depending on location) as fisheries in management objectives. Greater use should be made of these tools and approaches.

Fourth, further introductions of non-native oyster species to new areas should not be allowed. The cumulative impacts of the globalization of a few oyster species (and their hitchhikers) have been great, and few regions remain that are still free of introduced oysters.

Fifth, addressing threats originating within watersheds such as nutrient pollution, erosion, excessive sediment supply, and altered freshwater flows, will increase the effectiveness of conservation and management. Enhancing native populations will help restore natural biofiltration capacity in estuaries and bays.

The condition of oyster reef habitat is generally poor and the challenge in revitalizing native oyster reefs is great. Nevertheless we suggest many reasonable actions that will work on local to regional to global scales. Fundamental to ensuring success of these actions, oyster reefs and other shellfish-dominated habitats need to be managed as critical components of coastal ecosystems and the commitment must be built to restore their vital functions in coastal marine systems around the globe.



Monitoring restored oyster reefs in North Carolina.
© Rob Brumbaugh/TNC



Oyster restoration site in North Carolina. © Aaron McCall/TNC

KEY RECOMMENDATIONS

FOR REEF CONSERVATION AND RESTORATION

Ecological Significance

- **Shellfish are ecosystem engineers** that create conditions that allow many other plant and animal species in estuaries and coastal bays to thrive world-wide.
- **Shellfish provide many ecosystem services**, which need to be more fully integrated into policies and management frameworks.
- **Oyster reefs were in many regards the temperate equivalents of tropical coral reefs.** Both reef types possess a surface veneer of living animals overlaying consolidated calcareous frameworks of dead shells that can be meters thick.

Condition of Oyster Reefs

- **Oyster reefs in most ecoregions where they historically occurred are in poor condition and at risk of extirpation as functional ecosystems.**
 - 1) **In most individual bays and ecoregions there has been a >90% loss in oyster reef habitat. In some bays, losses are >99%.**
 - 2) **Globally, 85% of oyster reefs have been lost,** making oyster reefs one of the most severely impacted marine ecosystem on the planet.
- **There are a few bays and regions where reefs are in fair condition.** These bays present a real opportunity for conservation action. New approaches are needed to ensure that the same well-trodden and ineffective management path taken in more than 100 other bays is not followed.

Improve Protection

- **Protect the Last, Best Reefs.** Our work highlights that there are a few key areas remaining for conservation.
- **Develop MPAs for Oyster Reefs.** Oyster reefs and other shellfish habitats are rarely identified as a management or conservation feature within MPAs; they should be and they can work.
- **Recognize Reefs as Ecosystems in Protected Area Policies.** Shellfish reefs need to be recognized as habitats in representative protected area policies such as those arising nationally from commitments to the Convention on Biological Diversity.

- **Recognize Oyster Reefs as Critical Wetlands under the Ramsar Convention.** Oyster reefs should be specifically identified for protection under this convention and further, should be regarded with other similar wetlands (e.g., seagrasses, coral reefs, mangroves, and kelp forests) as an “under-represented wetland type.”
- **Expand Listings for Oysters as Imperiled Species and Threatened Habitats.** For some places and species, at-risk listings for oysters are needed and a number of countries have done so (e.g., UK, Netherlands, Ukraine, and Canada).
- **Develop Shellfish and Temperate Reef Commitments in Global Organizations.** International agencies and environmental organizations, many of which are based in the U.S. and EU, should bolster these efforts by encouraging commitments on temperate reefs; these could be part of an overall focus on temperate and tropical reefs.

Restore and Recover Reefs and Their Services

- **Set Restoration and Recovery Goals.** Regional and national goals need to be set for restoration and recovery. The condition estimates provided in this report can help.
- **Use Existing Restoration Funds Better.** Some of the tens of millions of dollars spent annually to recover fisheries should be invested in rebuilding the natural capital of reefs to provide for multiple benefits including fisheries where the interest, not the principal of our investments is harvested.
- **Support Public-Private Partnerships to Restore Natives.** The aquaculture industry, public agencies and environmental NGOs are natural partners for promoting the restoration of native oysters and their services, which could be profitable for businesses and reduce costs for restoration programs.
- **Develop New Funding Mechanisms Around Ecosystem Services: Nitrogen.** Nitrogen pollution has grown exponentially in recent decades and nitrogen markets are being developed. The ability of shellfish to sequester nitrogen in their tissues is one direct route for nitrogen reduction, and approaches are being developed to market them for this function.

- **Develop New Funding Mechanisms Around Ecosystem Services: Shoreline Protection.**

Oyster reefs can play a key role in helping to defend shorelines and reduce erosion, and there are a growing number of tests and applications of this approach.

- **Reduce Perverse Incentives that Make Restoration More Difficult.** One of the few potential “protections” for shellfish occurs in areas where human harvest is prohibited because of poor water quality. Unfortunately, restoration in such areas is sometimes not allowed because shellfish in these locations are regarded as an “attractive nuisance”; better policy approaches could be developed.

Manage Fisheries Sustainably

- **Develop and Adhere to Fishery Rebuilding Plans for Oyster Reefs.** The development of rebuilding plans for fisheries is increasingly common, but not for oysters.
- **Stop Fishing in Areas with Less than 1% of Shellfish Remaining.** It is still surprisingly common for harvest to be allowed when only ~ 1% of stocks remain.
- **Ensure Sustainable Fisheries in the Gulf of Mexico.** The oyster fisheries of the Gulf of Mexico need to be managed for what they represent: likely the last opportunity in the world to achieve both large-scale reef conservation and sustainable fisheries.
- **Learn from Successes.** In the few areas with shellfish reefs in good condition, we need to learn from and expand effective conservation and management approaches.
- **Use Private Fishing Rights More Effectively and Promote Greater Stewardship.** The extensive use of private rights approaches for shellfish (e.g., concessions of submerged lands) should provide a basis for more effective management.
- **Map Reefs to Assess Management Effectiveness.** To better manage for sustainable fisheries and reef rebuilding, the distribution of remaining reefs must be mapped.

Stop the Intentional Introduction and Spread of Non-native Shellfish

- **Follow ICES Protocols.** At a minimum all International Council for the Exploration of the Sea (ICES) codes of practice for marine introductions and transfers should be followed in aquaculture.
- **Stop Intentional Introductions.** Given the widespread impacts from the spread and globalization of just a few oyster species, we cannot recommend any further introductions.
- **Support Hatcheries and Business that Grow and Use Native Shellfish Seed** with incentives or other market forces.
- **Support Aquaculture that Relieves Pressure on Reefs and Wild Stocks.** When done well and combined with other fishery regulations, aquaculture can reduce pressure on harvest of wild reefs.

Improve Water Quality

- **Use Shellfish as Bioindicators.** Because of their close ties to many estuarine processes and their ability to bioaccumulate, oysters can be used as bioindicators for water quality and overall achievement of estuarine conservation and restoration targets.
- **Enhance or Establish Shellfish Partnerships Across Sectors.** There is much common ground between the aquaculture industry, environmental NGOs, and managers in helping to conserve and restore the coastal water quality that is vital to cultured and wild shellfish.
- **Support Sustainable Aquaculture.** Shellfish aquaculture can be done more sustainably than most other fisheries or aquaculture, and these businesses rely on clean coastal waters and are key stakeholders for preserving and improving water quality.

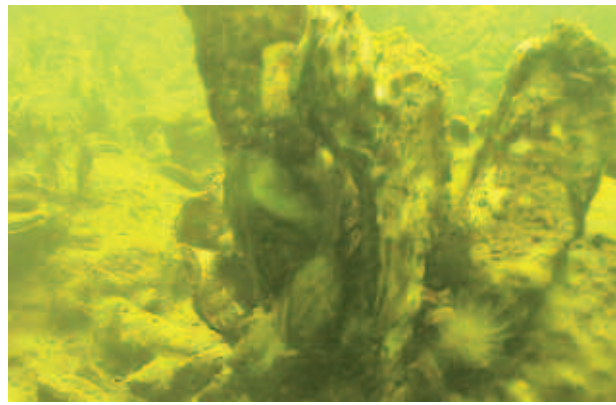
“...the most dazzling error does not become transformed into truth, no matter how long and firmly one may believe in it.” Karl Mobius, (1883)



INTRODUCTION

Oyster reefs and beds (hereafter just reefs) were once a dominant structural and ecological component of estuaries around the globe, fueling coastal economies for centuries. Oysters are ecosystem engineers; often one or a few species produce the underlying structure for entire ecosystems (Lenihan and Peterson 1998). Oyster reefs provide many services including fisheries; food and habitat for fish, crabs, and birds; water filtration; and shoreline stabilization and coastal defense; they have supported civilizations for millennia from Romans to railroad workers in California (Mackenzie 1997 a,b,c). In 1864 alone, 700 million European flat oysters (*Ostrea edulis*) were consumed in London, employing up to 120,000 men in Britain to dredge oysters (MacKenzie et al. 1997c). Shell piles in the southwest of France contain over 1 trillion shells apiece (Goulletquer and Heral 1997), underscoring both the productivity of the species and the scale of harvest. In the 1870s, intertidal reefs of the eastern oyster (*Crassostrea virginica*) extended for miles along the main axis of the James River in Chesapeake Bay but had largely disappeared by the 1940s (Woods et al. 2005). Roads in many coastal areas, including around Matagorda Bay, Texas, were paved with oyster shells (Doran 1965).

For millennia, people on every inhabited continent have exploited shellfish for food, ornamentation, currency, and as a mineral resource. The beds, banks, and reefs formed by the accumulation of countless generations of these bivalve molluscs settling upon one another have largely been taken for granted. Only very recently has there been recognition of the vital ecological roles they play in coastal bays and estuaries around the world.



Clockwise from top: Oyster reefs can take many forms, from intertidal bars and beds to extensive subtidal reefs. © St. Johns River Water Management District, © Rob Brumbaugh/TNC, Restoration site in North Carolina. © Aaron McCall/TNC

This report documents a global analysis designed to help illuminate the distribution and condition of oyster reefs, which have been among the most important and valuable resources to humans and among the most poorly understood as a habitat.

Numerous recent papers document the condition of and threats to marine ecosystems globally (Spalding et al. 1997, Bryant et al. 1998, Burke et al. 2001, Green and Short 2003, EPA 2005, Orth et al. 2006, Halpern et al. 2008), but most of these estimates of the condition of marine ecosystems are indirect and based on the distribution of assumed threats (e.g., trawling, sedimentation, pollution). Shellfish declines have been considered in part by others (Kirby 2004, Ruesink et al. 2005, Lotze et al. 2006); however, they did not directly estimate ecosystem condition except in a few places.

Despite their importance, oyster reefs and shellfish beds have not been well-managed and their plight has been largely overlooked by the conservation community. Scientists began to appreciate the role of oyster reefs as a form of structured habitat in the late 1800s, when Karl

Möbius (1883) coined the term *biocönose* to describe what he called the “social community” of European oyster reefs, supporting both oysters and myriad other species. As of the early 21st century, a robust literature exists that vividly describes the functional roles that shellfish reefs play in estuaries, ranging from providing habitat for other species to serving as natural buffers that stabilize shorelines to improving coastal water quality through removal of suspended material.

The shallow bays and coastal waters in which oysters and other habitat-forming shellfish have existed for millennia are the same coastal places that people find most desirable for commerce and settlement. Because of their proximity to human populations, shellfish beds are a readily exploitable resource, leading to overfishing in many places, and puts them at risk of other human impacts such as changes in water quality and water flow and habitat loss from dredging and coastal development. That said, this proximity also provides an opportunity to use restoration of shellfish fisheries and habitats as an entree into more enlightened and pro-active watershed management.

ECOSYSTEM SERVICES PROVIDED BY NATIVE SHELLFISH REEFS



Jekyll Island, Georgia. Oyster reef restoration. © Erika Nortemann/TNC

Bivalve shellfish provide a variety of ecologically and economically valuable services including filtering suspended particles from the water column, providing nursery habitat for fish, and stabilizing and protecting shorelines with intertidal reefs. As “ecosystem engineers” shellfish influence the environment around them in ways that benefit other species (Jones et al. 1994), and in doing so benefit people and our economy.

The ecological influence of shellfish is profound, in some instances providing the conditions that allow some species to persist or thrive at all. For example, shellfish remove suspended solids from surrounding waters, thereby increasing water clarity (reviewed by Newell 2004), enabling seagrass growth. This same filtration service can reduce the likelihood of harmful algal blooms (Cerrato et al. 2004, Newell and Koch 2004) that take an enormous economic toll on coastal communities. Shellfish can also help to remove excess nutrients from coastal bays through denitrification in surrounding sediments, which has tremendous economic value in areas where nutrient removal is a high priority for coastal policy makers (Newell et al. 2005).

Shellfish also serve as natural coastal buffers, absorbing wave energy directed at shorelines and reducing erosion from boat wakes, sea level rise, and storms (Meyer 1997, Piazza et al. 2005). In addition, shellfish reefs play an important role as habitat for other species; the fish produced on oyster reefs have significant value to coastal economies (Grabowski and Peterson 2007). Moreover, reef functions such as fish habitat and water filtration can enhance tourism and recreation by improving adjacent water quality, resulting in more desirable areas for tourists to visit (Freeman 1995, Lipton 2004).

Recognition of the “engineering” services provided by other ecosystems such as coral reefs and mangroves has resulted in greater protection for those ecosystems and management with multiple ecosystem services in mind (Gilbert and Janssen 1998, Day 2002). Oyster reefs should also be managed in ways that consider the value of these systems to surrounding coastal areas. Although there is increasing recognition that shellfish provide multiple ecosystem services, management for objectives beyond harvest has not yet become widespread. A shift in perception is needed to effectively manage shellfish for their complete suite of services. Just as important, perhaps, is the need to develop markets in which the services can be traded. Given the public and private funds being invested in reducing nitrogen pollution from land-based sources, nutrient trading markets likely have real potential for enhancing shellfish reef restoration and conservation and improving the health of coastal ecosystems.



© Kevin Schafer



METHODS

Focusing the Assessment on Oyster Reefs

This assessment focuses on native, wild shellfish that form structured habitats identified as reefs, beds, and aggregations. These categories are based on the degree to which the structured habitat is provided by the shellfish (modified from ASMFC 2007). Hereafter we will refer to all of these as “reefs.”

- **Reefs** are formed by epibenthic shellfish that provide the dominant structural component of the benthos, and whose accumulated mass provides significant vertical relief (≥ 0.5 m). Examples include the Eastern oyster (*Crassostrea virginica*), Pacific oyster (*Crassostrea gigas*), and numerous related species of *Crassostrea*. Blue mussels (*Mytilus* spp.) can also form impressive reef-like structures in parts of their range.
- **Beds** are formed by epibenthic shellfish that provide the major structural habitat component of the benthos, and occur at high densities forming macro-relief (< 0.5 m) on otherwise unstructured bottom. Examples include the Olympia oyster (*Ostrea conchaphila*), ribbed mussel (*Geukensia demissa*), horse mussel (*Modiolus modiolus*), green mussel (*Perna viridis*), European flat oyster (*Ostrea edulis*), and the Chilean oyster (*Tiostrea chilensis*).
- **Aggregations** can be formed by epibenthic shellfish as a secondary structure on top of other underlying hard substrate or physical features (e.g., rocky intertidal areas, mangrove roots and rhizomes). Examples include pen shells (*Pinna* spp., *Atrina* spp.), giant clams (*Tridacna gigas*), mangrove oyster (*Crassostrea rhizophorae*, *C. brasiliiana*, and *C. gasar*), Sydney rock oyster (*Saccostrea commercialis*), crested oyster (*Ostreola equestris*), and the slipper cupped oyster (*Crassostrea iredalei*).



© Barry Truitt/TNC

Bivalve shellfish can help to structure benthic communities in other ways, even when they do not provide the dominant physical structure. Shells, even at low densities, can provide nursery and nesting sites for fish and attachment points for macroalgae and a variety of invertebrates (e.g., bay scallop, *Argopecten irradians*). Burrowing shellfish can also cycle nutrients within the sediments, enabling conditions that are important for many other species that reside within and above sediments. Burrowing bivalves that play critical roles in ecosystems include the hard clam (*Mercenaria mercenaria*), Carolina marsh clam (*Polymesoda caroliniana*), Estuarine wedge clam (*Rangia cuneata*), and softshell clam (*Mya arenaria*) among many others.

Assessing the Condition of Oyster Reefs

Because reef structures are usually comprised of only one, or less commonly, a few species, the condition of oyster reefs can be directly assessed. Some records of the abundance and catch of these species span centuries and millennia (Rippon 2000). In this study, ecosystem condition was established based on the percent of shellfish reefs remaining compared to baselines measured from 20- 130 years ago.

We considered the condition of oyster reefs at two different scales: “bays” and ecoregions, based on ecoregion boundaries developed by Spalding et al. (2007). The term “bay” refers to estuaries, embayments, coastal counties, and portions of coastlines (e.g., Mobile Bay, Wadden Sea, Venice Lagoon) that are discrete, semi-enclosed water bodies. In most previous studies and published literature, “bay” was the term used most consistently to describe these ecological units. The condition of oyster reefs in bays and ecoregions was based on estimates of abundance taken from the primary and “gray” literature. The categories of



© Barry Truitt/TNC

condition are based on the percent of current to historical abundance of oyster reefs remaining: < 50% lost (good); 50-89 % lost (fair); 90-99% lost (poor); > 99% lost (functionally extinct).

Where possible we gathered direct estimates of the distribution of oysters and oyster reefs in the past and present either from the same publication or from multiple publications. Areal distribution data on reefs are extremely rare; although historical maps showing reefs are available for some places, recent surveys of oyster habitat distribution are not common, despite the emergence of many new methods for collecting such data.

The literature reviews were bolstered by formal surveys of scientists and managers to assess condition in bays; these surveys were administered on-line, in person, and by phone. The survey results were used to identify critical existing literature and to corroborate published data and anecdotal accounts. Survey results were not used without other supporting literature to assess condition.

Fishery statistics were the most commonly used information for identifying condition of oyster reefs. Many primary references indicated that oyster reefs had been abundant and supported large fisheries, usually from thousands of tonnes to millions of pounds or bushels of recorded catch, but are now greatly reduced and often collapsed entirely. There was often evidence that restrictions were placed on harvest or that there were concerns about incidence of disease, but harvest continued until oysters could no longer be fished commercially.



© Barry Truitt/TNC

Fully exploited populations or those close to exploitation at their maximum sustainable yield were identified as in fair condition (50-89 % of historical reef area lost). In cases where fisheries had collapsed and there was no evidence of renewal, the condition was identified to be at least poor (>90% lost). When references and surveys indicated that it was difficult to find any reefs or structures remaining in places where reefs had been extensive, we estimated that >99% of the habitat was lost, and the condition was identified as functionally extinct (National Research Council 1995, Jackson et al. 2001). There is abundant evidence from past and present that shellfisheries frequently continue well past the point at which 10% or less of the habitat remains (e.g., MacKenzie et al. 1997c, Kirby 2004). Unexploited or lightly exploited populations were identified as in good condition (< 50% lost).

In addition to fisheries literature, other sources such as restoration literature were also used. For a number of bays, anecdotal reports of abundance were consistent with trends identified through fishery statistics. In some bays and regions, there were multiple information sources, including literature, expert surveys, and the authors' personal observations, that provided consistent accounts of reef condition. Typically, there was no debate about the condition of the ecosystems, but only about the cause of the decline (e.g., Kirby 2004, Ogburn et al. 2007). For this analysis the condition of reefs within bays was firmly identified only if there were one or more literature citations on condition.

The condition of oyster reefs was also identified across coastal ecoregions using appropriate information for each ecoregion and national publications on the status of oyster populations (e.g., Red Lists) and fisheries (Mackenzie et al.

1997 a,b,c). The condition of oyster reefs in an ecoregion was identified if there were one or more references that characterized condition across numerous bays within the ecoregion or condition was firmly documented in three or more bays within each ecoregion. Usually there were multiple references for each bay and ecoregion (Appendix 1). When there were several estimates of condition in bays in an ecoregion and no other regional sources of status information, the condition estimates were averaged for all bays in the ecoregion and rounded to the nearest integer.

The global loss of oyster reefs was estimated by assuming that the abundance in bays and ecoregions was at the mid-point of their respective condition category (e.g., 95% habitat loss for ecoregions in poor condition) and then condition (loss) was averaged among all ecoregions.

These estimates of condition are conservative because (i) where there was question of status we gave a higher ranking (i.e., chose the category indicating less loss), (ii) for most bays and ecoregions it was clear that abundances were usually at the lower end of their condition ranking (e.g., Chesapeake Bay reefs are closer to 1% remaining than 10% remaining), (iii) these estimates are usually based on only part of the historical loss and reefs were likely in greater abundances prior to the maintenance of fishing records.

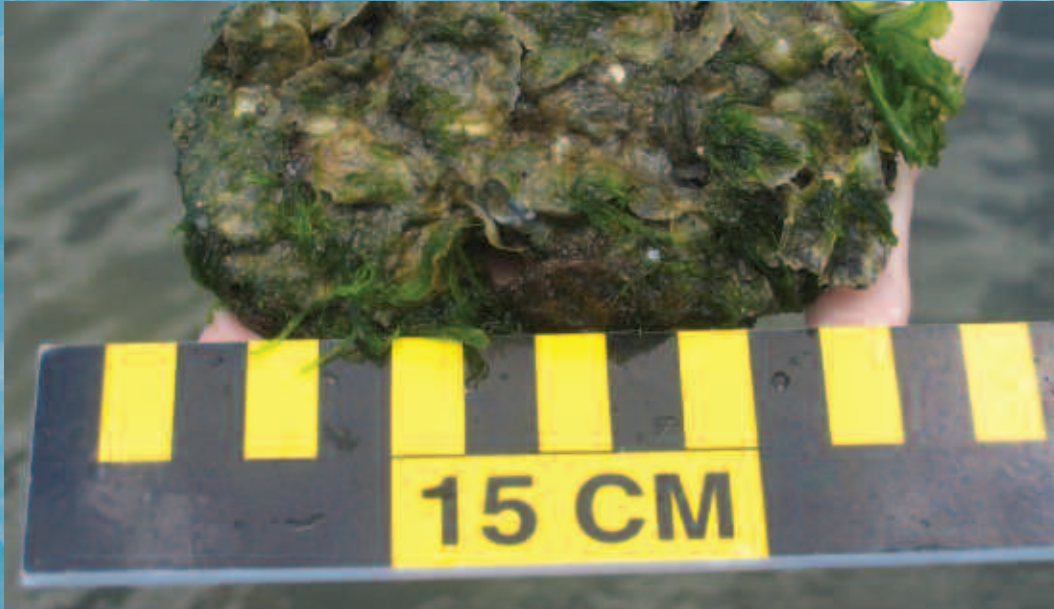
To compare current levels of wild oyster harvest among ecoregions, we used global commercial catch data developed by the Sea Around Us Project (Watson et al. 2004). These catch data are based primarily on the national catch statistics compiled by FAO, allocated to half-degree cells of latitude and longitude, and then summed by ecoregion. To account for yearly variation in recent catches, we used the average catch in tonnes of native oysters per ecoregion for the ten year period from 1995-2004.



Spatially explicit data on the abundance of native bivalves is rare.
© NOAA



Sampling shellfish beds off the coast of British Columbia.
© Brian Kingzett



RESULTS

Condition of Oyster Reefs Globally Across Bays and Ecoregions

A direct, global assessment of the condition of native oyster reefs from records of reef abundance and their harvest shows that in most of 144 bays in 40 ecoregions examined the condition of these ecosystems is poor overall (Figure 1; Appendix 1). While individual oysters are still present in most places, records of historical (past 20 to ~130 years) and recent abundances show that reefs that were once common are now often rare or extinct as ecosystems. Oyster reefs are at less than 10% of prior abundance in most bays (70%) and ecoregions (63%). They are functionally extinct with less than 1% of prior abundances remaining in many bays (37%) and ecoregions (28%), particularly in North America, Australia and Europe. Very few bays and ecoregions are in good condition. These results likely underestimate losses because of the lack of historical abundance records, which particularly affects assessments in South America, temperate Asia, and South Africa.

Globally 85% of oyster reefs in bays and ecoregions have been lost (Figure 1; Appendix 1). Global loss statistics are difficult to gather for estuarine and marine habitats. Nonetheless, global estimates for loss of coastal wetlands are approximately 50% with higher loss reported at some locations (e.g., USFW 1970, Burke et al. 2001, Zedler and Kercher 2005, Lotze et al. 2006, e.g., Airoldi and Beck 2007). Estimates of the loss of mangroves from countries with available multiyear data show that 35% of mangrove forests have disappeared in the past two decades

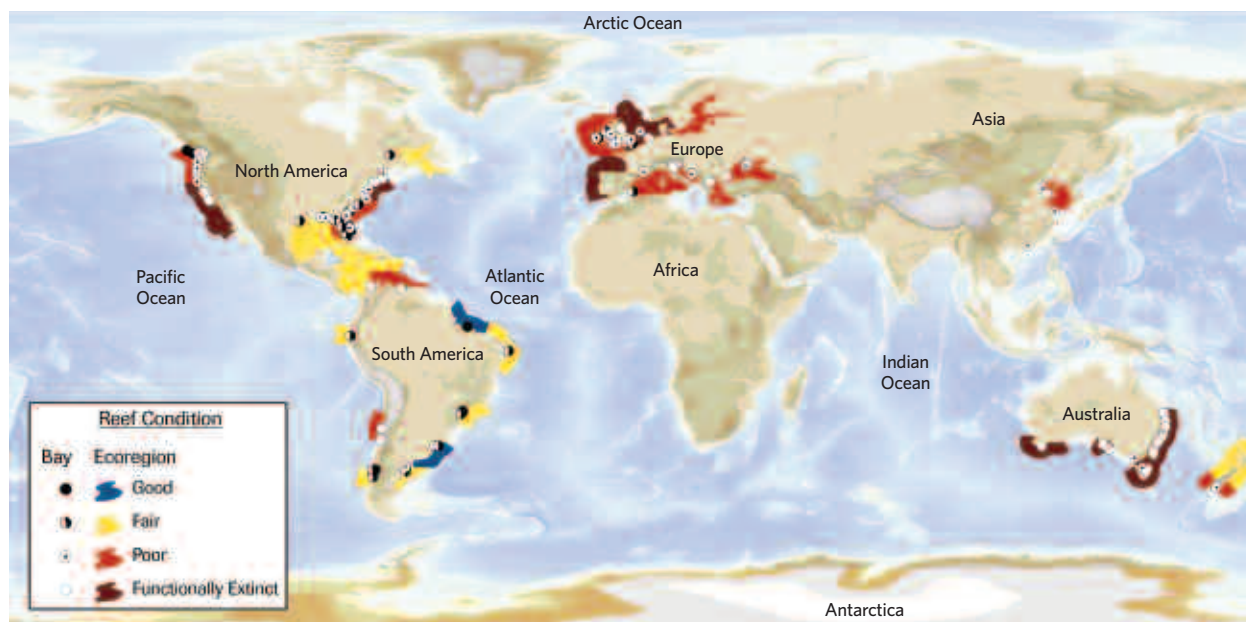


Figure 1. The global condition of oyster reefs in bays and ecoregions. The condition ratings of Good, Fair, Poor, and Functionally Extinct are based on the percent of current to historical abundance of oyster reefs remaining: < 50% lost (good); 50-89 % lost (fair); 90-99%lost (poor); > 99%lost (functionally extinct). Ecoregion boundaries are from Spalding et al. (2007). © TNC

(Valiela et al. 2001). In some countries, more than 80% of original mangrove cover has been lost due to deforestation (Spalding et al. 1997). Coral reef loss has been estimated at 20% globally (Wilkinson 2002), again with locally higher rates and, as with most marine ecosystems, widespread degradation has occurred even when reefs are not lost entirely (Pandolfi et al. 2003).

Most of the world's remaining wild capture of shellfish comes from five ecoregions (of 152 with reported catch) on the East Coast of North America (>75%), and the condition of oyster reefs in most of these bays and ecoregions is poor or worse (Figure 2). Only ten ecoregions in the world presently report wild oyster capture rates above 1000 tonnes averaged over a ten-year period (1995-2004). Only six ecoregions have average captures above 5500 tonnes and five of the six are on the East Coast of North America (Virginian to Southern Gulf of Mexico ecoregions).

Regional Summaries of the Condition of Shellfish Reefs

In addition to the bay and ecoregional scale estimates shown in Figure 1, we provide continental- or country-scale summaries of shellfish reef condition.

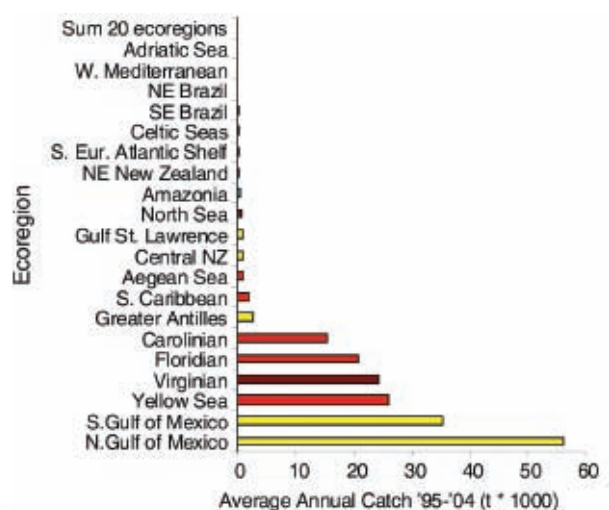


Figure 2 – Average annual catch (tonnes) of wild harvested native oysters per year by ecoregion from 1995-2004. The color codes on the bars correspond with the ecoregion condition in Figure 1. The last column is the sum of the average catch of the other 20 ecoregions in which reef condition was identified.

A note on data limitations: We could not identify the condition of oyster reefs for several regions including some of those covering parts of South Africa, China, Japan and the Koreas. Theses, anecdotal information, personal observations, and surveys in these areas suggest that wild oyster abundance was much higher in the past and that reefs have declined greatly in abundance. There is no indication that the patterns of loss are different than the well-described patterns in other regions, but there is not enough information for a firm estimate of condition.

Australia and New Zealand

Synthesized by Christine Crawford, Graham Edgar, and Boze Hancock



Figure 3. The condition of oyster reefs in Australia and New Zealand. © TNC

OVERVIEW OF CONDITION

Oysters, especially the native flat oyster, *Ostrea angasi*, and the Sydney rock oyster, *Saccostrea glomerata*, were very abundant in temperate and subtropical Australian waters before European settlement in the early 1800s. Evidence of shellfish harvest by aboriginal Australians is provided by the numerous middens scattered around the Australian coastline (Ogburn et al. 2007). The first settlers also documented oyster harvesting by aboriginal tribes. In the mid- to late 1800s intense exploitation of this resource occurred in most Australian states, and by the end of the 19th century most of these fisheries had been abandoned because there were insufficient shellfish remaining to support commercial harvest. These shellfish were harvested for the dinner table and for lime production; the shells were also used for road building and fill in construction sites. Considerable information is available on the decline in oyster reefs in all Australian states due to over fishing, disease and introduced pests. According to Ogburn et al. (2007) there is no evidence that any of these oyster beds have returned to their original population size or reef habitat type.

Native oysters still occur in many temperate regions of Australia, but they are sparsely distributed and reefs generally do not occur any more. Of significance to the management of oyster beds in Australia is a general lack of knowledge and understanding by the Australian public and State government managers of the dramatic decline in oyster resources and the ecological significance of this loss. There is no cultural tradition of community harvest and management of shellfish. The Australian native oyster reef ecosystem is largely gone and forgotten.

***O. angasi* (flat oyster)**

The native oyster fishery was regarded by Hone (1996) as the first fishery to be established in South Australia and the first to collapse. In South Australia fishing for *O. angasi* commenced in the 1840s in the York Peninsula region. An

Oyster Fisheries Act was introduced in 1853 in an attempt to control this industry and to encourage the establishment of artificial beds in areas where they no longer existed. By the 1870s a large fishery using dredges towed by sail boats existed in the Yorke and Eyre Peninsula regions, including at Coffin Bay, Oyster Bay and Boston Bay, and on Kangaroo Island. A total of 6 million oysters was reported to have been harvested annually from Coffin Bay at this time (Wallace-Carter 1987). Many of these natural beds were depleted before legislation was introduced in 1873 to control dredging. This legislation, which controlled the opening and closing of areas to harvest and some reseedling of depleted beds, allowed production of native oysters to continue in some areas, albeit in much lower numbers (Wallace-Carter 1987). The oyster stocks gradually declined and were severely reduced by the 1890s (Shepherd 1986). Oyster dredging continued until the 1930s, but at a much less intensive level than at the inception of the fishery. In 1935 a Royal Commission encouraged the cultivation of *O. angasi*, but numerous attempts were unsuccessful (Hone 1996). By 1945 there were no records of oysters being harvested. More than 80 years later only about two million oysters remain, sparsely scattered across this region, in contrast to the approximately 300 million which must have been here historically (Shepherd 1986).

The Tasmanian native oyster fishery flourished in the mid-1800s with beds being fished extensively and indiscriminately along much of the coastline. Many of these oysters were exported to mainland Australia and to England. The *Parliamentary Report on Fisheries of Tasmania, Report of the Royal Commission* (Fisheries of Tasmania 1882) provides records of more than 22 million oysters being harvested from five of the principal native beds during one of the best harvest years during the peak period in 1860-70.

By the 1880s the fishery was limited. The only natural beds that could be profitably worked were in the vicinity of Spring Bay, but the total yield was reduced to 100,000 oysters a year, from an area which had once provided 8.4 million (Fisheries of Tasmania 1882). This report to the Commissioners suggested that the decline was due to overfishing, mussel encroachment, disease, and inclement weather. The colonization and clearing of land for settlement and agriculture led to increased silt loads to nearby rivers and bays which was claimed to have killed many beds (Parliamentary Report 1885). However, overfishing is likely to have been one of the most significant factors in the population decline.

***Saccostrea glomerata* (Sydney rock oyster)**

Sydney rock oysters, *Saccostrea glomerata* (Gould 1850), occur on sheltered rocky shores predominately in the mid-intertidal zone, from Port Phillip Bay in Victoria up the east coast of Australia, across the tropical north and down the west coast as far south as Shark Bay in Western Australia; it also occurs in New Zealand. *S. glomerata* is generally the dominant oyster in estuaries on the mid-east coast of Australia. Much of the historical information about the oyster fisheries in New South Wales (NSW) and Queensland does not stipulate the species; however this information is

assumed to be predominately about Sydney rock oysters.

In NSW oysters were harvested almost immediately after the first settlement by Europeans in 1788. Large quantities of oysters were harvested in Port Jackson and the shells were used to produce lime for the construction of early buildings in Sydney (Smith 1985). Extensive oyster reefs were present in most NSW and southern Queensland estuaries at the time of European settlement; however these were extensively exploited during the 1850s – 1870s resulting in drastic declines in oyster populations.

The oyster industry in Queensland flourished from the 1870s to the 1920s and then declined. It was mainly located in Southern Queensland where oyster reefs, including reefs of the Sydney rock oyster, occurred in the intertidal zone (Smith 1985). The main oyster beds were in Moreton Bay and Great Sandy Strait with smaller beds in Tin Can Bay, Rodd'd Bay and Keppel Bay. Oysters were harvested by dredging in deeper water down to about four meters or in the intertidal zone by collecting juveniles by hand and redistributing them to promote growth. Approximately two-thirds of the harvest was exported to Sydney and Melbourne. For many years the oyster industry in southern Queensland was the largest fishery in the region and in one year more than 252,000 oysters (14 tons) were exported to southern colonies after their own oyster industries had declined (Smith 1985). Peak exports of oysters from Queensland occurred in 1891. Parasitic polychaete worms, collectively referred to as mudworm, were first noticed in oysters in Queensland at Southport Broadwater in 1895. The Queensland industry then declined rapidly, partly because of the increase in cultured oysters in New South Wales and partly due to overharvesting, disease, and mudworm. In 1902 Sydney rock oysters were discovered in Sandy Strait. The last dredge section in Queensland in the Maroochy River was forfeited in 1947 and dredging for oysters does not now occur.

***Malleus meridianus* (hammer oyster)**

The lesser-known hammer oyster (*Malleus meridianus*) occurs on sheltered and moderately exposed reef and sand at depths of 0-200 m from Fremantle, WA to Gulf St Vincent, SA (Edgar et al. 2000). Sometimes up to 2 m high, beds of this species occur in upper Spencer Gulf, South Australia, but are not extensive. Because no trawling is allowed in this area, these reefs presumably persist (S. Shepherd pers. comm. 2007). Low hammer oyster reefs in Gulf St Vincent were described by Shepherd and Sprigg (1976), but a resurvey by Tanner (1983) showed that they had disappeared, Tanner concluded that this was a likely result of prawn trawling in the 1970s-90s.

O. chilensis

O. chilensis occurs throughout New Zealand primarily on soft sediment to 200m (New Zealand Ministry of Fisheries 2007a, 2007b). It is most abundant in the Tasman Bay, Golden Bay, and Marlborough Sound area on the northern section of the South Island, and in the Foveaux Strait between the southern end of the South Island and Stewart

Island. The Foveaux Strait has been the primary fishery for more than 130 years. *O. chilensis* is well studied in New Zealand, particularly for the Foveaux Strait dredge fishery, and a recent and rigorous stock assessment indicates that current population levels are ~20% of virgin spawning stock biomass (New Zealand Ministry of Fisheries 2007a). In the mid 1980s a *Bonamia exitiosa* epizootic reduced the population to less than 10% of its virgin level (New Zealand Ministry of Fisheries 2007a). Since the 1980s the population has experienced several cycles of stock increases and subsequent *Bonamia* epizootics.

Exploitation of the Nelson/Marlborough oyster fishery at the north end of the South Island of New Zealand began to increase in the early 1960s. By 1986 a total allowable catch of 500t was imposed, but between 2000 and 2004 the catches had declined to between 0t and 150t (New Zealand Ministry of Fisheries 2007b).

THREATS AND CAUSES OF DECLINE

Smith (1985) listed 14 reasons for oyster population declines in Queensland, Australia. These reasons include a variety of economic and marketing issues, such as competition from New Zealand oysters on the Sydney and Melbourne markets, the rise of the NSW industry associated with unreliable and irregular shipping to southern states during and after the First World War, increased labor costs and shortage of experienced labor, the management system of auctioning areas which could be dredged, and lack of security for management of oyster areas with licences renewed annually. Environmental problems include an over-abundance of predators, such as rays, bream, mussels, and crabs; unsuitable sites and culture methods selected for oyster ranching; silting up of oyster beds; conflicting uses of oyster grounds; and diseases, especially mudworm disease but possibly also QX disease. Social problems for the industry included theft of oysters from allocated areas and greed of companies and individuals who tried to monopolize the industry. The mudworm disease was considered to have had the greatest negative economic impact on the industry.

A recent paper by Ogburn and others (2007) observes that although large subtidal reefs of both *S. glomerata* and *O. angasi* were very common in estuaries along the east coast of Australia at the time of European settlement, these reefs are now absent. Kirby (2004) hypothesizes that these reefs were destroyed by overfishing using destructive methods such as dredging. However, Ogburn et al. (2007) believe that the permanent loss of subtidal oyster reefs in Australian east coast estuaries is due to the introduction of a new and virulent species of mudworm (polydroid complex of spionid polychaete worms) from New Zealand. They suggest that "the loss of oyster reefs has led to profound, and most likely, irreversible changes in the ecological structure and function of Australian east coast temperate and sub-tropical estuaries."

According to Shepherd (1986) the decline of native flat oyster populations in South Australia was due to ecological disturbance of the seabed. Adult oysters were removed by

dredging, which reduced the area of preferred substrate for settling larvae. Dredging also disturbed the sediment which settled out as a thin layer of silt over the seabed, further reducing the availability of substrate for settlement. Also the alga *Caulerpa cactoides*, which prefers silty substrate, gradually expanded over most of the old oyster beds.

In New Zealand, *O. chilensis* remains at risk of exploitation and from outbreaks of the pathogen *Bonamia exitiosa*. The dredge fishery has also been responsible for significant habitat alteration. *O. chilensis* is thought to have concentrated on bryozoan biogenic reefs that were formed in Foveaux Strait by the frame-building bryozoan *Cinctipora elegans* and associated epifauna (Cranfield et al. 2003). Since the 1970s these reefs have been substantially altered by dredge fishing. By 1998 none of the reefs surveyed in the late 1970s remained, but had released large volumes of mobile sediments, subsequently impacting the oyster population. Declines in the Nelson/Marlborough oyster fishery are also thought to be the result of limitations in substrate availability and food, and disease events (New Zealand Ministry of Fisheries 2007b).

CURRENT NOTEWORTHY ACTIONS

The only known remaining oyster reef habitat in temperate Australia is in Georges Bay on the east coast of Tasmania. A small fishery exists for *O. angasi* in this bay, and regulators have recently allocated two licenses for harvesting oysters. Harvesting must be by hand and the total allowable catch (TAC) is set annually; for 2008 it was 96,000 oysters per license. At present the harvest is constrained by lack of market demand. An assessment of this fishery by the Australian Government in relation to ecologically sustainable management of fisheries concluded that it would not be detrimental to the survival or conservation status of this species in the short term; nevertheless a number of risks were identified. Although the assessment recognized the limited number of substantial beds of *O. angasi* in Tasmanian waters, it is unlikely that it recognized that this is the only known remaining reef habitat for this species in its broad distribution across southern Australia.

As part of an assessment of the health of Georges Bay in 2005, the seabed habitat was mapped, including the location of oyster beds (Mount et al. 2005). The oysters occupied two main areas: (i) silty sand habitat below the deep edge of seagrass beds, primarily mature animals scattered across the bottom at maximum densities of 40-50 m⁻², and (ii) dense beds around Humbug and Lords Points. A comparison of Wilson's map from 1987 with a May 2002 Quickbird satellite image shows that most of the beds identified in 1987 were still obvious in 2005, although one bed seems to have disappeared (Mount et al. 2005).

Recreational fishing of *O. anagasi* is permitted across its distribution, although the harvest is low because of sparse distribution and subtidal habitat. In NSW recreational fishers are limited by regulation to a daily bag limit of 50 native oysters (Sydney rock *S. glomerata* or flat oysters *O. angasi*) and 50 blue mussel (*Mytilus edulis*). Pipis, cockles,

and mussels are hand-gathered commercially by endorsed fishers in the "Estuary General Fishery" (D. Masters pers. comm.).

Culture of native oysters has been attempted on several occasions and in several locations in Tasmania. A Flat Oyster Culture Program was established in 1991 with substantial Tasmanian government support. It involved harvesting and translocating small native oysters from Georges Bay to marine farms in southern Tasmania for ongrowing to market. The population of native oysters in Georges Bay was surveyed in 1987 prior to the establishment of this program (Wilson 1991). It was estimated that over 24 million oysters were present in a series of beds occupying approximately 33 ha. However, this program ended abruptly in 1994 when the oyster disease Bonamiasis was discovered in translocated oysters. The translocated spat were also heavily predated by several species of fish.

It is noteworthy that although much of the oyster reef habitat was destroyed by the end of the 19th century, small oyster populations still exist in most bays and estuaries but at very low densities compared to the preharvest period. Reef habitat has not returned, even in relatively pristine estuaries with limited human impacts. Ogburn et al. (2007) suggest that active restoration of subtidal reefs in southeastern Australian estuaries is not possible because of the presence of mudworm, but that hypothesis has not been tested. The oyster disease Bonamiasis is also thought to have hindered the reestablishment of reefs.

The New Zealand Ministry of Fisheries continues to monitor the *O. chilensis* fishery closely. Despite the monitoring effort the landings continue to decline; Foveaux Strait landings declined from 89 million oysters in the early 1980s to 7.37 million in the 2006-2007 fishing season. This catch was well below the 14.95 million oyster catch limit set for the season. The fishing industry voluntarily shelved 50% of the total allowable commercial catch for the 2008 season.



Oyster beds in Georges Bay, Tasmania. At just 2 m depth they show the variety of other species living on the bed – i.e. very much an ecosystem rather than a monospecific community. © Graham Edgar

China, Japan and Korea

Synthesized by Guofan Zhang, Li Li, Fei Xu, and Ximing Guo

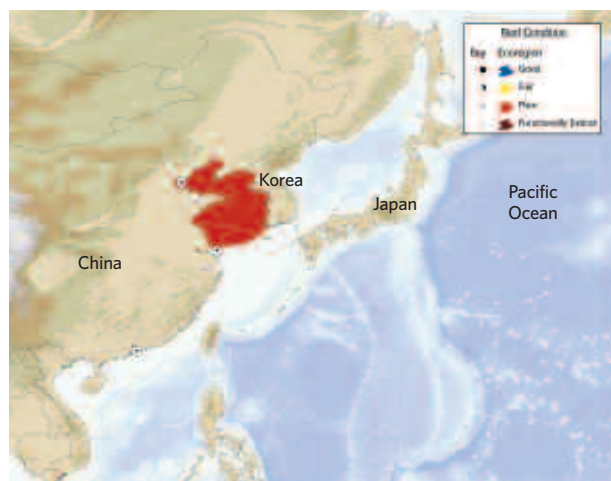


Figure 4. The condition of oyster reefs in Asia. © TNC

OVERVIEW OF CONDITION

This region of the world poses special challenges for characterizing the status of oyster reefs, the greatest of which is that historical records for natural reefs are very poor. These areas of Asia are at the epicenter of oyster diversity and natural reefs were once widespread throughout the region. The taxonomy of oysters in this area is difficult, however: China alone has between 15 and 23 oyster species (Zhang and Zikang 1956, Li 1989, Li and Qi 1994, Xu and Zhang 2008). The cultivation of oysters has been practiced for at least 1,000 years in the region. In recent decades the scale of coastal aquaculture for many species has increased dramatically. Unlike most regions of the world, oyster aquaculture here is based primarily on native oyster species. There has also been substantial growth and urbanization of many coastal cities which bring the problems of coastal development, pollution, and freshwater diversions. All of these issues, and overfishing, present challenges for native oyster reefs.

Currently all of the oyster production from this region comes from some form of aquaculture. Cultivation practices range from augmenting bottom habitat through the addition of shell and predator exclusion structures to large-scale suspended culture. Some of these cultivation practices provide some measure of reef habitat. For instance, oyster culture (*C. gigas*, *C. sikamea*, and *C. ariakensis* in mixed assemblages) in southern Japan (Kyushu Island, Ariake Bay, and Shiranui Bay) involves the creation of managed shell “reefs” throughout the bays. In south China (Guangxi and Fujian Provinces) structures are placed on the bottom in intertidal habitats to collect spat and sometimes provide grow-out allowing for the creation of some oyster habitat which only partially resembles natural oyster reefs. In most areas with either *C. gigas* cultivation (Honshu, Japan, southern Korea, and northern China) or *C. angulata* (central and southern China), oysters are suspended in

the water column in a manner that does not mimic natural oyster habitat.

While oysters occur throughout the region, we focus on the northern regions of China where there is some recent historical information on the change in condition and conservation of native oyster reefs. There are currently about 20 areas along the China coast with a recent history of supporting oyster reefs, including Dalian Bay reef in Liaoning; Hangu oyster reef in Tianjin (Fang et al. 2007); Dajiawa oyster reef, Weifang, Shandong Province; Xiaomiaohong oyster reef, Nantong, Jiangsu Province; and Jinmen oyster reef, Fujian Province (Yao 1985).

In most of these areas, however, environmental conditions have changed dramatically in the past 30 years and most of the historical reefs have disappeared. Overall, the condition of reefs in the bays and ecoregion are poor. *C. ariakensis* is declining from north to south across China’s coastline and is at great risk in China.

THREATS

Overfishing, particularly in the past, and the growth of aquaculture have been major issues for shellfish reefs throughout the region. Habitat loss has been an important threat recently. With the rapid development of coastal industries and cities in the past 30 years, much of the oyster habitat was lost in China’s coastal shallow sea. In the past 30 years alone, reefs in Bohai Bay have seen drastic declines including the Hangu oyster reef with 70% loss (Fang et al. 2007) and the Dajiawa oyster reef with 90% loss. Mariculture has also impacted the oyster reefs. In the Yellow Sea, algal farming has expanded rapidly in places such as Sanggou Bay and Dalian Bay, and the algae has smothered and reduced benthic populations including oysters. The aquaculture of *C. gigas* has also caused major changes on the remaining Dajiawa oyster reefs in the Yellow Sea.

Today the condition of and threats to oyster reefs once formed by *Crassostrea ariakensis* in the Laizhou Bay and Nantong Sea are typical of the condition of oyster reefs elsewhere in China. The Dajiawa oyster reef in Laizhou Bay, initially formed by a combination of Pacific oyster, *C. gigas*, and Jinjiang oyster, *C. ariakensis* (Geng et al. 1991, Wang et al. 2004, Wang et al. 2007), has declined to less than 10% of its original area. Several factors contributed to the decline. Overfishing was a major issue from the 1960s to 1980s as oysters were collected for food and lime. Direct habitat loss was also a significant problem as nearby cities expanded and reefs were bombed to provide access for commercial ships. Pollution from the chemical industries in the area caused further deterioration (Deng and Jin 2000). Hydrologic alterations from water withdrawals in the Yellow River have reduced the reproductive success of *C. ariakensis*. From 1972 to 1999, the Yellow River often experienced drastic reductions in water flow leading to greatly elevated salinity, particularly between March and June, the key reproductive period for *C. ariakensis* (Yan 2003). During this time, *C. gigas* expanded its distribution and abundance in the bay.

The Xiaomiaohong oyster reefs occupy an area of about 3.5 km² in the Nantong Sea, Jiangsu Province (Zhang 2004). The oysters lower on the reefs are primarily *C. ariakensis* and those on the upper layer are *C. plicatula* (Zhang 2004, Zhang et al. 2007). Unlike the Dajiawa reefs in Laizhou Bay, some of the changes in Xiaomiaohong oyster reefs are driven more by natural processes, particularly the dynamic changes in the Yangtze River estuary. Before the shift of the Yangtze River estuary, the freshwater flows were conducive to reproduction, growth, and survival of *C. ariakensis*, which formed extensive subtidal reefs. As the flow and delta has shifted in the estuary, salinities have changed dramatically and allowed *C. plicatula*, which tolerates higher salinities and intertidal conditions, to increase in abundance and occupy more of the reef.

CURRENT NOTEWORTHY ACTIONS

Measures have been taken to restore and conserve *C. ariakensis* in Laizhou Bay. River flows have been managed more sustainably, and an MPA was established in 2006. The culture of Pacific oysters within the MPA and nearby waters has been abolished to reduce competition with this species, and a stock enhancement program was established for *C. ariakensis*. Over an eight-year period, these measures are proving effective, and the total abundance of *C. ariakensis* is increasing.

An MPA was established in 2006 to help protect the remaining Xiaomiaohong oyster reefs. In general it has helped to conserve the habitat and promote better water management practices. However, the MPA has not completely protected the reefs from poaching and illegal harvest. Local fishermen prefer *C. ariakensis* because of their larger size and tend to ignore *C. plicatula*. As a result, *C. plicatula* remains abundant on the reef while *C. ariakensis* is decreasing.



Oyster reef in Nantong Sea, Jiangsu province. © Guofan Zhang

South America

Synthesized by Alvar Carranza and Omar Defeo



Figure 5. The condition of oyster reefs in South America. © TNC

OVERVIEW OF CONDITION

There are 13 native, habitat-forming species of Ostreidae in South America and three introduced oyster species (Harry 1985, Toro and Aguila 1996, Jozefowicz and O'Foighil 1998, Camus 2005, Ruesink et al. 2005, Shilts et al. 2007, Varela et al. 2007, Carranza et al. 2009a, Castilla and Neill 2009). Similarly, at least 14 species of mussels in South America form beds, banks, or aggregations that contribute significantly to ecosystem function (Klappenbach 1965, Zaiuso 2004, Borthagaray and Carranza 2007, Wood et al. 2007, Carranza et al. 2009b). Several species also sustain important artisanal fisheries or aquaculture systems (Ciocco et al. 1998, Lasta et al. 1998, Toro et al. 2004, Acosta et al. 2006).

Despite the extensive literature describing the ecology and culture of oysters and mussels worldwide, until recently there has been no assessment of their diversity, distribution, and conservation status for South America (Carranza et al. 2009a, Carranza et al. 2009b). Such an assessment is critical because increasing coastal development pressure threatens most nearshore habitats along these coasts, including mangroves and other ecosystems on which bivalves depend. To obtain our first estimates, we exchanged information with a number of active researchers working on oyster and mussel ecology and management, and received invaluable input to our analysis through expert surveys and through a workshop convened during the VII Latin-American Malacological Congress (Valdivia, Chile, November 8-9 2008). Along with an extensive literature search, we were able to generate condition estimates for some shellfish populations within estuaries and overall condition estimates at an ecoregional scale. To date, we are unaware of any studies that more directly measure the extent or rate of decline for South American shellfish populations. This shortage of information may be due to a lack of management interest in these systems, but is also probably limited by the amount of economic support this kind of research receives in South American countries. The most troubling finding was that nearly half of the assessed shellfish populations

were either moderately or highly threatened by overfishing and environmental degradation. Overall for oyster reefs, 31% of the populations were assessed in good condition, 44% were fair, 19% were poor, and one population (6 %) was functionally extinct.

THREATS

Although the condition of native oysters and mussels in South America may not yet be as dire as that in many other regions of the world, shellfish on these coasts are following the same declining trends as populations elsewhere. In addition to the ecological considerations, these declines are critical socio-economically because the success of the regional development of aquaculture practices is closely tied to the conservation of natural banks of seed. Several species in particular are jeopardized by the extensive loss of mangroves, their primary settlement habitat. The mangrove oyster *C. rhizophorae* is on Colombia's Red List of threatened species after dramatic reductions in the population occurred in the large coastal lagoon Ciénaga Grande de Santa Marta. Alterations in river flow and loss of mangrove habitat are the primary drivers of this loss, and recovery is hindered by unauthorized harvest of oysters from remnant populations. Fishing, including illegal harvest, is a pervasive threat that, particularly when coupled with other factors such as mangrove loss and alterations in river flow, poses real challenges to conservation (A. Gracia, pers. comm. 2008). This trend is not exclusive to South American mangrove oysters: the Chilean flat oyster *Ostrea chilensis* was rapidly overexploited since the fishery started in 1978. Similarly, there is evidence of declines in one of the most important populations of *O. puelchana* in the North Patagonian Gulfs ecoregion (M. Pascual pers. comm.). *Crassostrea gasar* in the Eastern Brazil ecoregion and *Crassostrea rhizophorae* in the Central Caribbean ecoregion are in need of urgent conservation actions (Carranza et al. 2009a).

As in other parts of the world, a lack of data has hindered the assessment of actual condition of populations, even in those cases where populations are, apparently, in good condition, representing a unique opportunity for conservation. In this vein, activities enhancing coordination between conservation and restoration initiatives at a continental scale are needed, and the development of a standardized methodology and metrics for assessing the condition of oyster and mussel populations are stressed.

CURRENT NOTEWORTHY ACTIONS

Community-based management and co-management in Chile is providing opportunities to enhance conservation and enable sustainable fishing. Such rights-based approaches could be employed more broadly within South America, as in other areas of the globe. In addition, several traditional management policies have been adopted in Chile (e.g., minimum legal size limits). The Chilean Fishery Subsecretary also created two genetic reserves aiming to protect the stocks of *C. chorus* and *O. chilensis*. The implementation of Coastal Marine Protected Areas (CMPA) opened new avenues for bivalve conservation in this country, and the recovery of natural banks of *C. chorus* in

the Lafken CMPA has been reported.

In Brazil, there are a number of ongoing initiatives linking poverty alleviation with sustainable extractive activities in Pernambuco, Rio Grande do Norte, Paraíba, Bahia, São Paulo, and Santa Catarina states. To this end, US\$3 million is being invested in Pernambuco, Rio Grande do Norte, and Paraíba. The Brazilian model of co-management for natural resources, known as “reservas extrativistas” (RESEX), developed with the active participation of fishers, government agencies, and partners in São Paulo and Santa Catarina, is considered a promising tool for conserving native shellfish populations in the country (Carranza et al. 2009a).

In Argentina, the San Matías Gulf offers a rare opportunity to study the structure of one of the best remaining populations of the puelche flat oyster, *O. puelchana*, in the world. Restoration and conservation efforts are currently directed to: (i) carry out extensive surveys to evaluate the state of the three main grounds and compare them with previous surveys; (ii) determine age and growth; (iii) assess biomass and demography of San José populations; and (iv) initiate seeding experiments using hatchery seed to evaluate an alternative for restoring depleted beds.

Restoration is emerging as an important community-based strategy in various countries in South America, most often coupled with aquaculture development. For example, a project is underway that is intended to restore the population of El Sótano, a traditional mussel bed located in an area characterized by strong recruitment in the Argentinean San Matías Gulf, and there are several ongoing initiatives in Chile. As with rights-based approaches such as co-management, these restoration projects are directed toward sustainable fishing and enhanced conservation. In Venezuela there are initiatives to restore beds in the Mochima National Park using a community-based approach. A South American Network on Shellfish Conservation and Restoration, involving scientists from around the continent is being developed to bolster conservation and restoration initiatives, link research teams, and provide a framework for pursuing support for shellfish conservation initiatives.



A bed of *Choromytilus chorus* in Chile. © Luis Prado

Europe

Synthesized by Laura Airoidi, Antonella Fatone, Matt Kay and Mike Beck

Parts of text are excerpted and adapted from Airoidi and Beck (2007) with permission

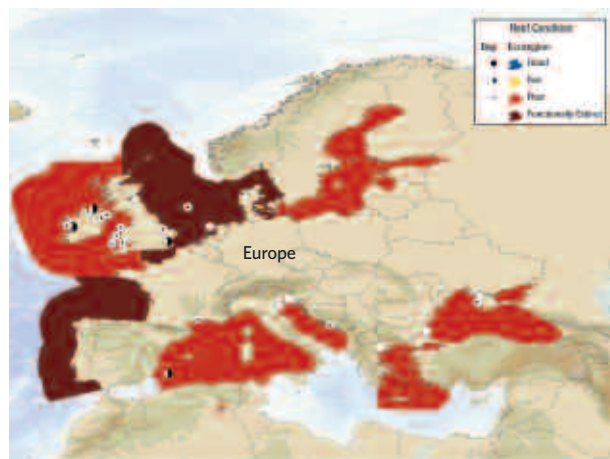


Figure 6. The condition of oyster reefs in Europe. © TNC

OVERVIEW OF CONDITION

The native European flat oyster (*Ostrea edulis*) used to be very abundant throughout its range (Korringa 1952). The natural distribution of *O. edulis* is along the European Atlantic coasts from Norway to Morocco and across the coasts of the Mediterranean and Black Seas. Their abundance declined significantly during the 19th and 20th centuries and wild native beds were considered scarce in Europe as early as the 1950s (Korringa 1952, MacKenzie et al. 1997c). In Europe oysters have been an extremely popular food for centuries. Both ancient Greeks and Romans highly valued oysters. Romans fished and imported them from all over European and Mediterranean coastlines and cultivated them extensively (Gunther 1897), and in some British estuaries there are archaeological signs of overexploitation of native oyster beds that date back to the first century (Rippon 2000). In the 18th and 19th centuries, large offshore oyster grounds in the southern North Sea and the English Channel produced up to 100 times more than today's 100–200 t (UK Biodiversity Group 1999, Berghahn and Ruth 2005).

Virtual extinction of native oyster beds has been documented in the Wadden Sea, where wild oysters largely disappeared by 1950 (Wolff 2000, Wolff 2005, Worm et al. 2005); in Helgoland (Germany), where beds largely disappeared by the mid-1900s (Korringa 1952); in the Dutch Eastern Scheldt (OSPAR Commission 2005, van den Berg et al. 2005); in Belgium (OSPAR Commission 2005); in all deeper waters of the southern North Sea, such as in the Oyster Grounds (OSPAR Commission 2005); in most areas of Galicia (Cano and Rocamora 1996); in many coastal lagoons of the Adriatic sea (Magliocchetti Lombi et al. 1988, Mizzan et al. 2005) and in some bays in the Black Sea (Zaitsev 2006, Micu and Todorova 2007). In the Firth of Forth (Scotland), which in past centuries had hosted one

of the most famous oyster banks, no oysters were found in 1957 (Dodd 2005). Dramatic stock decreases have been reported as well on the Atlantic coasts in French Brittany, the Netherlands, Denmark, Norway, Ireland and England and in the Mediterranean Sea (Korringa 1952, UK Biodiversity Group 1999, Barnabe and Doumenge 2001). In the United Kingdom, where 700 million oysters were consumed in London alone in 1864, the catch fell from 40 million in 1920 to 3 million in the 1960s and has not recovered (Tyler-Walters 2001).

Remains of wild native oyster beds still occur in various regions, including the rivers and flats bordering the Thames Estuary, the Solent, River Fal, the west coasts of Scotland and Ireland (Kennedy and Roberts 1999, UK Biodiversity Group 1999, Tyler-Walters 2001), the western part of the Swedish Kattegat region of the Baltic (Lozan 1996), the Limfjord region of Denmark (Korringa 1952), the Adriatic Sea, where *O. edulis* is still captured in the wild (Barnabe and Doumenge 2001), the Mar Menor (Spain), where a large flat oyster population, estimated at more than 100 million individuals, previously produced large amounts of spat (Cano and Rocamora 1996, Ramón et al. 2005), and areas of the Black Sea, where the species was still valuable commercially until the 1970s (Zaitsev 2006). Limited information, however, is available about the current status of these oyster reefs and there is debate about whether the fragmented patches of wild oyster habitats are self-sustaining or owe their survival to the inputs of larvae from cultivated oysters (Korringa 1952).

Currently, aquaculture provides the main supply of native oysters in most European countries (MacKenzie et al. 1997c, Ocean Studies Board 2004). This industry has been seriously affected by epidemic diseases in recent decades, with documented losses of commercial stocks above 80% in France (Kennedy and Roberts 1999, Ocean Studies Board 2004), and most Mediterranean native oyster beds are in such poor conditions that they are unable to support intensive culture (Barnabe and Doumenge 2001). Although marketplace demand for native oysters remains strong, the introduced Pacific oyster, *Crassostrea gigas*, which is easier to cultivate than the native oyster, now provides the major share of oyster production in Europe (Cano and Rocamora 1996, Kennedy and Roberts 1999, Lotze 2005).

THREATS

There is some documentation of the decline and loss of native oyster reefs, mainly from fishery landing records. The richest natural oyster beds in Europe until the 19th century were probably around Britain, from Stornoway to the Solway in the west and from the Orkney Islands to the Firth of Forth in the east (Berghahn and Ruth 2005). In the mid-19th century these were heavily exploited; dredging of the oyster beds was one of the largest fisheries, employing about 120,000 men around the coast in the 1880s (Tyler-Walters 2001), with an annual yield of >50 million oysters (Berghahn and Ruth 2005). Oyster reefs at Strangford Lough, in Ireland, once supported up to 20 oyster dredging boats (Kennedy and Roberts 1999). In the Wadden Sea, the commercial oyster fishery started in

the eleventh century and flourished in the 18th century: in 1765 large oyster beds between Texel and Wieringen supported a profitable fishery of 145 vessels, with catches over 100,000 oysters per year per vessel (Wolff 2005).

By the late 19th century, beds of *O. edulis* were already severely depleted or physically destroyed around most European coasts (Ocean Studies Board 2004). Overfishing and wasteful exploitation, combined with outbreaks of disease, habitat loss and change or destruction, reduction in water quality and other large-scale environmental alterations, adverse weather conditions, and the introduction of non-native stocks or species of oysters (and associated parasites and diseases, such as the protozoans *Bonamia ostreae* and *Marteilia refringens*) for aquaculture and other non-native species (e.g., the invasive gastropod *Crepidula fornicata*) were blamed for the decline (Korringa 1952, Wolff 2000, Berghahn and Ruth 2005, Laing et al. 2005). There is limited information about current trends in and threats to remaining native oyster reefs in Europe.

Ostrea edulis is a relatively long-lived species that reproduces sporadically (Korringa 1952). Thus, presumably, population recovery times could be long, perhaps up to 20 yr. Further, in many regions the loss of standing stocks has been so severe that natural replenishment of damaged grounds is limited (Laing et al. 2005). *O. edulis* is considered to be highly sensitive to substrate loss, smothering, contamination by synthetic compounds (particularly tributyltin (TBT) antifouling paints used on ships and leisure craft, which, in the early 1980s, caused stunted growth of oysters and probably affected reproductive capacity), oxygen depletion, reduced freshwater inputs, introduction of microbial pathogens/parasites, introduction of non-native species, and direct extraction (UK Biodiversity Group 1999, Hiscock et al. 2005). All these factors together with insufficient broodstock impair recovery and restoration efforts (Laing et al. 2005).

The main factors that probably threaten native oyster reefs now include illegal fishing, by-catch in trawl fisheries, poor water quality and pollution, changes to the environment (e.g., habitat loss due to coastal development), and the introduction of non-native competitors, predators and diseases (OSPAR Commission 2005). A recent report on the feasibility of restoration of native oyster stocks in the UK (Laing et al. 2005) identified the disease Bonamiasis as the biggest biological factor limiting the potential for stock restoration.

CURRENT NOTEWORTHY ACTIONS

Although the sparse remains of wild native oyster beds are probably one of the most endangered marine habitats in Europe, *Ostrea edulis* has rarely been the target of any specific large-scale protection measure, conservation legislation, or convention. Oyster reefs have just recently been listed as a conservation feature in Annex I of the European Commission (EC) Habitats Directive. Since 2003, *O. edulis* beds have been included in the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) list of threatened and/or declining species

and habitats (OSPAR Commission 2005). *Ostrea edulis* is also included in the Red lists of some regions (e.g., Wadden Sea, Black Sea). Indirect protection of native oyster reefs may also come from a number of EC Directives related to shellfish, such as the 91/67/EC, the 95/70/EC and the new 2006/88/EC, which set community-wide rules to prevent the introduction and spread of the most serious diseases affecting bivalve molluscs, and the Shellfish Waters Directive.

Fisheries for native oysters are regulated (sometimes prohibited) at a national level (e.g., Hiscock et al. 2005, Zaitsev 2006), and there is a range of national and local legislation related to issues of water quality but other national or regional conservation initiatives are rare. There is little evidence that this current low level of management attention is leading to recovery of stocks. In the United Kingdom, *O. edulis* is included in a Species Action Plan under the U.K. Biodiversity Action Plan (UK Biodiversity Group 1999) and naturally occurring native oyster beds are considered a nationally scarce habitat, although complex regulations still allow some harvesting (Laing et al. 2005).

There is a strong interest in stock restoration of native *Ostrea edulis* in many European countries, both to revitalize the fishery and to re-establish a native biotope that was once common. For example, in the UK Defra and Seafish commissioned a report on the feasibility of restoring native oyster stocks in the UK that includes an examination of biological, technical, economic, and legislative considerations (Laing et al. 2005). The report points out that there is clear evidence of the potential for success of *Ostrea edulis* stock regeneration especially in disease-free areas, and recommends the restocking of strategic areas, the relaying of cultch, and the use of sanctuaries as important components of successful restoration programs. The report also pointed out that there is a basic genetic similarity among wild European *O. edulis* populations, so the source of stocks would not be critical, and that there is evidence that disease-resistant stocks can be developed or might have already arisen at some sites. Restoration efforts are restrained by a lack of awareness of the poor condition and risks of these habitats.



Ostrea edulis is now functionally extinct throughout most of its native European range. © Keith Hiscock

North America

Synthesized by Robert Brumbaugh, Bill Arnold, Loren Coen, Boze Hancock, Matt Kay, Mark Luckenbach



Figure 7. The condition of oyster reefs in North America. © TNC

OVERVIEW OF CONDITION

The ten or more ecoregions comprising the coastal areas of North America have the best information of all the ecoregions on status of oyster reefs habitat. Although historic reports describe oyster reefs large enough to pose a hazard to navigation, today only the ecoregions in the Gulf of Mexico remain in fair condition. Oyster reefs elsewhere on the continent are either in poor condition or functionally extinct as reefs.

The oyster reefs that occur in estuaries throughout the Gulf of Mexico and the Atlantic coast of the U.S. belong primarily to one species, *Crassostrea virginica*, the Eastern oyster, whose full range extends south to Brazil and north to Nova Scotia, Canada. In virtually all of these locations, oysters are found in single-species assemblages, with some small accumulations of oysters in the genus *Ostrea* (primarily *O. equestris*). In some East Coast estuaries the ecological function of oysters is likely to be completely lost. For example, the oyster reefs in the Hudson-Raritan Bay and Narragansett Bay are functionally extinct. Recent assessments (Scarpa and Bushek 2001) suggest that there are presently no *C. rhizophorae* in the continental U.S., despite historical accounts; this may be a result of misidentifications or extirpation (Scarpa and Bushek 2001, J. Scarpa pers. comm. 2008).

The loss of *C. virginica* reef habitat is staggering in some estuaries. In the Maryland waters of the Chesapeake it is estimated that 90% or more of historic oyster reef acreage has been lost to direct damage from overharvest and sedimentation of remnant reefs (Rothschild et al. 1994, Smith et al. 2005). Oyster reefs along the Georgia coast appear to have suffered even greater declines in

geographic extent. Area alone does not tell the entire story, however, because density of oysters in remaining reefs is difficult to measure relative to historical numbers. In Apalachicola Bay, catch per unit effort (CPUE) is estimated to have fallen by a factor of ~10 even though reef area appears to have changed little over the past 100 years.

The native Olympia oyster (*Ostrea conchaphila*) along the West Coast of North America is not reported to form the tall three-dimensional reefs that *C. virginica* does on the East Coast. Nevertheless, there are records of extensive areas of reef-like habitat from southern California, Oregon, Washington, and parts of British Columbia. These beds were the focus of intense fisheries through the late 1800s and early 1900s. As harvests declined the intertidal areas were extensively manipulated and oysters were translocated around the coast (particularly from WA south to San Francisco Bay) to support the industry. The wild fishery collapsed and very few beds of wild native oysters remain today. In many bays they are functionally extinct. Some of the best beds are in more remote portions of the coast of British Columbia and the province has a Species at Risk plan that should help to facilitate long-term conservation efforts. The native “Olympia oyster” may actually be two different *Ostrea* species. As taxonomists have discovered for oysters in the Indo- and Western Pacific, species identifications can be challenging because morphologies exhibited under various environmental conditions can vary widely. The original classification dating back to the 1800s suggests that there are two West Coast species, *Ostreola lurida* and *Ostrea conchaphila*, with the former dominating the northern range, and the latter dominating a more southern range. A recent genetic assessment supports this classification (Polson et al. 2009).

THREATS

Populations of *Crassostrea virginica* in the many bays and estuaries of the U.S. East Coast share a common history of being over-exploited to the point of population collapse, and then failing to recover. This failure appears related to many factors, including disease, pollution, and eutrophication. In some cases, these stressors are thought to be exacerbated by the mass removal of the oysters’ own filtering capacity (Newell 1988, Newell et al. 2007). Similarly, on the eastern coast of Canada, the Gulf of St. Lawrence supported an intense and productive oyster fishery that maintained high yields into the 1910s. Following reports of destructive harvest and declines in the 1800s, the fishery most abruptly declined around 1915 when Malpeque disease arrived with shipments of oysters imported from outside the region. The fishery has recovered somewhat but natural reefs remain rare.

As with Eastern oysters, the intensive fishing pressure on Olympia oysters (*O. conchaphila*) on the West Coast of North America soon led to declines in many estuaries

NEW HOPE FOR CHESAPEAKE BAY OYSTERS?



Oysters from a reef restoration site in the Piankatank River, Virginia. © TNC

The tragic decline in Chesapeake Bay oyster reefs and the oyster fishery they supported is extremely well-chronicled. Surveys as early as the late 1800s revealed dramatic declines in the overall extent of viable reefs in the lower estuary and diminishing numbers of oysters in areas that had been—for a few decades at least—the mainstay of the largest oyster fishery in the United States (Winslow 1882). The rapid changes in physical structure of reefs is vividly apparent in comparisons of historic navigation charts between the late 19th century and mid-20th century in places such as the James River, the largest tributary in the lower estuary (Woods et al., 2005). As with other areas in the U.S. where dramatic declines in oyster landings occurred, the management objective of maximizing fisheries landings has proved unsustainable in the Chesapeake Bay, particularly against the backdrop of changing environmental conditions (Kirby and Miller 2005).

The loss of oysters from the Chesapeake has had profound effects in the region, both ecologically and socially. Fishermen in Maryland and Virginia were pitted against one another, sometimes violently, in so-called 'oyster wars' involving poaching across state lines in the Potomac River (Wennersten 1981). Ecologically, the loss of oysters' filtering capacity may have profoundly altered water quality in the estuary, jeopardizing seagrasses, another vitally important habitat (Newell 1988; Cerco and Noel 2007). Such impacts have spurred calls for dramatic changes in oyster management—ranging from moratorium on the wild oyster fishery (Horton and Eichbaum 1992) to introductions of non-native oysters as a means of bolstering the fishing industry. The latter issue was reviewed by a National Research Council panel (NRC 2004) and has been scrutinized further in an Environmental Impact Study by state and federal regulatory agencies (USACE 2009).

Despite the dire situation, there is hope that the native oyster, *Crassostrea virginica*, can, with active restoration and wholesale changes in management approaches, stage a comeback in the estuary. Restoration efforts for the native oyster show promise that oysters can be restored (Brumbaugh et al. 2000), and there is evidence that in places where fishing pressure has been minimized it is possible for oysters to develop resistance to parasites that have posed a particular challenge in recent decades (Ryan Carnegie, VIMS, Personal Communication). Most recently, two 'blue ribbon' style panels were convened in Maryland and Virginia reached similar conclusions (MOAC 2008; VBROP 2007). First, both panels noted that significant areas need to be restored and set aside strictly for their ecological function. To date, only small sanctuaries have been restored and set aside, so this is a fundamental shift from the historic management approaches. Second, aquaculture should play a larger role in providing Chesapeake Bay oysters for the marketplace. Again, this shift away from relying solely on public fisheries and wild harvest is a significant shift in management philosophy, particularly for Maryland where there has been less emphasis on private leasing than in Virginia. While there is a need to ensure that aquaculture is conducted responsibly, this shift could enable significant progress by relieving pressure on natural reefs and wild populations that are currently estimated to be near 1% of historic abundances overall.

OLYMPIA OYSTER REEFS IN BRITISH COLUMBIA

CONSERVATION PRIORITIES & RESTORATION BENCHMARKS

The estuaries along the Pacific West Coast of North America are dominated by non-native oysters and clams. There once were, however, extensive and thriving reefs and beds of many native bivalve shellfish throughout the coast from British Columbia to California. Many and likely most of the temperate bays on this coast had large and sometimes huge beds of native Olympia oysters, *Ostrea conchaphila*. For example, there used to be huge beds of Olympia oysters in San Francisco Bay (Fig.1 below), supporting a substantial fishing industry. After the wild beds were depleted, however, native oysters were shipped down from Washington state, Willapa Bay in particular, and placed in holding beds in San Francisco Bay to supply the local markets. Interestingly, the author Jack London, a San Francisco native, was once both an oyster pirate and policeman (see his "Tales of the Fish Patrol"). Only a handful of oysters remain in the Bay today with no true beds and they are functionally extinct. Functional extinction is the common state in bays throughout the coast.



Measuring densities at oyster beds in Nootka Sound © Brian Kingzett

The Olympia oyster can still be found in many bays but only as small clumps or pockets of individual oysters. Even in some of the most heavily altered estuaries in Southern California they can be found clinging to rip rap, seawalls and other artificial hardened structures revealing their tenacious nature and the potential for restoration. Presently few people in the region know that the Pacific oyster, *Crassostrea gigas*, is not native to this coast. *C. gigas*, is the main farmed species of bivalve on the west coast of North America, as it is globally. *C. gigas* is increasingly found in the wild as well, to such an extent that it has become an important competitor with the remaining native oysters in some places (Trimble et al. 2009).

Despite the loss of Olympia oysters throughout much of its range, there are a few healthy beds of Olympia oysters in remote areas of Northwest Vancouver Island (Gillespie 2009). From a conservation standpoint, these beds are critically important as the last and best reefs remaining of native Olympia oysters in North America. They are also of vital importance for informing restoration goals elsewhere on the Pacific coast as it is rare to have direct data on the characteristics of intact beds and their communities.



Fig. 1 San Francisco Bay oyster beds. Adapted from California Fish Bulletin 123 (Sacramento, CA, 1963).

In 2008, a team of scientists and conservationists from various organizations including Puget Sound Restoration Fund, the Shellfish Centre at Vancouver Island University, Canadian Department of Fisheries and Oceans, and The Nature Conservancy surveyed some of these last remaining beds to inform conservation and restoration. What was found in Nootka Sound was remarkable given the state of flat oysters on the Pacific coast and elsewhere globally.

In Nootka Sound, the inlets and drainages are steep and the intertidal benches tend to be small. In the primary inlet that was surveyed, the average densities of native Olympias was over 300 oysters/m² across the three biggest benches, a total intertidal area of 20,000 square meters. In randomly located quadrats, the densities reached higher than 1,100 oysters/m². In most of this area, the native oysters covered the bottom and provided the primary structure for many other plants and animals. Even in these areas though, *C. gigas* was frequently found in the beds and the infaunal bivalves were dominated by non-native species.

This information is already informing restoration goals for projects in the region. The Canadian government previously has identified *O. conchaphila* as a Species at Risk and is finalizing a management and monitoring plan. Few of the remaining populations have been comprehensively surveyed. The surveys are being published scientifically elsewhere and the implications of this work for coastal ecology can be found in a forthcoming book by Rowan Jacobsen.

with no subsequent recovery. Other factors likely contributed to the declines, or at least exacerbated the impacts of destructive fishing practices. For example, declines of Olympia oysters in south Puget Sound are at least partly attributed to pollution from a pulp mill. A second example is Coos Bay, Oregon, where oysters that were believed to be plentiful prior to European colonization were absent when colonists first arrived. Local lore has it that a massive forest fire, followed by heavy rains, caused intense sedimentation that smothered oyster populations. This sequence of events, if true, represents the largest naturally-driven decline in oyster populations contained in this study. A third example is sedimentation in San Francisco Bay. Unlike Coos Bay, this sedimentation was not a natural event but rather was caused by gold mining activities within the watershed that sent vast quantities of sediment down river into the estuary beginning in the mid 1800s.

The commercial fishery for *Ostrea conchaphila* in British Columbia was short lived and stocks have failed to recover since the fishery collapsed in the 1930s and '40s. Fishery decline and failure to recover has been attributed to extremely low recruitment and high juvenile mortality caused by harsh environmental conditions. Stafford (1918) cautioned that beds were thin and dominated by larger size classes—a condition he interpreted as suggestive of low recruit survivorship. Harvest was destructive to the fragile beds and little enhancement was practiced.

CURRENT NOTEWORTHY ACTIONS

The ecosystem services provided by oyster reefs are gaining recognition in North America, particularly in the United States. Restoration efforts that historically were focused exclusively on enhancing fishery landings are increasingly focused on the return of other services, such as shoreline protection, provision of fish habitat, and improvement of water quality. Nearly every coastal state has some form of restoration for ecological outcomes underway, though these efforts are still small relative to the magnitude of loss. New and expanded sources of funding will be necessary for large-scale restoration efforts, and improved coordination between fisheries and other environmental objectives are needed to ensure that reefs are restored and managed as critically important ecosystems. Additional documentation of the economic value of restored reefs may help to propel these efforts in the future.



Restored Oyster Reef at the Virginia Coast Reserve. © Barry Truitt/TNC



THREATS

Overview of Threats and Causes of Decline

As illustrated in the regional reviews, shellfish populations face many threats from land and sea which have contributed to profound losses of reefs world-wide and continue largely unabated today. The major stresses include overfishing, destructive fishing, sedimentation, disease, changes in freshwater inflow, introduced species, and excess nutrients and pollutants.

Aggressive fishing practices that directly alter the physical structure of reefs have been implicated in rapid declines in both fisheries productivity and overall reef condition in many estuaries. Fishing practices involving the translocation of shellfish within and between bays has increased the incidence and severity of disease and parasite outbreaks that have all but eliminated fisheries in many coastal areas. Coastal development including land-reclamation (filling) and dredging of shipping channels has taken a toll on reefs. In tropical areas the widespread deforestation of mangroves, which are a primary attachment substrate, have had major effects on mangrove oyster populations. Likewise, activities occurring upstream continue to cause problems as human populations increase in coastal watersheds. Altered river flows, construction of dams, poorly managed agriculture, and urban development can all impact the quality and quantity of water and local sediment supply (too much sediment, in particular, is a problem for shellfish) that largely determines whether shellfish reefs persist or perish.



Clockwise from top left: Non-native bivalves can outcompete native species. Here green mussel *Perna viridis* overgrows the native eastern oyster in Florida. © Jon Fajans, Reef scarring from boat propellers in South Carolina. ©Mike Yianopoulos, SCDNR, Boat wakes cause impacts to shorelines and can threaten intertidal oyster reefs. © Loren Coen, SCCF

After reviewing the literature dating back to the 1700s and 1800s describing declines in oyster fisheries, it is clear that the dramatic loss of oyster reefs across the globe stems from a common sequence of causes (Mackenzie 1997 a,b,c, NRC 2004). Typically extensive harvest of wild populations results in the loss of reef structures. Most declines start with destruction of the primary structural complexity, often through dredging/trawling, which increases likelihood of stresses from anoxia, sedimentation, disease, and non-native species. Often years of declining harvest are followed by introductions of non-native oysters directly in the wild or released from aquaculture. There is often a population crash caused, at least proximally, by overharvest or disease. While oyster diseases occur in native populations, in many places the incidence of disease is believed to be associated with transfers of non-native oysters for aquaculture and from ballast waters (National Research Council 2004). Other anthropogenic factors cause declines, such as changes in freshwater inflow and sediments and loadings of nutrients and toxic pollution. These factors can be very important in some bays.

Despite the wealth of historic information, there is a contemporary debate within fisheries management circles about the causes of reef declines. Much of this debate seems to focus on laying blame rather than on remedying the mostly agreed-upon poor conditions of reefs themselves. Extensive direct harvest, particularly using techniques that destroy underlying structures, has had large impacts on these populations, stressing them and leaving them more susceptible to other impacts. These shellfish live in some of the most highly developed coastal watersheds and degradation of water quality and changes in flow are important. The spread of non-native species and their associated predators, pests, and diseases has also affected oyster reefs and in many places the pressure to spread non-natives continues today. Fixing the problems will at some level demand addressing all of these factors at sea and on land.



RECOMMENDATIONS

Recommendations for Conservation, Restoration, and Management

The catastrophic loss of shellfish reefs has been centuries and even millennia in the making. But this loss is not just a problem of the past; it is a problem of the present and future. While many of these losses happened historically, we are still managing these species and their reefs in ways that almost assure that they will continue to decline. Most wild *Ostrea edulis* populations in Europe were removed between 100 and nearly 1000 years ago, but in just the past decade (1990s), a wild population in the Gulf of Thessaloniki (Greece) collapsed from more than 1000 tonnes of harvest annually to a point where it is now difficult to find just 60 individual oysters with a dredge (Virvilis and Angelidis 2006). There are likely multiple causes of this decline, and parasitic infections are highly prevalent in the few remaining oysters. One of the last (if not the last) remaining *Ostrea anagasi* beds in all of Australia was recently re-opened for harvest. The few remaining remnants of Olympia oyster beds in the U.S. Pacific Northwest are still generally open for harvest. In the Chesapeake Bay, harvests continue at approximately 1% of their peak exploitation rates.

There are many obstacles to successful management of shellfish reefs as habitats, but perhaps the biggest challenge is the perception among managers that there is not a problem. Oyster reefs are not generally recognized as habitats in policy or practice. Fisheries in many areas have yielded large quantities of oysters or mussels even as the reefs themselves become degraded and vanish. In addition there is a common perception that non-native shellfish in aquaculture can replace natives. However, native oysters need to be recognized for the reef habitat that they provide. A paradigm shift is needed in the regulatory and management communities and in the general public that will lead to shellfish ecosystem restoration and conservation not just for fisheries production, but specifically to return a full array of critical ecosystem services.

Few groups or agencies have a broad or global focus on temperate coastal ecosystems such as seagrasses, salt marshes, or shellfish reefs. Instead, a bay-by-bay method of management has led to

piecemeal conservation efforts rather than a broad, cohesive conservation strategy. To get from current practices to more holistic management, a regime shift will need to occur. There are historical precedents for such shifts in perception and actions. Until recently wetlands were mainly perceived as disease-infested swamps that should be dredged, diked, drained, refilled, and reclaimed. That perception has changed and the values of wetlands are now better appreciated. While degradation continues, it has slowed. The global focus on coral reefs has also changed substantially in the past 15 years starting with a series of global papers and analyses including *Reefs at Risk* (Bryant et al. 1998). We hope this *Shellfish Reefs at Risk* report will act as a similar catalyst to change the conservation and management of shellfish reefs which, in many regards, are the temperate equivalents of coral reefs.

At a minimum, the following strategies will be needed to turn the tide. No one strategy will be right for each area or threat and it is assumed that multiple strategies will be needed in most places. The strategies are grouped into five common themes:

- **Improve Protection** for reefs of native shellfish;
- **Restore and Recover Reefs** back to functioning ecosystems that provide multiple services to humans;
- **Manage Fisheries Sustainably** for ecosystems and livelihoods;
- **Stop the Intentional Introduction and Spread of Non-native Shellfish**; and
- **Improve Water Quality**

Improve Protection

- **Protect the Last, Best Reefs.** Our work emphasizes the fact that there are a few key areas remaining that are priority candidates for conservation. These include some of the best and sometimes last remaining shellfish reefs for certain species in Australia (Georges Bay, Tasmania), Pacific North America (Vancouver Island, British Columbia), and in several bays in the Gulf of Mexico. The opportunities in Europe are more difficult to ascertain but must be explored. For example, in the Mediterranean Sea, Mar Menor (Spain) was considered to have one of the best preserved natural beds of *O. edulis*, but its current status has not been studied since the mid-1990s (Ramón et al. 2005). Other areas where conservation opportunities should be explored include the west coasts of Scotland and Ireland, the western part of the Swedish Kattegat region of the Baltic, and the Limfjord region of Denmark.
- **Develop MPAs for Oyster Reefs.** Oyster reefs and other shellfish habitats are very rarely identified as a management or conservation feature within MPAs. China recently established one protected area primarily for shellfish. In the U.S. a few states have recently established spawner sanctuaries for shellfish, but these are mostly small-scale relative to their historic population size and aerial extent. North Carolina, for example, has established a network of nine oyster reef sanctuaries, and is working to re-establish reefs with old shells and limestone rubble. These kinds of MPAs should be expanded to other
- important areas, particularly because the likelihood that existing reefs serve as propagule sources to seed other locations is greater for shellfish than most species.
- **Recognize Reefs as Ecosystems in Protected Area Policies.** Shellfish reefs need to be recognized as habitats in representative protected area policies. Many of these policies have been developed by nations as part of their signed agreement to the Convention on Biological Diversity, which, among other things, commits them to establishing representative networks of coastal and marine protected areas by 2012. Most nations do not recognize shellfish habitats in their representative area policies. The European Union recently added oyster reefs as a habitat for protection under Natura 2000; however reefs should be elevated to a priority habitat type given their functional extinction throughout much of Europe.
- **Recognize Oyster Reefs as Critical Wetlands under Ramsar Convention.** The Convention on Wetlands of International Importance of 1971 or Ramsar Convention (named after the Iranian town in which the convention was signed) was the first modern multi-national agreement aimed at conserving natural resources. It encourages the designation of sites containing representative, rare, or unique wetlands. Oyster reefs should be specifically identified for protection under this convention and further, should be regarded with other similar wetlands (e.g., seagrasses, coral reefs, mangroves, and kelp forests) as an “under-represented wetland type.” There are presently 1,831 wetland sites, totaling 170 million hectares, designated for inclusion in the Ramsar List of Wetlands of International Importance (www.ramsar.org); few of these were identified to help protect shellfish populations.
- **Expand Listings for Oysters as Imperiled Species and Threatened Habitats.** For some places and species, at-risk listings for oysters are needed. Oysters have been identified as imperiled or threatened by a number of countries mainly in Europe including the United Kingdom, Netherlands, Germany, Sweden and Ukraine. The OSPAR convention for the Northeast Atlantic identifies *O. edulis* beds as a threatened or declining habitat. In Canada, Olympia oysters, *O. conchaphila*, have been identified as a Species at Risk and a draft management plan has been developed (Gillespie 2009). No similar plan exists in the United States for *O. conchaphila* despite the fact that Olympia oysters beds are in worse condition there. In Australia, *O. angasi* reef habitat could be nominated for listing as a threatened ecological community under the Environment Protection and Biodiversity Conservation Act of 1999.
- **Develop Shellfish and Temperate Reef Commitments in Global Organizations.** Few global organizations and agencies have a focus on temperate reefs or wetlands, much less shellfish. International agencies and environmental organizations, most of which are based in the U.S. and EU, should initiate new programs to bring attention to temperate reefs, as they have for tropical reefs, and seek commitments from participating countries on conservation measures. Assessments by IUCN of the status of shellfish ecosystems could bolster these commitments.



Oyster mats used for restoration in Indian River Lagoon
© Anne Birch/TNC

Restore and Recover Reefs and Their Services

Reef restoration is needed on a scale commensurate with reef loss (Figure 1). Existing funds could be used more effectively and there are opportunities to develop new funding streams for rebuilding reefs. Doing so would provide a host of environmental services including sustainable fisheries, habitat for other species, water filtration, and shoreline protection. In some areas, the barriers to successful restoration still need to be understood.

- **Set Restoration and Recovery Goals.** Regional and national goals need to be set for restoration and recovery. The condition estimates and categories provided in this report can help in that development. Goals should be set (i) to ensure that abundances and condition do not slip in to lower categories and (ii) to raise oyster reef abundances within bays and regions so that these areas increase from one condition category to the next.
- **Use Existing Restoration Funds Better.** There are significant opportunities to use existing funds better. In the U.S. alone, tens of millions of dollars have been spent in the past decade to recover fisheries in places like Chesapeake Bay and to regain fishery production following hurricanes in the Gulf of Mexico. Often billed as restoration, the outcomes of these investments are measured mainly in near-term harvests. Assisting oystermen to overcome the effects of natural disasters and the legacy of poor past management are important goals, but wise investments should be more than short-term (e.g., put-and-take of oysters). More of these funds should be invested in rebuilding the natural capital of reefs to provide for multiple benefits including fisheries where the interest, not the principal of our investments, is harvested.
- **Support Public-Private Partnerships to Restore Native Species.** The aquaculture industry, public agencies, and environmental NGOs are natural partners for promoting the restoration of native oysters and their services. Together these groups could promote businesses to help produce native oyster species that can be sold for market and in the process generate funds and seed oysters for habitat and population restoration. For example, public-private partnerships could be profitable for businesses and reduce costs for native Olympia oyster restoration on the West Coast of the U.S (J. Madeira pers. comm.).
- **Develop New Funding Mechanisms Around Ecosystem Services: Nitrogen.** Nitrogen pollution, a primary cause of the degradation of coastal estuaries and water quality, has grown exponentially in recent decades. The costs of both nitrogen pollution and the manufactured solutions to address it are enormous, which is why there is growing interest in cap-and-trade mechanisms to control this type of pollution. Nitrogen markets are being tested along the mid-Atlantic coasts in the U.S. in which credits are traded for mechanisms such as the planting of riverine buffers on farmlands and new designs for chicken coops to contain wastes. The ability of shellfish to sequester nitrogen in their tissues is one direct way to bring about nitrogen reduction. In Sweden, the filtration power of mussels in aquaculture is being used to sequester nitrogen in an effort to avoid the cost of constructing another wastewater treatment facility (Lindahl et al. 2005). The amount of nitrogen potentially sequestered or removed by shellfish is large, especially when the ability of benthic shellfish to remove nitrogen through denitrification in adjacent sediments is considered. Further research is needed to establish the credit equation (i.e., how much nitrogen is sequestered or removed per oyster or reef). It is likely to be no more variable than the amount of nitrogen sequestered or removed by a vegetated shoreline buffer (or the amount of carbon sequestered across the lifetime of a given planted sapling). A market for this service could pump significant funding into shellfish restoration.
- **Develop New Funding Mechanisms Around Ecosystem Services: Shoreline Protection.** The impacts of climate change and coastal habitat loss are being manifested in the increasing inundation and erosion of shorelines globally. The costs of these impacts and the manufactured solutions to address them are growing rapidly. At the same time there is growing interest in using ecosystem-based adaptations or green infrastructure to help abate these threats. Oyster reefs can play a key role in helping to defend shorelines and reduce erosion, and there are a growing number of tests and applications of this approach. The value of a reef for shoreline protection should be accounted for before any further degradations are allowed. Furthermore, the costs and benefits of natural and manufactured solutions should be weighed for any project. Funds should be sought for further demonstration tests of the use of oyster reefs for shoreline protection. For methods see: <http://www.oyster-restoration.org/>
- **Reduce Perverse Incentives that Make Restoration More Difficult.** One of the few potential “protections” for shellfish occurs in areas where human harvest is prohibited because of poor water quality. Unfortunately, restoration in such areas is sometimes actively discouraged or not allowed because shellfish in these locations are regarded as an “attractive nuisance” that could entice illegal harvest from polluted waters (and lead to concomitant human health issues). In some cases,

managers remove shellfish from these areas and further exacerbate the poor condition of reefs. What is essentially a regulatory and enforcement challenge is, therefore, condemning some rivers and bays to a continued decline. In the U.S., leadership from the Interstate Shellfish Sanitation Conference (ISSC) in finding new solutions to this enforcement challenge would go a long way toward removing these perverse incentives that allow reefs and water quality to degrade further.



Sanctuaries are a useful tool for rebuilding and protecting spawning populations. © Linda Walters, University of Central Florida

Manage Fisheries Sustainably

- **Develop and Adhere to Fishery Rebuilding Plans.** The collapse of fisheries is a global problem that affects people and livelihoods. It is a core responsibility of management to disallow, reduce, and recover from these disasters. In many fisheries rebuilding plans are being developed, and there have been some important successes. However, the development of rebuilding plans for oysters is rare. At a minimum, they should be managed to the same standard as other fisheries.
- **Stop Fishing in Areas with Less Than 1% of Shellfish Remaining.** There should be no question that when stocks are below 1% of historical abundance that fishing should be stopped until the reef is successfully rebuilt. For most other fisheries action is taken if stocks fall below 10% of prior abundances and the same approach should be followed for shellfish. Unfortunately these guidelines have not been followed for shellfish and it is still common to see harvest allowed when only around 1% of stocks remain.
- **Ensure Sustainable Fisheries in the Gulf of Mexico.** While scientists and managers focus on the dozen or so estuaries that dominate typical oyster discourse such as Chesapeake Bay, the needs and opportunities elsewhere are often overlooked. The oyster fisheries in the Gulf of Mexico (U.S. and Mexico) need to be managed for what they represent: likely the last opportunity in the world to achieve both large-scale reef conservation and sustainable

fisheries. These beds currently represent the most significant wild harvests left in the world. There is real opportunity for sustainable fisheries in the Gulf of Mexico, but even those reefs have been declining. Changes towards more sustainable long-term oyster harvest is needed if the Gulf is to avoid the fate of most wild, native oyster fisheries globally.

- **Use Fishery Funds to Sustain Long-term Harvests, not just short-term put-and-take gains.** See **Use Existing Restoration Funds Better.**
- **Learn from Successes.** Managers need to study the few areas with healthy shellfish reefs in order to learn from these successes and expand effective conservation and management approaches. In Chile, more sustainable shellfish harvests have been achieved using a mixture of protected areas for important populations, cooperative fishery management, user rights, and aquaculture to reduce harvests on wild stocks (Castilla et al. 2007). This approach should be replicated elsewhere.
- **Use Private Fishing Rights More Effectively and Promote Greater Stewardship.** Private rights approaches for shellfish (e.g., lease and concessions of submerged lands) have been used extensively in many countries including the U.S.; these rights should provide the basis for more effective management (Beck et al. 2004) and are believed to be key to restoring fisheries. Greater monitoring and stewardship of the shellfish resources should be required for leases in order for individuals to maintain exclusive rights. Extending leasing opportunities to conservation organizations and other private firms could also facilitate the testing of new approaches for restoration and harvest using these leases.
- **Map Reefs to Assess Management Effectiveness.** To better manage for sustainable fisheries and reef rebuilding, the distribution of reefs must be mapped. In many places the distribution of oyster habitat was known better 100 years ago (e.g., Drake 1891, Moore 1907, 1913), than it is today. Nearshore habitat mapping, using for



Non-native bivalves can outcompete native species. Here green mussel *Perna viridis* overgrows the native eastern oyster in Florida. © Jon Fajans

example side scan sonar, is now relatively cheap and needs to be used much more often.

Stop the Intentional Introduction and Spread of Non-native Shellfish

Much of the spread of non-native species happened in the past but the pressure to spread non-native oysters is still strong today globally from Ireland to Chesapeake Bay to South America. Shellfish culture has been the second greatest source of marine invasive species after ballast water (Molnar et al. 2008); these non-natives include the imported shellfish, their diseases and many associated predators, competitors, and hitchhiker species (Ruesink et al. 2005, Molnar et al. 2008).

- **Follow ICES Protocols.** At a minimum all International Council for the Exploration of the Sea (ICES) codes of practice for marine introductions and transfers should be followed in aquaculture to ensure that new non-natives are not released in to the wild (ICES 2004). These protocols reduce but do not eliminate the risks of new introductions (NRC 2003).
- **Stop Intentional Introductions.** The ICES protocols however only look at impacts case by case or bay by bay and do not account for the cumulative impacts of introductions. Given the widespread impacts from the spread and globalization of just a few oyster species, we cannot recommend any further introductions.
- **Support Hatcheries and Business that Grow and Use Native Shellfish Seed** with incentives or other market forces. See also **Support Public-Private Partnerships to Restore Natives.**
- **Support Aquaculture that Relieves Pressure on Reefs and Wild Stocks.** Aquaculture when done well and combined with other fishery regulations can reduce pressure on harvest of wild reefs.

Improve Water Quality

The fate of oysters is tied to overall estuarine condition. Improving estuaries will require significant effort, much of which will need to be watershed-based. Indeed watershed management is likely to be one of the bigger challenges for conserving shellfish and other coastal ecosystems. The recommendations outlined here focus on those explicitly tied to shellfish; a broader set of water quality recommendations is beyond the scope of this document. While improving water quality is a daunting task, there are actions that can help.

- **Use Shellfish as Bioindicators.** Because of their close ties to many estuarine processes and their ability to bioaccumulate, oysters can be used as bioindicators for water quality and for achievement of estuarine conservation and restoration targets (Volety et al. in press). Shellfish could also be used as indicators for water flow. Currently, flows and shellfish reefs are managed at local, often disconnected scales. Improvements could include integrating shellfish reefs as management targets for catchment (watershed) management councils.
- **Enhance or Establish Shellfish Partnerships Across Sectors.** The aquaculture industry, environmental NGOs, and managers should seek common ground to help conserve and restore the coastal water quality that is vital to cultured and wild shellfish. The decline of oyster reefs may be harbingers for further environmental declines in coastal estuaries as they tend to decline first, which are followed by other habitats and species (Lotze et al. 2006).
- **Support Sustainable Aquaculture.** Shellfish aquaculture can be carried out more sustainably than most other fisheries and aquaculture. These businesses rely on clean coastal waters and are key stakeholders for preserving and improving water quality.
- **See Develop New Funding Mechanisms Around Ecosystem Services: Nitrogen.**



Measuring brown tide outbreak in Chesapeake Bay. © Rob Brumbaugh/Chesapeake Bay Foundation

A NOVEL SOLUTION TO A CONTEMPORARY THREAT TO OYSTER REEFS IN THE INDIAN RIVER LAGOON, FLORIDA



Volunteers working on oyster reef restoration in Indian River Lagoon. © Anne Birch/TNC



Oyster mats deployed in Indian River Lagoon. © Cheryl Mall/TNC



Restoration efforts are enabling oysters to recover from damage caused by boat wakes within Canaveral National Seashore, Florida. © Anne Birch/TNC

Declines in oyster reefs in many estuaries noted in this report are historic in nature, the legacy of excessive and destructive fishing practices that peaked in the 18th through early 20th century. In some locations, such as the Indian River Lagoon, Florida, the losses are quite contemporary and stem from novel sources of stress on oyster reefs. Scientists in the 1990s used aerial photography to compare the present day extent of live oyster reefs to reefs in the 1950s and noticed a dramatic decline in live oyster reef area. The declines were occurring even within the boundaries of the Canaveral National Seashore, a protected area managed by the U.S. National Park Service, where extractive forces such as dredging or excessive harvest were not permitted. The declines were accompanied by a commensurate increase in the area of 'dead margins', mounded areas of disarticulated shells resembling sand dunes or snow drifts above the level of mean high tide (Grizzle et al. 2002). Additional research made it clear that these changes were related to the impacts of boat wakes associated with increases in boating traffic in the area over that timeframe (Walters et al. 2002, Wall et al. 2005).

A collaborative effort to reverse these declines through restoration was initiated in 2005 between The Nature Conservancy and the University of Central Florida. Working within the boundaries of the Canaveral National Seashore, a pilot project was initiated to test the efficacy of using 'oyster mats' developed by Linda Walters, a professor at the University of Central Florida. The mats are constructed using aquaculture grade mesh with a specific number of shells firmly attached so that they are both resistant to the movement of water caused by boat wakes and are oriented vertically to provide a good structural representation of a healthy reef's surface. The vertical orientation of oysters on reefs helps to increase recruitment and long-term survival of oysters, and provides a refuge for small fish and other organisms associated with the reefs (Soniat et al 2005). The dead margins are graded back to normal elevation. When deployed on top of the shells from the leveled dead margins, the mats reduce the wave energy and provide a stable place for oyster larvae to settle and grow.

Between 2005 and 2009, The Nature Conservancy's Indian River Lagoon Program organized an army of volunteers, nearly 10,000 people in all, to help assemble and deploy the thousands of mats necessary to restore approximately 20 acres of degraded reefs within the Canaveral National Seashore. Community groups of all kinds became engaged in the effort. Novel partners emerged such as the Royal Caribbean Cruise Ships '*Mariner of the Seas*' and '*Freedom of the Seas*' whose crews have provided the invaluable service of drilling

holes in hundreds of thousands of shells during the ship's time at sea, enabling the shells to be affixed to the oyster mats back on shore.

With this project, the University of Central Florida and The Nature Conservancy have shown that the mats are effective at stabilizing degraded reefs, provide a perfect substrate for young oysters to re-colonize the reefs and help support a diverse assemblage of other species (Barber, A.L. 2007). In just a few years, the declines from decades of increasing boating traffic have been stemmed and are being reversed. Mats deployed early in the restoration effort have become entombed in the reef's surface and the restored areas are becoming virtually indistinguishable from natural reefs found farther from areas with boating traffic. Importantly, underpinning this restoration work is science, and as restoration efforts expand, careful monitoring and documentation will be key to understanding how the reefs and their associated community respond to restoration and whether additional protective measures are necessary to ensure their long-term persistence.



CONCLUSIONS

Oyster reefs once dominated many temperate estuaries globally and were, in many regards, the temperate equivalents of coral reefs. Recorded and anecdotal accounts of historical extraction of oysters indicate the existence of vast reefs with significant structural complexity. This report provides thorough and direct estimates of condition of this critical coastal marine habitat.

There are many obstacles to successful management of oyster reefs, but the biggest is simply perception among managers that there is not a problem. In addition there is a common perception that non-native shellfish in aquaculture can replace natives. Put simply, native oysters need to be recognized for the reef habitat that they provide. A paradigm shift is needed in the regulatory and management communities and with the public in general that leads to shellfish habitat conservation and restoration not just for fisheries production, but specifically to return a full array of critical ecosystem services.

The oyster abundance categories in this report can assist in setting much-needed goals for restoration and conservation. Realistic conservation goals include (i) ensuring that abundances do not slip into lower categories and (ii) more appropriately, increasing reef quality and abundance such that reefs can be moved up from one category to the next. While there is no exact level at which reef ecosystems become self sustaining, it must be higher than 10% of historic areas.



Oyster beds at Virginia Coast Reserve. © Diana Garland

We have outlined sensible options for improving the condition and management of shellfish reefs in five key areas:

Improve Protection for native shellfish reefs. Native, wild oyster reefs need to be recognized explicitly as a priority for habitat management and conservation and in development of protected area policies. They are an imperiled habitat with little protection in place for the few remaining examples. Because they are typically found nearshore, and are relatively static features in the coastal zone, shellfish reefs are conducive to being managed through area-based approaches such as marine protected areas (MPAs) and community concessions.

Restore and Recover Reefs back to functioning ecosystems that provide multiple services to humans. Reef recovery and restoration is needed on a scale commensurate with losses. Existing funds can be used better and new funding streams are possible for rebuilding reefs and their services.

Manage Fisheries Sustainably for both ecosystem condition and livelihoods. In addition to using quantitative stock assessment methods for shellfish populations, their reefs must be managed with more than just fisheries landings in mind. Other ecosystem services such as water filtration, nutrient removal, shoreline protection, and provision of fish habitat should receive the same consideration (or greater, depending on location) as fisheries in management objectives. Greater use should be made of these tools and approaches.

Stop the Intentional Introduction and Spread of Non-native Shellfish. Further introductions of non-native oyster species to new areas should not be allowed. The cumulative impacts of the globalization of a few oyster species (and their hitchhikers) have been great, and few regions remain that are still free of introduced oysters.

Improve Water Quality. Addressing threats originating within watersheds such as nutrient pollution, erosion, excessive sediment supply, and altered freshwater flows, will increase the effectiveness of conservation and management. Enhancing native populations will help restore natural biofiltration capacity in estuaries and bays.

We believe that the recommendations in this report will enable oyster reefs formed by native shellfish to recover where they have been affected by human activities along the coast and to persist for the long-term in places where they exist today in fair to good condition, providing ecological and economic benefits to societies around the globe.

“The nation behaves well if it treats the natural resources as assets which it must turn over to the next generation increased and not impaired in value.”

- Theodore Roosevelt



REFERENCES

© Anne Birch/TNC

- Acosta, V., A. Prieto, and C. Lodeiros. 2006. Índice de condición de los mejillones *Perna perna* y *Perna viridis* (Bivalvia: Mytilidae) bajo un sistema suspendido de cultivo en la Ensenada de Turpialito, Golfo de Cariaco, Venezuela. *Zootec Trop* 245:177-192.
- Airoldi, L., and M. W. Beck. 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review* 45:345-405.
- ASMFC. 2007. The Importance of Habitat Created by Shellfish and Shell Beds Along the Atlantic Coast of the U.S., prepared by L.D. Coen, and R. Grizzle, with contributions by J. Lowery and K.T. Paynter, Jr., 108pp.
- Barber, A.L. 2007. Restoration of intertidal oyster reefs affected by intense recreational boating activity in Mosquito Lagoon, Florida. Master's Thesis, University of Central Florida. Orlando. 111 pp.
- Barnabe, G., and F. Doumenge. 2001. *Mariculture of Mediterranean species*. Academic Press, San Diego.
- Beck, M. W., T. D. Marsh, S. E. Reisewitz, and M. L. Bortman. 2004. New tools for marine conservation: the leasing and ownership of submerged lands. *Conservation Biology* 18:1214-1223.
- Berghahn, R., and M. Ruth. 2005. The disappearance of oysters from the Wadden Sea: a cautionary tale for no-take zones. *Aquatic Conservation* 15:91-104.
- Booker, M. M. 2006. Oyster growers and oyster pirates in San Francisco Bay. *Pacific Historical Review* 75:63-88.
- Borthagaray, A., and A. Carranza. 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. *Acta Oecologica* 31:243-250.
- Brumbaugh, R.D. and L.D. Coen. 2009. Contemporary approaches for small-scale oyster reef restoration to address substrate versus recruitment limitation: A review and comments relevant for the Olympia oyster, *Ostrea lurida* (Carpenter, 1864). *J. Shellfish Res.* 28:147-161.
- Brumbaugh, R.D., L. Sorabella, C. Garcia, W. Goldsborough and J. Wesson. 2000. Making a case for community-based oyster restoration: An example from Hampton Roads, Virginia, U.S.A. *J. Shellfish Research* 19: 467-472.
- Bryant, D., L. Burke, J. McManus, and M. Spalding. 1998. *Reefs at Risk: A map-based indicator of potential threats to the world's coral reefs*. World Resources Institute, Washington, DC.
- Burke, L., Y. Kura, K. Kassem, C. Revenga, M. Spalding, and D. E. McAllister. 2001. Pilot analysis of global ecosystems: coastal ecosystems. World Resources Institute, Washington, DC.
- Camus, P. 2005. Introduction of species in Chilean marine environments: not always exotic, not always evident. *Revista Chilena de Historia Natural* 78:155-159.
- Cano, J., and J. Rocamora. 1996. Growth of the European flat oyster in the Mediterranean Sea (Murcia, SE Spain). *Aquaculture International* 4:91-104.
- Carranza, A., O. Defeo, and M. W. Beck. 2009a. Diversity, conservation status and threats for native oysters (Ostreidae) in the Atlantic and Caribbean coasts of South America. *Aquatic Conservation* 19:344-353.
- Carranza, A., O. Defeo, M. W. Beck, and J. C. Castilla. 2009b. Linking fisheries management and conservation in bioengineering species: the case of South American mussels (Mytilidae). *Rev Fish Biol Fisheries*.
- Castilla, J., and P. Neill. 2009. Marine bioinvasions in the Southeastern Pacific: status, ecology, economic impacts, conservation and management. Pages 439-457 in G. Rilov and J. Crooks, editors. *Biological invasions of marine ecosystems: patterns, effects, and management*. Springer-Verlag, Heidelberg.
- Castilla, J. C., S. Gelcich, and O. Defeo. 2007. Successes, lessons, and projections from experience in marine benthic invertebrate artisanal fisheries in Chile. Pages 25-42 in T. R. McClanahan and J. C. Castilla, editors. *Fisheries management: progress towards sustainability*. Blackwell Press, London.
- Cerco, C.F., and M.R. Noel. 2007. Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? *Estuaries and Coasts* 30: 331-343.
- Cerrato, R. M., D. A. Caron, D. J. Lonsdale, J. M. Rose, and R. A. Schaffner. 2004. Effect of the northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide alga *Aureococcus anophagefferens*. *Marine Ecology-Progress Series* 281:93-108.
- Ciocco, N., M. Lasta, and C. Bremec. 1998. Bivalves fisheries: mussel, scallops (tehuelche and patagonian) and other species. Pages 143-166 in *The Argentine Sea and its fisheries resources*. Vol.2. Molluscs of interest for fisheries. Culture and reproductive strategies of bivalves and echinoids.
- Cranfield, H., B. Manighetti, K. Micheal, and A. Hill. 2003. Effects of oyster dredging on the distribution of bryozoan biogenic reefs and associated sediments in Foveaux Strait, southern New Zealand. *Continental Shelf Research* 23:14-15.
- Day, J. C. 2002. Zoning: Lessons from the Great Barrier Reef Marine Park. *Ocean & Coastal Management* 45:139-156.
- Deng, J., and X. Jin. 2000. Study on fishery biodiversity and its conservation in Laizhou Bay and Yellow River estuary. *Zoological Research (in Chinese)*. 21:76-82.
- Dodd, J. 2005. Native oysters. *Scottish Natural Heritage*. in <http://www.snh.org.uk>.
- Doran, E., Jr. 1965. Shell roads in Texas. *Geographical Review* 55:223-240.
- Drake, G. 1891. On the sounds and estuaries of Georgia with reference to oyster culture. *US Coast and Geodetic Survey Bulletin* 19:179-209.
- Edgar, G. J., N. S. Barrett, D. J. Graddon, and P. R. Last. 2000. The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* 92:383-397.
- EPA. 2005. *National Coastal Condition Report II* EPA, Washington, DC.
- Fang, E., W. Li, and J. Yu. 2007. Sustainable use of live oyster reef in Bohai Gulf. *Modern Fisheries Information (in Chinese)* 22:12-14.
- Fisheries of Tasmania. 1882. *Fisheries of Tasmania: Report of Royal Commission*. 92.
- Freeman, M. 1995. The benefits of water quality improvements for marine recreation: a review of the empirical evidence. *Marine Resource Economics* 10:385-406.
- Geng, X., M. Fu, X. Xu, and P. Li. 1991. The evolution of modern oyster bioherms and their ecological character with significance of paleo-environment. *Science in China (Series B, in Chinese)* 8:867-875.
- Gilbert, A. J., and R. Janssen. 1998. Use of environmental functions to

- communicate the values of a mangrove ecosystem under different management regimes. *Ecological Economics* 25:323-346.
- Gillespie, G. 2009. Status of the Olympia oyster, *Ostrea lurida*, in British Columbia, Canada. *Journal of Shellfish Research* 28: 59-68.
- Goulletquer, P., and M. Heral. 1997. Marine molluscan production trends in France from fisheries to aquaculture. Pages 137-164 in C. L. MacKenzie, V. G. Burrell Jr., A. Rosenfield, and W. L. Hobart, editors. The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3, Europe. U.S. Department of Commerce, Seattle.
- Grabowski, J. H., and C. H. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. Pages 281-298 in K. Cuddington, J. Byers, W. Wilson, and A. Hastings, editors. *Ecosystem engineers: plants to protists*. Academic Press, Boston.
- Green, E. P., and F. T. Short. 2003. *World atlas of seagrasses*. University of California Press, Berkeley.
- Grizzle, R.E., J.R. Adams and L.J. Walters. 2002. Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida Lagoon potentially related to boating activities. *J. Shellfish Research* 21: 749-756.
- Gunther, R. T. 1897. The oyster culture of ancient Romans. *Journal of the Marine Biological Association of the United Kingdom* 4:360-365.
- Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A global map of human impact on marine ecosystems. *Science* 319:948-952.
- Harry, H. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). *The Veliger* 28:121-158.
- Hiscock, K., J. Sewell, and J. Oakley. 2005. Marine Health Check 2005. A report to gauge the health of the UK's sea-life. WWF-UK. Online. Available HTTP: http://www.wwf.org.uk/filelibrary/pdf/marine_healthcheck05.pdf. in.
- Hone, P. 1996. Summary of existing data collected for the shellfish environmental monitoring program (SEMP) 1992 to 1994. South Australian Research and Development Institute, Adelaide.
- Horton, T. and W.M. Eichbaum. 1992. *Turning the Tide: Saving the Chesapeake Bay*. Island Press, Baltimore MD.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jozefowicz, C., and D. O'Foighil. 1998. Phylogenetic analysis of southern hemisphere flat oysters based on partial mitochondrial 16S rDNA gene sequences. *Molecular Phylogenetics and Evolution* 10:426-435.
- Kennedy, R. J., and D. Roberts. 1999. A survey of the current status of the flat oyster *Ostrea edulis* in Strangford Lough, Northern Ireland, with a view to the restoration of its oyster beds *Biology and the Environment: Proceedings of the Royal Irish Academy* 99B:79-88.
- Kirby, M. X. 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries. *Proceedings of the National Academy of Science* 101:13096-13099.
- Kirby, M.X. and H.M. Miller 2005. Response of a benthic suspension feeder (*Crassostrea virginica* Gmelin) to three centuries of anthropogenic eutrophication in Chesapeake Bay. *Est. Coastal Shelf Sci* 62: 679-689.
- Klappenbach, M. 1965. Lista preliminar de los Mytilidae brasilenos con claves para su determinacion y notas sobre su distribucion. *Anais da Academia Brasileira de Ciencias* 37:327-351.
- Korringa, P. 1952. Recent advances in oyster biology. *The Quarterly Review of Biology* 27:266-308.
- Laing, I., P. Walker, and F. Areal. 2005. A feasibility study of native oyster (*Ostrea edulis*) stock regeneration in the United Kingdom. FC1016, Defra and Seafish.
- Lasta, M., N. Ciocco, C. Bremec, and A. Roux. 1998. Bivalve and gastropod molluscs. Pages 115-142 in *The Argentine Sea and its fisheries resources*. Vol.2. Molluscs of interest for fisheries. Culture and reproductive strategies of bivalves and echinoids.
- Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* 8:128-140.
- Li, X. 1989. A comparative morphology of mantle cavity in some Chinese oysters. *Oceanologica et Limnologia Sinica* 20:502-507.
- Li, X., and Z. Qi. 1994. Studies on the comparative anatomy, systematic classification and evolution of Chinese oysters. *Stud. Mar. Sin.* 35:143-173 (in Chinese).
- Lindahl, O., R. Hart, B. Hernroth, S. Kollberg, L. Loo, L. Olrog, A. Rehnstam-Holm, J. Svensson, S. Svensson, and U. Syversen. 2005. Improving marine water quality by mussel farming – a profitable solution for Swedish society. *Ambio* 34:129-136.
- Lipton, D. 2004. The value of improved water quality to Chesapeake Bay boaters. *Marine Resource Economics* 19:265-270.
- Lotze, H., H. Lenihan, B. Bourque, R. Bradbury, R. Cooke, M. Kay, S. Kidwell, M. Kirby, C. Peterson, and J. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806-1809.
- Lozan, J. 1996. Nutzung und Veraenderungen von Mollusken und Krebsen der Ostsee. Pages 197-201 in J. Lozan, R. Lampe, W. Matthaeus, H. Rumohr, and H. Von Westernhagen, editors. *Warnsignale aus der Ostsee*, Berlin.
- MacKenzie, C. L., V. G. Burrell Jr., A. Rosenfield, and W. L. Hobart. 1997a. The history, present condition and future of the molluscan fisheries of North and Central America and Europe. Volume 1, Atlantic and Gulf Coasts. U.S. Department of Commerce, Seattle, Washington.
- MacKenzie, C. L., V. G. Burrell Jr., A. Rosenfield, and W. L. Hobart. 1997b. The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 2, Central America. U.S. Department of Commerce, Seattle, Washington.
- MacKenzie, C. L., V. G. Burrell Jr., A. Rosenfield, and W. L. Hobart. 1997c. The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3, Europe. U.S. Department of Commerce, Seattle, Washington.
- Magliocchetti Lombi, P., R. Perdicaro, and M. L. Bianchini. 1988. Hydrologic and trophic conditions of the Marano-Grado Lagoon (Northern Italy) relatively to oysters populations (*Ostrea edulis* and *Crassostrea gigas*). *Oebalia* 14:139-157.
- Maryland Oyster Advisory Commission (MOAC). 2008. Maryland Oyster Advisory Commission's 2007 Interim Report and Preliminary Thoughts Concerning Maryland's Chesapeake Bay Oyster Management Program. Submitted to the Governor and General Assembly January 4, 2008.
- Meyer, B. L. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology* 5:93-99.
- Micu, D., and V. Todorova. 2007. The Black Sea: biodiversity of the western Black Sea. *MarBEF Newsletter* 7:26-29.
- Mizzan, L., R. Trabucco, and G. Tagliapietra. 2005. Nuovi dati sulla

- presenza e distribuzione di specie alloctone del macrozoobenthos della laguna di Venezia. *Boll. Mus. civ. St. Nat. Venezia* 56:69-89.
- Mobius, K. 1883. The oyster and oyster-culture. Pages 683-751 in United States Commission of Fish and Fisheries, Part VIII. Report of the Commissioner for 1880. Government Printing Office, Washington, DC
- Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and Environment* 6:485-492.
- Moore, H. F. 1907. Survey of oyster bottoms of Matagorda Bay, Texas. U.S. Government Printing Office, Washington, D.C.
- Moore, H. F. 1913. Condition and extent of the natural oyster beds and barren bottoms of Mississippi east of Biloxi. U.S. Government Printing Office, Washington, D.C.
- Mount, R., C. Crawford, C. Veal, and C. White. 2005. Bringing back the bay: marine habitats and water quality in Georges Bay. Break O'Day Council, Hobart.
- National Research Council. 1995. Understanding marine diversity: a research agenda for the nation. National Academy Press, Washington, D.C.
- National Research Council. 2004. Non-native oysters in the Chesapeake Bay. National Academy Press, Washington, D.C.
- New Zealand Ministry of Fisheries. 2007a. Status of New Zealand fisheries - dredge oyster (Foveaux Strait - OYS 5). New Zealand Ministry of Fisheries, http://services.fish.govt.nz/fishresourcespublic/Plenary2007/OYU5_07.pdf
- New Zealand Ministry of Fisheries. 2007b. Status of New Zealand fisheries - dredge oyster (OYS 7 - Nelson/Marlborough). New Zealand Ministry of Fisheries Report, http://services.fish.govt.nz/fishresourcespublic/Plenary2007/OYS%207_07.doc.
- Newell, R., W. Kemp, J. Hagy, C. Cerco, J. Testa, and W. Boynton. 2007. Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Comment on Pomeroy et al. (2006). *Marine Ecology Progress Series* 341:293-298.
- Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? Pages 536-546 in Understanding the estuary: advances in Chesapeake Bay research. Chesapeake Research Consortium, Baltimore, MD.
- Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollusks: a review. *Journal of Shellfish Research* 23:51-61.
- Newell, R. I. E., T. R. Fisher, R. R. Holyoke, and J. C. Cornwell. 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. in R. F. Dame and S. Olenin, editors. *The Comparative Roles of Suspension Feeders in Ecosystems*. Springer, Netherlands.
- Newell, R. I. E., and E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793-806.
- NRC. 2004. Non Native Oysters in the Chesapeake Bay. Committee on Nonnative Oysters in the Chesapeake Bay, Ocean Studies Board. National Academies Press, Washington DC.
- Ocean Studies Board. 2004. Nonnative oysters in the Chesapeake Bay. National Academy Press, Washington, DC.
- Ogburn, D. M., I. White, and D. P. McPhee. 2007. The disappearance of oyster reefs from eastern Australian estuaries— impact of colonial settlement or mudworm invasion? *Coastal Management* 35:271-287.
- Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56:987-996.
- OSPAR Commission. 2005. Case reports for the initial list of threatened and/or declining species and habitats in the OSPAR maritime area. in http://www.ospar.org/documents/dbase/publications/p00198_Case_reports_for_initial_list_of_species_and_habitats_2005_version.pdf.
- Pandolfi, J., R. Bradbury, E. Sala, T. Hughes, K. Bjorndal, R. Cooke, D. McArdle, L. McClenachan, M. Newman, G. Paredes, R. Warner, and J. Jackson. 2003. Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. *Science* 301:955-958.
- Parliamentary Report. 1885. Fisheries Inspectors: Reports for 1884; 1885, No 90.
- Piazza, B. P., P. D. Banks, and M. K. La Peyre. 2005. The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. *Restoration Ecology* 13:499-506.
- Polson, M., and D. Zacherl. 2009. Geographic distribution and intertidal population status for the Olympia oyster, *Ostrea lurida*, from Alaska to Baja. *Journal of Shellfish Research* 28: 69-77.
- Polson, M., W. E. Hewson, D. J. Eemisse, P. K. Baker, D. C. Zacherl. 2009. You say conchaphila, I say lurida: molecular evidence for restricting the Olympia Oyster (*Ostrea lurida* Carpenter 1864) to temperate western North America. *Journal of Shellfish Research* 28:11-21.
- Ramón, M., J. Cano, J. B. Peña, and M. J. Campos. 2005. Current status and perspectives of mollusc (bivalves and gastropods) culture in the Spanish Mediterranean. *Boletín Instituto Espanol Oceangrafía* 21:361-373.
- Rippon, S. 2000. The transformation of coastal wetlands: exploitation and management of marshland landscapes in north west Europe during the Roman and Medieval periods. British Academy, London.
- Rothschild, B. J., J. S. Ault, M. H. Gouletquer, and M. Heral. 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Marine Ecology Progress Series* 111:29-39.
- Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology Evolution and Systematics* 36:643-689.
- Shepherd, S. 1986. Coastal Waters. Pages 182-199 in C. Nance and D. Speight, editors. *A Land Transformed: Environmental Change in South Australia*. Longman Cheshire, Adelaide.
- Shepherd, S. A., and R. Sprigg. 1976. Substrate, sediments and subtidal ecology of Gulf St Vincent and Investigator Strait. in C. Twidale, M. Tyler, and B. Webb, editors. *Natural History of the Adelaide Region*. Royal Society of South Australia, Adelaide.
- Shilts, A., M. Pascual, and D. O'Foighil. 2007. Systematic, taxonomic and biogeographic relationships of Argentine flat oysters. *Molecular Phylogenetics and Evolution* 44:467-473.
- Smith, G. 1985. The Queensland Oyster Fishery - an illustrated history. Queensland Department of Primary Industries, Brisbane.
- Smith, G., D. Bruce, E. Roach, A. Hansen, R. Newell, and A. McManus. 2005. Assessment of Recent Habitat Conditions of Eastern Oyster *Crassostrea virginica* Bars in Mesohaline Chesapeake Bay. *North American Journal of Fisheries Management* 25:1569-1590.
- Soniat, T.M., C.M. Finelli, J.T. Ruiz. 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. *J. Exp. Mar. Biol. Ecol.* 310: 163-182.
- Spalding, M., F. Blasco, and C. Field, editors. 1997. *World Mangrove Atlas*. International Society for Mangrove Ecosystems, Okinawa, Japan.
- Spalding, M. D., H. E. Fox, B. S. Halpern, M. A. McManus, J. Molnar, G. R.

- Allen, N. Davidson, Z. A. Jorge, A. L. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* 57:573-583.
- Stafford, J. 1918. The native oyster of British Columbia. Report of the Commissioner of Fisheries.
- Tanner, J. 1983. Three decades of habitat change in Gulf St Vincent, South Australia. *Transactions of the Royal Society of South Australia* 129:65-73.
- Toro, J., and P. Aguila. 1996. Genetic differentiation of populations of the oyster *Ostrea chilensis* in southern Chile. *Aquatic Living Resources* 9:75-78.
- Toro, J., A. Alcapan, J. Ojeda, and A. Vergara. 2004. Response to genetic selection for growth rate in individuals of *Ostrea chilensis* Philippi (Bivalvia: Ostreidae), maintained under laboratory conditions. *Revista de biologia marina y oceanografia* 39:53-59.
- Trimble, A.C., J. Ruesink, and B. R. Dumbauld. 2009. Factors preventing the recovery of a historically overexploited shellfish species, *Ostrea lurida* Carpenter 1864. *Journal of Shellfish Research* 28: 97-106.
- Tyler-Walters, H. 2001. *Ostrea edulis* beds on shallow sublittoral muddy sediment. in Plymouth, Marine Biological Association of the United Kingdom. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme. http://www.marlin.ac.uk/biotopes/Bio_BasicInfo_IMX.Ost.htm
- UK Biodiversity Group. 1999. UK Biodiversity Group Tranche 2 Action Plans - Volume V: Maritime species and habitats. English Nature. Online: http://www.ukbap.org.uk/Library/Tranche2_Vol5.pdf in.
- USACE. 2009. Draft Programmatic Environmental Impact Statement for Oyster Restoration in Chesapeake Bay. Volumes 1 & 2. United States Army Corps of Engineers. Norfolk, Virginia. <http://www.nao.usace.army.mil/OysterEIS/EIS/homepage.asp>
- USFW. 1970. National estuary study. US Department of the Interior, Washington.
- Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: one of the world's threatened major tropical environments. *Bioscience* 51:807-815.
- van den Berg, J., G. Koznyeff, H. Lin, J. McDarby, M. Peletier, R. Planque, and P. Wilson. 2005. Japanese oysters in Dutch waters. *Nieuw Archief voor Wiskunde* 5/6:130-141.
- Varela, E., C. Beasley, H. Schneider, I. Sampaio, N. Marques-Silva, and C. Tagliaro. 2007. Molecular phylogeny of mangrove oysters (*Crassostrea*) from Brasil. *Journal of Molluscan Studies* 73:229-234.
- Virginia Blue Ribbon Oyster Panel (VBROP). 2007. Recommendations of the Virginia Blue Ribbon Oyster Panel. Virginia Marine Resources Commission, Newport News, Virginia. 11 pp.
- Virvilis, C., and P. Angelidis. 2006. Presence of the parasite *Marteilia* sp. in the flat oyster (*Ostrea edulis* L) in Greece. *Aquaculture* 259:1-5.
- Volety, A. K., M. Savarese, S. G. Tolley, W. S. Arnold, P. Sime, P. Goodman, R. H. Chamberlain, and P. H. Doering. in press. Eastern oysters (*Crassostrea virginica*) as an indicator for restoration of Everglades ecosystems. *Ecological Indicators*.
- Wall, L.M., L.J. Walters, R.E. Grizzle, and P.E. Sacks. 2005. Recreational boating activity and its impact on the recruitment and survival of the oyster *Crassostrea virginica* on intertidal reefs in Mosquito Lagoon, Florida. *J. Shellfish Research* 24: 965-973.
- Wallace-Carter, E. 1987. For they were fishers: the history of the fishing industry in South Australia. Amphitrite Publishing House, Adelaide.
- Walters, L.J., K. Johnson, L.M. Wall, N. Martinez and R. Grizzle. 2002. Shell movement and juvenile survival of the oyster *Crassostrea virginica* on intertidal reefs adjacent to waters with intense boating activity in the Indian River Lagoon, Florida. *J. Shellfish Research* 21: 415-416.
- Wang, H., X. Guo, X. Liu, G. Zhang, S. Zhang, and F. Xu. 2007. Classification of "Jinjiang" oysters in China. *Marine Sciences* 31:85-86.
- Wang, H., X. Guo, G. Zhang, and F. Zhang. 2004. Classification of Jinjiang oysters *Crassostrea ariakensis* (Gould, 1861) from China based on morphology and phylogenetic analysis. *Aquaculture* 242:137-155.
- Watson, R., A. Kitchingman, A. Gelchu, and D. Pauly. 2004. Mapping global fisheries: sharpening our focus. *Fish and Fisheries* 5:168-177.
- Wennersten, J.R. 1981. *The Oyster Wars of Chesapeake Bay*. Tidewater Publishers, Centerville, MD. 159 pp.
- Wilkinson, C., editor. 2002. Status of coral reefs of the world: 2002. Australian Institute of Marine Science, Townsville, Australia.
- Wilson, J. 1991. Survey of the Flat Oyster Stocks in Georges Bay. Department of Primary Industries and Fisheries, Marine Research Laboratory, Taroona, Tasmania.
- Winslow, F. 1882. Methods and Results. Report of the oyster beds of the James River, Va. And of Tangier and Pocomoke Sounds, Maryland and Virginia. U.S. Coast and Geological Survey, Appendix No. 11. U.S. Government Printing Office, Washington, DC.
- Wolff, W. 2005. The exploitation of living resources in the Dutch Wadden Sea: a historical overview. *Helgoland Marine Research* 59:31-38.
- Wolff, W. J. 2000. Causes of extirpations in the Wadden Sea, an estuarine area in the Netherlands. *Conservation Biology* 14:876-885.
- Wood, A., S. Apte, E. MacAvoy, and J. Gardner. 2007. A molecular phylogeny of the marine mussel genus *Perna* (Bivalvia: Mytilidae) based on nuclear (ITS1&2) and mitochondrial (COI) DNA sequences. *Molecular Phylogenetics and Evolution* 44:685-698.
- Woods, H., W. J. Hargis, Jr., C. H. Hershner, and P. Mason. 2005. Disappearance of the natural emergent 3-dimensional oyster reef system of the James River, Virginia 1871-1948. *Journal of Shellfish Research* 24:139-142.
- Worm, B., M. Sandow, A. Oschlies, H. K. Lotze, and R. A. Myers. 2005. Global patterns of predator diversity in the open oceans. *Science* 309:1365-1369.
- Xu, F., and S. Zhang. 2008. An Illustrated Bivalvia Mollusca Fauna of China Seas. Science Press, Beijing.
- Yan, F. 2003. Causes of zero flow of the Yellow River and humanistic consideration. *Journal of Catastrophology* (in Chinese) 18:91-96.
- Yao, Q. 1985. The discovery of oyster reef in waters northeast to the Jinmen island, Fujian, and paleogeographical significance. *Journal of Oceanography in Taiwan Strait* 4:108-109.
- Zaitsev, Y. 2006. Black sea red data book (online). in. <http://www.grid.unep.ch/bsein/redbook/index.htm>.
- Zaixso, H. 2004. Bancos de cholga *Aulacomya atra atra* (Molina) (Bivalvia: Mytilidae) del golfo San Jose (Chubut, Argentina): Diversidad y relaciones con faunas afines. *Revista de Biología Marina y Oceanografía* 39:61-78.
- Zedler, J. B., and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30:39-74.
- Zhang, R. 2004. The geomorphology-Sedimentology character of oyster reef in Xiaomiaohong tidal channel, Jiangsu Province. *Oceanologia et Limnologia sinica* 35:1-7.
- Zhang, R., Y. Wang, Z. Zhang, and J. Jiang. 2007. Geomorphology and evolution of the Xiaomiaohong Oyster reef off Jiangsu coast, China. *Oceanologia et Limnologia sinica* 38:259-265.
- Zhang, X., and L. Zikang. 1956. Studies of oysters in China. *Acta Zoologica Sinica* 8:65-94.

APPENDIX 1

© Anne Birch/TNC

Condition by Bays and Ecoregions

Table S1: Condition of oyster reefs in ecoregions and their bays. The condition is based on the percent of current to historical abundance of oyster reefs remaining, where:

3 <50% lost (good) **2** 50-89 % lost (fair) **1** 90-99% lost (poor) **0** >99% lost (functionally extinct)

Ecoregion	Bay	Condition				Species	References
		3	2	1	0		
Adriatic Sea						<i>O. edulis</i>	(1-8)
	Grado lagoon					<i>O. edulis</i>	(5, 7)
	Gulf of Trieste					<i>O. edulis</i>	(7, 9)
	Po Delta lagoons					<i>O. edulis</i>	(1, 8)
	Venezia (lagoon)					<i>O. edulis</i>	(2, 3)
	Limski Kanal					<i>O. edulis</i>	(4)
	Mali Ston Bay					<i>O. edulis</i>	(10)
Aegean Sea						<i>O. edulis</i>	(11, 12)
	Thessaloniki Bay					<i>O. edulis</i>	(11, 12)
Amazonia						<i>C. rhizophorae</i>	(13)
	Furo Do Cafe					<i>C. rhizophorae</i>	(13)
Baltic Sea						<i>O. edulis</i>	(14-16)
Bassian						<i>O. angasi</i>	(17)
	Cloudy Bay					<i>O. angasi</i>	(18, 19)
	D'Entrecasteaux Channel					<i>O. angasi</i>	(17, 19-21)
	Derwent River					<i>O. angasi</i>	(17, 19-23)
	Georges Bay, Tasmania					<i>O. angasi</i>	(17, 19, 24)
	Huon River					<i>O. angasi</i>	(17, 19, 20)
	Port Esperance					<i>O. angasi</i>	(18, 19)
	Port Phillip Bay					<i>O. angasi</i>	(25-31)
	Southport					<i>O. angasi</i>	(18, 19)
	Spring Bay					<i>O. angasi</i>	(18, 19)
	Swanport					<i>O. angasi</i>	(18, 19)
	Tamar River					<i>O. angasi</i>	(17, 19-21, 32)
Black Sea						<i>O. edulis</i>	(33, 34)
	Karkinits'ka Bay					<i>O. edulis</i>	(33)
	Dzharylgats'ka Bay					<i>O. edulis</i>	(33)
	Primorsko to Cape Maslen					<i>O. edulis</i>	(34)
Cape Howe						<i>S. glomerata</i> , <i>O. angasi</i>	(35-38)
	Clyde River					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
	Georges River					<i>S. glomerata</i> , <i>O. angasi</i>	(35-38)
	Nelson Lagoon					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
	Wonboyne Lake					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
Carolinian						<i>C. virginica</i>	(39, 40)
	Beaufort County, SC					<i>C. virginica</i>	(41-43)
	Charleston County, SC					<i>C. virginica</i>	(41-43)
	Georgetown County, SC					<i>C. virginica</i>	(41-43)
	Georgia Coast					<i>C. virginica</i>	(39, 40, 44-46)

Ecoregion	Bay	Condition				Species	References
		3	2	1	0		
	Mosquito Lagoon					<i>C. virginica</i>	(47, 48)
	Wilmington, NC					<i>C. virginica</i>	(49)
Celtic Seas						<i>O. edulis</i>	(50-64)
	Belfast Lough					<i>O. edulis</i>	(50-52, 65, 66)
	Bertraghboy Bay					<i>O. edulis</i>	(52, 67)
	Cardigan Bay					<i>O. edulis</i>	(50, 62, 66)
	Carlingford Lough					<i>O. edulis</i>	(50-52, 65, 66)
	Galway Bay					<i>O. edulis</i>	(51, 52, 68-70)
	Kilkieran Bay					<i>O. edulis</i>	(51, 52, 67, 69)
	Lough Foyle					<i>O. edulis</i>	(50-52, 65, 66, 68, 71)
	Menai Strait					<i>O. edulis</i>	(50, 54, 62)
	Milford Haven					<i>O. edulis</i>	(50, 53, 54, 62)
	Strangford Lough					<i>O. edulis</i>	(51, 72, 73)
	Swansea					<i>O. edulis</i>	(50, 53, 62)
Central Chile						<i>T. chilensis</i>	(74)
	Coquimbo					<i>T. chilensis</i>	(74)
	Valparaíso					<i>T. chilensis</i>	(74)
	La Herradura					<i>T. chilensis</i>	(74)
Central New Zealand						<i>O. chilensis</i>	(75, 76)
Guayaquil						<i>O. columbiensis</i>	(77)
	Tumbes, Perú					<i>O. corteziensis</i> , <i>O. columbiensis</i>	(77, 78)
Chiloense						<i>T. chilensis</i>	(79)
	Ancud, Chiloe					<i>T. chilensis</i>	(79)
	Bay of Pullinque					<i>T. chilensis</i>	(79)
	Bay of Yaldad					<i>T. chilensis</i>	(79)
	Calbuco					<i>T. chilensis</i>	(79)
	Castro					<i>T. chilensis</i>	(79)
	Channel of Rilán					<i>T. chilensis</i>	(79)
	Estuary of Quempillén					<i>T. chilensis</i>	(79)
	Guaitecas					<i>T. chilensis</i>	(79)
	Island of Melinka					<i>T. chilensis</i>	(79)
	Quetalmaue					<i>T. chilensis</i>	(79)
East China Sea							
	Shenzhen, Pearl River						(80)
Floridian						<i>C. virginica</i>	(35, 81-85)
	Biscayne Bay					<i>C. virginica</i>	(83)
	Caloosahatchee River					<i>C. virginica</i>	(84, 86)
	Charlotte Harbor					<i>C. virginica</i>	(81-83)
	Estero Bay					<i>C. virginica</i>	(81, 82)
	Lake Worth					<i>C. virginica</i>	(83)
	Loxahatchee River					<i>C. virginica</i>	(83)
	Naples and Dollar Bays					<i>C. virginica</i>	(81, 82)
	Rookery Bay					<i>C. virginica</i>	(81-83)
	South Indian River					<i>C. virginica</i>	(83)
	Sebastian River					<i>C. virginica</i>	(83)
	St. Lucie					<i>C. virginica</i>	(83)
	Tampa Bay					<i>C. virginica</i>	(85)
Greater Antilles						<i>C. spp</i>	(87, 88)

Ecoregion	Bay	3 2 1 0				Species	References
		Condition					
Gulf of Maine/Bay of Fundy							
	Great Bay					<i>C. virginica</i>	(16, 89,
Gulf of St. Lawrence - E. Scotian Shelf						<i>C. virginica</i>	(89, 91-94)
	Gulf of St Lawrence					<i>C. virginica</i>	(89, 91-94)
Leeuwin						<i>O. angasi</i>	(95, 96)
	Oyster Harbour					<i>O. angasi</i>	(95, 97-101)
Manning-Hawkesbury						<i>S. glomerata</i> , <i>O. angasi</i>	(35, 36, 38)
	Camden Haven Estuary					<i>S. glomerata</i> , <i>O. angasi</i>	(36, 102, 103)
	Clarence River					<i>S. glomerata</i>	(36)
	Hawkesbury River					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
	Pambula River					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
	Port Stephens					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
	Sydney Harbor					<i>S. glomerata</i> , <i>O. angasi</i>	(36, 38)
	Wallis Lake					<i>S. glomerata</i> , <i>O. angasi</i>	(36)
North Patagonian Gulfs						<i>O. puelchana</i>	(104, 105)
	Banco Las Grutas					<i>O. puelchana</i>	(105, 106)
	Golfo San José					<i>O. puelchana</i>	(106)
	Golfo San Matías					<i>O. puelchana</i>	(105)
North Sea						<i>O. edulis</i>	(107, 108)
	Dogger Bank English Channel					<i>O. edulis</i>	(50)
	Firth of Forth					<i>O. edulis</i>	(50, 54, 59)
	Rivers Crouch andRoach					<i>O. edulis</i>	(50, 53, 57, 58)
	The Wash					<i>O. edulis</i>	(50)
	Wadden Sea					<i>O. edulis</i>	(14, 15, 109-119)
Northeastern Brazil						<i>C. rhizophorae</i>	(120)
	Itamaracá					<i>C. rhizophorae</i>	(120)
Northeastern New Zealand						<i>O. chilensis</i>	(76, 121)
Northern California						<i>O. conchaphila</i>	(122, 123)
	Elkhorn Slough					<i>O. conchaphila</i>	(122, 124-127).
	Morro Bay					<i>O. conchaphila</i>	(122, 125-127)
	San Francisco Bay					<i>O. conchaphila</i>	(35, 122, 123, 127-139)
Northern Gulf of Mexico						<i>C. virginica</i>	(35, 81, 91, 140-144)
	Apalachicola Bay					<i>C. virginica</i>	(91, 143, 145-150)
	Cedar Key					<i>C. virginica</i>	(35, 81, 82)
	Galveston Bay					<i>C. virginica</i>	(141, 142, 151-156)
	Mobile Bay					<i>C. virginica</i>	(157-159)
	Mississippi Sound					<i>C. virginica</i>	(35, 140)
	Pensacola Bay					<i>C. virginica</i>	(160-162)
OR, WA, Vancouver Coast and Shelf						<i>O. conchaphila</i>	(163, 164)
	Barclay Sound					<i>O. conchaphila</i>	(35, 165-167)
	Coos Bay					<i>O. conchaphila</i>	(164, 168-172)
	Humboldt Bay					<i>O. conchaphila</i>	(35, 122, 125, 127)
	Kyuquot Sound					<i>O. conchaphila</i>	(173)
	Netarts Bay					<i>O. conchaphila</i>	(164, 170, 174, 175)
	Nootka Sound					<i>O. conchaphila</i>	(173)
	Willapa Bay					<i>O. conchaphila</i>	(123, 135, 163, 176-179)
	Yaquina Bay					<i>O. conchaphila</i>	(164, 170, 171, 180-182)

		3210					
Ecoregion	Bay	Condition				Species	References
Puget Trough/Georgia Basin						<i>O. conchaphila</i>	(163, 166, 176, 177, 179, 183)
	Boundary Bay					<i>O. conchaphila</i>	(173)
	Ladysmith Harbor					<i>O. conchaphila</i>	(173)
	Puget Sound - Northern					<i>O. conchaphila</i>	(176,177)
	Puget Sound - Southern					<i>O. conchaphila</i>	(135, 163, 176-178, 183-185)
Rio de la Plata						<i>O. puelchana</i>	(186, 187)
	Banco Ingles					<i>O. puelchana</i>	(186)
	Isla de Flores					<i>O. puelchana</i>	(187)
South Australian Gulfs						<i>O. angasi</i>	(30, 188)
	Boston Bay					<i>O. angasi</i>	(188-190)
	Coffin Bay					<i>O. angasi</i>	(188-190)
	Kangaroo Island					<i>O. angasi</i>	(188-190)
	Oyster Bay					<i>O. angasi</i>	(188-190)
	Port Lincoln					<i>O. angasi</i>	(188-190)
South European Atlantic Shelf						<i>O. edulis</i>	(191-193)
Southeastern Brazil						<i>C. gasar</i>	(194-196)
	Cananéia					<i>C. gasar</i>	(196)
	Cananéia-Iguape Estuaries					<i>C. gasar</i>	(195, 197)
	Guaratuba					<i>C. gasar</i>	(194)
Southern California Bight						<i>O. conchaphila</i>	(122, 125)
Southern Caribbean						<i>C. rhizophorae</i>	(88, 198)
	Laguna de Tacarigua					<i>C. rhizophorae</i>	(199)
Southern Gulf of Mexico						<i>C. virginica</i>	(200, 201)
Southern New Zealand						<i>O.chilensis</i>	(121, 202)
	Foveaux strait					<i>O.chilensis</i>	(121, 202)
Southwestern Caribbean						<i>C. rhizophorae</i>	(88, 203, 204)
	Cienaga Grande De Santa Marta					<i>C. rhizophorae</i>	(204)
Tweed-Moreton						<i>S. glomerata</i>	(35-38)
	Great Sandy Strait					<i>S. glomerata</i>	(35, 37, 38)
	Moreton Bay					<i>S. glomerata</i>	(35-38)
	Tin Can Bay					<i>S. glomerata</i>	(35, 38)
	Wide Bay					<i>S. glomerata</i>	(35, 38)
Uruguay-Buenos Aires Shelf						<i>O. puelchana,O.equestris</i>	(105, 205)
Virginian						<i>C. virginica</i>	(91, 107, 123, 206)
	Chesapeake Bay					<i>C. virginica</i>	(123, 207-218)
	Delaware Bay					<i>C. virginica</i>	(123, 211, 219-225)
	Great South Bay					<i>C. virginica</i>	(35)
	Hudson Raritan Estuary					<i>C. virginica</i>	(35, 107, 123, 226-228)
	Narragansett Bay					<i>C. virginica</i>	(107, 229-235)
	Pamlico Sound					<i>C. virginica</i>	(49, 123, 140, 218, 236-242)
Western Mediterranean						<i>O. edulis</i>	(107, 243)
	Gulf of Lion					<i>O. edulis</i>	(3, 243, 244)
	Mar Menor Lagoon					<i>O. edulis</i>	(244-246)
Yellow Sea						<i>C. ariakensis, C. gigas</i>	(80, 247-250)
	Bohai Bay					<i>C. ariakensis, C. gigas</i>	(248, 249)
	Laizhou Bay (Dajiawa Reef)					<i>C. ariakensis, C. gigas</i>	(247, 248, 250)
	Laizhou Bay (Xiaoqinghe Reef)					<i>C. ariakensis, C. gigas</i>	(80)
	Nantong Sea (Xiaomiaohong Reef)					<i>C. ariakensis, C. gigas</i>	(251)

Appendix 1 References

1. Parenzan P (1989) The history of *Crassostrea gigas* growing spontaneously in the Mediterranean. *Thalassia Salentina* 19:39-48 (in Italian).
2. Mizzan L, Trabucco R, & Tagliapietra G (2005) New data on the presence and distribution of allocthonous species of macrozoobenthos in the Venice lagoon. *Bolletino del Museo Civico di Storia Naturale Venezia* 56:69-89 (in Italian).
3. Saavedra C, Zapata C, Guerra A, & Alvarez G (1993) Allozyme variation in european populations of the oyster *Ostrea edulis*. *Marine Biology* 115(1):85-95.
4. Hrs-Brenko M (1980) The settlement of mussels and oysters in the northern Adriatic Sea. *Nova Thalassia* 4:67-85.
5. Magliocchetti Lombi P, Perdicaro R, & Bianchini ML (1988) Hydrologic and trophic conditions of the Marano-Grado Lagoon (Northern Italy) relatively to oysters populations (*Ostrea edulis* and *Crassostrea gigas*). *Oebalia* 14:139-157.
6. Barnabe G & Doumenge F (2001) Mariculture of Mediteranean species (Academic Press, San Diego).
7. Vesnaver R & Orel G (2001) Gulf of Trieste and surroundings: fishery, aquaculture and curiosities from past times. (in Italian). <http://www.adriaticonline.org/construct.asp?par=menu.asp;1989&st=1>.
8. Prioli G (2001) National census of shellfish production from Consorzio Unimar. Unimar Osservatorio tecnico-biologico (Roma, Italy).
9. Orel G & Zamboni R (2004) Proposals for a pluriannual management strategy of the coastal area in the Gulf of Trieste. (in Italian). http://www.adriaticonline.org/construct.asp?par=pg:/reposurp/Download_Pesca_New/01_scientifico_testo.pdf&st=1.
10. Bratos A, Bolotin J, Peharda M, & Njire J (2002) Seasonal distribution of the oyster *Ostrea edulis* (Linnaeus, 1758) larvae in the bay of Mali Ston, Adriatic Sea. *Journal of Shellfish Research* 21:763-767.
11. Virvilis C & Angelidi P (2006) Presence of the parasite *Marteilia* sp. in the flat oyster (*Ostrea edulis* L) in Greece. *Aquaculture* 259:1-5.
12. Virvilis C, Angelidis P, & Photis G (2003) Presence of the parasite *Marteilia* spp in the shellfish of the Thermaikos Gulf in northern Greece. *Bulletin of the European Association of Fish Pathologists* 23(4):157-162.
13. Marques-Silva NS, et al. (2006) Settlement dynamics of the encrusting epibenthic macrofauna in two creeks of the Caeté mangrove estuary (North Brazil). *Wetlands Ecology and Management* 14:67-78.
14. Kristensen PS (1997) in The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3 Europe, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle).
15. Strand O & Volstad JH (1997) in The history, present condition, and the future of the molluscan fisheries of North and Central America and Europe, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle), pp 7-24.
16. Lotze H, et al. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806-1809.
17. Sumner C (1972) Oysters and Tasmania, part 1. *Tasmanian fisheries research* 6:1-15.
18. Fisheries of Tasmania (1882) *Fisheries of Tasmania: Report of Royal Commission*.
19. Australian Department of the Environment and Heritage (2004) *Assessment of the Tasmanian native oyster fishery*. (DEH, Canberra).
20. Edgar G & Samson C (2004) Catastrophic decline in mollusc diversity in eastern Tasmania and its concurrence with shellfish fisheries. *Conservation Biology* 18:1579-1588.
21. Sumner C (1974) Oysters and Tasmania, part 2. *Tasmanian fisheries research* 8:1-12.
22. Australian Department of the Environment and Heritage (2006) *Developmental fishing for native oysters in Tasmanian state waters*. (DEH, Canberra).
23. Australian Department of the Environment and Heritage (2007) *Assessment of the Tasmanian native oyster fishery*. (DEH, Canberra).
24. Mitchell I, Crawford C, & Rushton M (2000) Flat oyster (*Ostrea angasi*) growth and survival rates at Georges Bay, Tasmania. *Aquaculture* 191:309-321.
25. Hickman N, Mantzaris S, & Rawlinson P (2000) *Native Flat Oyster Investigation*. Final Report (Marine and Freshwater Resources Institute, Victoria).
26. Bennett S (1867) *The history of Australian discovery and colonization* (Harvard University, Boston).
27. Hickman NJ & O'Meley CM (1988) *Culture of the Australian flat oyster (Ostreag angasi) in Victoria*. (Department of Conservation Forests and Lands, Fisheries Division).
28. Black J (1966) Port Phillip survey 2 - benthic communities. *Memoirs of the Natural History Museum of Victoria* 32:129-170.
29. Cohen B, Currie D, & McArthur M (2000) Epibenthic community structure in Port Phillip Bay, Victoria, Australia. *Marine and Freshwater Research* 51:689-702.
30. Nell J (2001) The history of oyster farming in Australia. *Marine Fisheries Review* 63:14-25.
31. Wilson R, Heislars, S., and G. Poore (1998) Changes in benthic communities of Port Philip Bay, Australia, between 1969 and 1995. *Marine and Freshwater Research* 49:847-861.
32. Wilson R (1970) Oyster farming spreads to Tasmania. *Australian Fisheries* 29:7-8.
33. *Black Sea Red Data Book* (2008) (<http://www.grid.unep.ch/bsein/redbook/index.htm>).
34. Micu D & Todorova V (2007) The Black Sea: biodiversity of the western Black Sea. *MarBEF Newsletter* 7:26-29.
35. Kirby M (2004) Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences* 101:13096-13099.
36. Ogburn DM, White I, & McPhee DP (2007) The disappearance of oyster reefs from eastern Australian estuaries - impact of colonial settlement or mudworm invasion? *Coastal Management* 35:271-287.

37. Roughly T (1922) Oyster culture on the Georges River, New South Wales. Technical Education Series No 25 (Technological Museum, Sydney).
38. Smith G (1985) The Queensland Oyster Fishery - an illustrated history (Queensland Department of Primary Industries, Brisbane).
39. Bahr LM & Lanier WP (1981) The ecology of intertidal oyster reefs of the south Atlantic coast: A community profile. (National Coastal Ecosystems Team, USFW, Washington, DC).
40. Cowman CF (1981) in Proceedings of the North American Oyster Workshop, ed Chew KK (Louisiana State University Press, Baton Rouge), pp 128-131.
41. Battle J (1890) An investigation of the coast waters of South Carolina, with reference to oyster culture. Bull. U.S. Fish Comm. for 1890:303-330.
42. South Carolina Department of Natural Resources (2008) SC oyster bed imaging project (http://www.dnr.sc.gov/GIS/images/doqqq_status08.pdf, Charleston).
43. Burrell Jr. VG (2003) South Carolina oyster industry: a history (V.G. Burrell, Charleston).
44. Drake G (1891) On the sounds and estuaries of Georgia with reference to oyster culture. US Coast and Geodetic Survey Bulletin 19:179-209.
45. Harris D (1980) Survey of the intertidal and subtidal oyster resources of the Georgia Coast. (Georgia Department of Natural Resources).
46. Burrell Jr. VG (1997) in The history, present condition, and the future of the molluscan fisheries of North and Central America and Europe: Volume 1, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle), pp 171-185.
47. Grizzle RE (1990) Distribution and abundance of *Crassostrea virginica* (Gmelin, 1791) (eastern oyster) and *Mercenaria* spp. (quahogs) in a coastal lagoon. Journal of Shellfish Research 9:347-358.
48. Grizzle RE, Adams JR, & Walters LJ (2002) Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida lagoon potentially related to boating activities. Journal of Shellfish Research 21:749-756.
49. Street MW, Deaton AS, Chappell WS, & Moorside PD (2005) North Carolina Coastal Habitat Protection Plan. (NC Department of Environment and Natural Resources, Morehead City).
50. Laing I, Walker P, & Areal F (2005) A feasibility study of native oyster (*Ostrea edulis*) stock regeneration in the United Kingdom. CARD Project FC1016 Native Oyster Stock Regeneration - A review of Biological, Technical and Economic Feasibility (Defra and Seafish).
51. Went A (1962) Historical notes on the oyster fisheries of Ireland. Proceedings of the Royal Irish Academy 62:195-223.
52. Browne T (1904) Report on the shell-fish layings on the Irish Coast, as respects their liability to sewage contamination. (HMSO, Dublin).
53. Davidson PE (1976) Surveys of oyster grounds River Crouch/Roach and River Blackwater. (Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Burnham-on-Crouch,).
54. Eyton TC (1858) *A history of the oyster and the oyster fisheries* (J. Van Voorst, London).
55. Crisp DJ (1964) The effects of the severe winter of 1962-'63 on marine life in Britain. Journal of Animal Ecology 33:165-210.
56. Shelbourne J (1957) The 1951 oyster stock in the rivers Crouch and Roach, Essex. Fisheries Investigations, London (Series 2) 2:1-27.
57. Rees H, Waldock R, Matthieson P, & Pendle M (2001) Improvements in the Epifauna of the Crouch Estuary (UK) following a decline in TBT concentrations. . Marine Pollution Bulletin 42:137-144.
58. Howell BR (1969) Oyster stocks on the rivers Crouch and Roach. ed Ministry of Agriculture Fisheries and Food (Fisheries Laboratory, Burnham-on-Crouch, Surveys and Reports by Staff).
59. Donnan D (2003) What has happened to the natives! CEFAS Shellfish News 16:10-11.
60. Dare PJ, Bell MC, Walker P, & Bannister RCA (2004) Historical and current status of cockle and mussel stocks in The Wash (CEFAS Lowestoft).
61. Hugh-Jones T (2003) The Loch Ryan native oyster fishery. Shellfish News 15:17-18.
62. Cooke A (2003) Native oyster beds in Wales. Shellfish News 15:19-20.
63. Millar RH (1968) Changes in the population of oysters in Loch Ryan between 1957 and 1967. Marine Research 1:1-8.
64. Mair JM, Moore CG, Kingston PF, & Harries DB (2000) A review of the status, ecology and conservation of horse mussel *Modiolus modiolus* beds in Scotland. (Scottish Natural Heritage).
65. Roberts D & D. MJ (1983) Utilization of mollusc resources in Northern Ireland. . Journal of Molluscan Studies 12(A):162-166.
66. Maguire JA, et al. (2007) Management recommendations for the sustainable exploitation of mussel seed in the Irish Sea (Irish Marine Institute, Environment and Health Series).
67. Barry MD (1981) Distribution and ecology of oysters, *Ostrea edulis* (L.) in Kilkieran and Bertraghboy Bays, Connemara, Co. Galway. Irish Fisheries Investigation Series B 24:2-18.
68. Culloty SC & Mulcahy MF (2001) Living with bonamiasis: Irish research since 1987. Hydrobiologia 465:181-186.
69. Hugh-Jones D (1994) Farming the European flat oyster (*Ostrea edulis*) in Ireland today. . Bulletin of the Aquacultural Society of Canada 94:3-8.
70. Whilde A (1971) Conservation and management of oysters in Ireland. Biological Conservation 4(1):70.
71. McKelvey F, Andrew T, & Cunningham P (1996) Recruitment potential of native oysters *Ostrea edulis* in Lough Foyle (International Council for the Exploration of the Sea, Copenhagen).
72. Kennedy RJ & Roberts D (1999) A survey of the current status of the flat oyster *Ostrea edulis* in Strangford Lough, Northern Ireland, with a view to the restoration of its oyster beds Biology and the Environment: Proceedings of the Royal Irish Academy 99B:79-88.
73. Roberts D, et al. (2004) Strangford Lough ecological change investigation (SLECI). Report to Environment and Heritage Service (Queen's University, Belfast).

Appendix 1 References

74. DiSalvo LH & Martínez E (1985) Culture of *Ostrea chilensis* Philippi 1845 in a North-central Chilean bay. *Biología Pesquera* 14:16-22 (in Spanish).
75. New Zealand Ministry of Fisheries (2007) Status of New Zealand fisheries - dredge oyster (OYS 7 - Nelson/Marlborough). (New Zealand Ministry of Fisheries Report, http://services.fish.govt.nz/fishresourcespublic/Plenary2007/OYS%207_07.doc).
76. Jeffs AG & Creese RG (1996) Overview and bibliography of research on the Chilean oyster *Tiostrea chilensis* (Philippi, 1845) from New Zealand waters. *Journal of Shellfish Research* 15:305-311.
77. CPPS (2004) Action Plan for the protection of the marine environment and coastal areas in the Southeastern Pacific. (Comision Permanente del Pacifico Sur, Guayaquil, Ecuador).
78. Ancieta F, Vera J, Berger CC, & Viacava MC (1979) Diagnosis of aquaculture in Perú. *Revista de la Comisión permanente del pacífico Sur* 10:3-11 (in Spanish).
79. Toro J & Chaparro O (1990) in *Cultivo de Moluscos en America Latina*, ed Hernandez A (CIID-Canadá, Bogota, Colombia), Vol 23 pp 1-264.
80. Guo X, et al. (2006) Oysters and oyster farming in China: a review. *Journal of Shellfish Research* 25(2):734.
81. Smeltz HA (1897) The oyster-bars of the west coast of Florida: their depletion and restoration. *Bulletin of the United States Fish Commission* 17:305-308.
82. Swift F (1897) The oyster grounds of the west Florida coast: their extent, condition and peculiarities. *Bulletin of the United States Fish Commission* 17:285-287.
83. Gambordella M, McEachron L, Beals C, & Arnold WS (2007) Establishing baselines for monitoring the response of oysters in southeast Florida to changes in freshwater input. Final Report to the Florida FWCC Fish and Wildlife Research Institute (Cooperative Agreement No. CA H 5284-05-0005, St. Petersburg, Florida).
84. New York Times (March 3, 1884) The cowboys of Florida. *New York Times*.
85. O'Keife K, Arnold W, & Reed D (2006) Tampa Bay oyster bar mapping and assessment. Final Report to the Tampa Bay Estuary Program.
86. Volety AK, et al. (in press) Eastern oysters (*Crassostrea virginica*) as an indicator for restoration of Everglades ecosystems. *Ecological Indicators*.
87. Zeller D, Booth S, Mohammed E, & Pauly D (2003) From Mexico to Brazil: central Atlantic fisheries catch trends and ecosystem models. *Fisheries Centre Research Reports* 11(6) (UBC, Vancouver).
88. Ellison AM (2008) Managing mangroves with benthic biodiversity in mind: moving beyond roving banditry. *Journal of Sea Research* 59:2-15.
89. Milewski I & Chapman A (2002) Oysters in New Brunswick: more than a harvestable resource. (Conservation Council of New Brunswick, Fredericton, New Brunswick).
90. Trowbridge P (2005) Environmental indicator report: shellfish. New Hampshire Estuaries Project, ed New Hampshire Department of Environmental Services.
91. MacKenzie C (1996) History of oystering in the United States and Canada, featuring North America's greatest oyster estuaries. *Marine Fisheries Review* 58:1-78.
92. Denys N (1908) The description and natural history of the coasts of North America (Acadia) (The Champlain Society, Toronto).
93. Cairns DK (1995) in *The north Atlantic fisheries: successes, failures, and challenges*, An Island Living Series, eds Arnason A & Felt L (Institute of Island Studies, Charlottetown), Vol 3, pp 95-133.
94. Perley M (1852) Reports on the sea and river fisheries of New Brunswick (Simpson, Fredericton) 2nd Ed.
95. Saville-Kent W (1895) in *Western Australia Year Book for 1894-1895*, (Richard Pether, Government Printer, Perth), pp 232-239.
96. Morton B, Lam K, & Slack-Smith S (2003) First report of the European flat oyster *Ostrea edulis*, identified genetically, from Oyster Harbour, Albany, south-western Western Australia. *Molluscan Research* 23:199-208.
97. Brearley A (2005) Earnst Hodgkin's Swanland; Estuaries and coastal lagoons of South-western Australia (University of Western Australia Press, Crawley).
98. Vancouver RN (1801) A voyage of discovery to the north Pacific Ocean and round the world (John Stockdale, London).
99. Saville-Kent W (1894) in *Western Australia Year Book for 1893-1894*, (Richard Pether, Government Printer, Perth), pp 179-190.
100. Baudin TN (1809) The Journal of the Post Captain Nicolas Baudin, Commander-in-Chief of the Corvettes Geographe and Naturaliste. Assigned by the order of the Government to be a "Voyage of Discovery". (Libraries Board of South Australia, Adelaide).
101. Nind S (1831) Description of the natives of King George's Sound (Swan River Colony) and adjoining country. *Journal of the Royal Geographical Society of London* 1:21-51.
102. Black AB (1876) Report on the Camden Haven fishery. Report of the Royal Commission, appointed on the 29th September, 1876 to inquire into the best mode of cultivating the oyster together with the minutes of evidence, and appendices (Oyster Culture Commission, Sydney).
103. Reid G (1876) An Essay of New South Wales. The Mother Colony of the Australias (Thomas Richards, Government Printer, Sydney).
104. Avila M, Seguel M, Plaza H, Bustos E, & Otazía R (1995) Assessment of the situation and perspectives on aquaculture in Chile. (CORFO-IFOP).
105. Carranza A, Defeo O, & Beck MW (2008) Diversity, conservation status and threats for native Oysters (Ostreidae) in the Atlantic and Caribbean coasts of South America. *Aquatic Conservation: Marine and Freshwater Ecosystems*.
106. Lasta ML, Ciocco NF, Bremec CS, & Roux AM (1998) in *The Argentinean sea and its fisheries: Vol. 2. molluscs relevant for fisheries. culture and reproductive strategies of bivalves and equinoideans*, ed Boschi EE (Instituto Nacional de Investigación y Desarrollo Pesquero), pp 115-142.
107. MacKenzie CL (1997) in *The history, present condition, and future of the molluscan fisheries of North and Central America and Europe: Volume 1*, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle), pp 87-117.

108. Berghahn R & Ruth M (2005) The disappearance of oysters from the Wadden Sea: a cautionary tale for no-take zones. *Aquatic Conservation* 15:91-104.
109. Munch-Petersen S & Kristensen P (2001) On the dynamics of stocks of blue mussels (*Mytilus edulis* L.) in the Danish Wadden Sea. *Hydrobiologia* 465:31-43.
110. Buhs F & Reise K (1997) Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig-Holstein: Spatial patterns and a long-term decline. *Helgolander Meeresuntersuchungen* 51:343-359.
111. Reise K (1998) in *Umweltatlas Wattenmeer Bd. 1 Nordfriesisches und Dithmarscher Wattenmeer*, (Landesamt fuer den Nationalpark Schleswig-Holsteinisches Wattenmeer, Umweltbundesamt. Ulmer, Stuttgart), pp 168-169.
112. Vollmer M, Guldberg M, Maluck M, Marrewijk D, & Schlicksbier G (2001) Landscape and cultural heritage in the Wadden Sea Region - Project Report. (Common Wadden Sea Secretariat, Wilhelmshaven, Germany).
113. Enghoff I (2000) Fishing in the southern North Sea region from the 1st to the 16th century AD: evidence from fish bones. *Archaeofauna* 9:59-132.
114. Lozan J (1994) in *Warnsignale aus dem Wattenmeer*, eds Lozan J, Rachor E, Reise K, von Westernhagen H, & Lenz W (Blackwell, Berlin), pp 215-226.
115. Neudecker T (1990) The history of the former German oyster fishery and mariculture: 400 years of crown law on oyster (4.2.1587). *Deutsche Hydrographische Zeitung Ergaenzungsheft Reihe B* 22:518-525.
116. Michaelis H & Reise K (1994) in *Warnsignale aus dem Wattenmeer*, eds Lozan J, Rachor E, Rachor E, Von Westernhagen H, & Lenz W (Blackwell, Berlin), pp 106-116.
117. Dahl K, Borchardt T, Dankers N, & Farke H (1994) Status, trends, regulation and ecological effects of the Wadden Sea fishery. *Ophelia Supplement* 6:87-97.
118. Herlyn M & Millat G (2000) Decline of the intertidal blue mussel (*Mytilus edulis*) stock at the coast of Lower Saxony (Wadden Sea) and influence of mussel fisher on the development of young mussel beds. *Hydrobiologia* 426:203-210.
119. Dankers N, Brinkman A, Meijboom A, & Dijkman E (2001) Recovery of intertidal mussel beds in the Waddensea: use of habitat maps in the management of the fishery *Hydrobiologia* 465:21-31.
120. Medeiros C, Kjerfve B, Araujo M, & Neumann-Leitao S (2001) in *Coastal Marine Ecosystems of Latin America*, eds Seeliger U & Kjerfve B (Springer-Verlag, Berlin).
121. New Zealand Ministry of Fisheries (2007) Status of New Zealand fisheries - dredge oyster (Foveaux Strait - OYS 5). (New Zealand Ministry of Fisheries, http://services.fish.govt.nz/fishresourcespublic/Plenary2007/OYU5_07.pdf).
122. Shaw WN (1997) in *The history, present condition, and future of the molluscan fisheries of North and Central America and Europe: Volume 2*, eds MacKenzie CL, Burrell Jr. VG, Rosenfield A, & Hobart WL (NOAA, Seattle).
123. Ingersoll E (1881) in *The history and present condition of the fishery industries*, ed Goode GB (US Department of the Interior 10th Census of the United States, Washington, DC), pp 1-252.
124. Browning B (1972) *The natural resources of Elkhorn Slough: Their present and future use*. California Department of Fish and Game Coastal Wetland Series #4.
125. Polson M & Zacherl D (in press) Geographic distribution and intertidal population status for the Olympia oyster, *Ostrea lurida*, from Alaska to Baja. *Journal of Shellfish Research*.
126. MacGinitie G (1935) Ecological aspects of a California marine estuary. *American Midland Naturalist* 16:629-765.
127. Barret E (1963) The California oyster industry. *Fish Bulletin* 123:1-103.
128. Nichols FH, Cloern JE, Luoma SN, & Peterson DH (1986) The modification of an estuary. *Science* 231:567-573.
129. Galvin J (1971) *The First Spanish Entry into San Francisco Bay 1775* (John Howell Books, San Francisco, CA).
130. Margolin M (1978) *The Ohlone Way* (Heyday Books, Berkeley).
131. Von Kotzebue O (1821) *A Voyage of Discovery into the South Sea and Beerings Straits* (Longman, Hurst, Rees Orme, and Brown, London).
132. Smith SE & Kato S (1979) in *San Francisco Bay: the urbanized estuary*, ed Conomos TJ (American Association for the Advancement of Science, San Francisco, CA).
133. von Chamisso A (1936) *A sojourn at San Francisco Bay 1816* (The Book Club of California, San Francisco).
134. Packard E (1918) *The molluscan fauna from San Francisco Bay*. University of California Publications in Zoology 14(2).
135. Townsend CH (1893) Report of observations respecting the oyster resources and oyster fishery of the Pacific coast of the United States. U.S. Commission of Fish and Fisheries Report 1889-1891 (U.S. Government Printing Office, Washington D.C.).
136. Booker M (2006) Oyster growers and oyster pirates in San Francisco Bay. *Pacific Historical Review* 75:63-88.
137. Galtsoff P & Luce S (1930) Oyster industry of the Pacific coast of the United States: Report of the United States Commissioner of Fisheries for the fiscal year 1929. Bureau of Fisheries Report.
138. Broughton J (1997) Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: ichthyofaunal evidence from the Emeryville Shellmound, California. *Antiquity* 71:845-862.
139. Broughton JM (2002) Prey spatial structure and behavior affect archaeological tests of optimal foraging models: examples from the Emeryville shellmound vertebrate fauna. *World Archaeology* 34:60-83.
140. National Marine Fisheries Service (2002) Fisheries statistics and economics. <http://www.st.nmfs.gov>.
141. Butler PA (1954) Summary of our knowledge of the oyster in the Gulf of Mexico. *Fishery Bulletin of the Fish and Wildlife Service* 55:479-489.
142. Stevenson CH (1893) Report on the coast fisheries of Texas. US Commission of Fish and Fisheries for 1889-1891 (U.S. Government Printing Office, Washington, D.C.).

Appendix 1 References

143. Dugas RJ, Joyce EA, & Berrigan ME (1997) in The history, present condition, and future of the molluscan fisheries of North and Central American and Europe, Volume 1, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle).
144. Chew K (1982) Proceedings of the North American Oyster Workshop (Louisiana State Univ. Press, Baton Rouge).
145. Ingle R & Dawson C (1953) A survey of Apalachicola Bay, Florida. State of Florida Board of Conservation (State of Florida Board of Conservation).
146. Danglade E (1917) Condition and extent of the natural oyster beds and barren bottoms in the vicinity of Apalachicola, Florida. (US Department of Commerce Bureau of Fisheries).
147. USFW (1970) National estuary study. (US Department of the Interior, Washington).
148. Livingston R, Howell R, Niu X, Lewis F, & Woodsum G (1999) Recovery of oyster reefs (*Crassostrea virginica*) in a Gulf estuary following disturbance by two hurricanes. *Bulletin of Marine Science* 64:465-483.
149. Rockwood CE (1973) A management program for the oyster resource in Apalachicola Bay, Florida. (Florida State University, Tallahassee).
150. Livingston R (1983) Resource atlas of the Apalachicola estuary (Florida Sea Grant College).
151. Carter LJ (1970) Galveston Bay: test case of an estuary in crisis. *Science* 167:1102-1108.
152. Alten LE (1983) Indians of the upper Texas coast (Adademic Press, New York).
153. Hofstetter RP (1982) in Proceedings of the North American oyster workshop, ed Chew KK (Louisiana State University, Baton Rouge), pp 96-100.
154. Reid G (1957) Biological and hydrographic adjustment in a disturbed gulf coast estuary. *Limnology and Oceanography* 2:198-212.
155. Stanley D (1992) Historical trends: water quality and fisheries, Galveston Bay. (University of North Carolina Sea Grant College Program, Greenville).
156. Lester J & Gonzales L (2002) The state of the bay - a characterization of the Galveston Bay ecosystem. (EPA, Washington, DC).
157. May EB (1971) A survey of the oyster and oyster shell resources of Alabama. *Alabama Marine Resources Bulletin* (4):1-52.
158. Heck Jr. KL & Spitzer PM (2004) Introduction to oyster reefs. (Mobile Bay National Estuary Program, Mobile, AL).
159. Tatum WM, Van Hoose MS, Havard RW, & Clark MC (1995) The 1991 atlas of major public oyster reefs of Alabama and a review of oyster management efforts. (Alabama Marine Resources Bulletin).
160. Little E & Quick JA (1976) Ecology, resource rehabilitation, and fungal parasitology of commercial oysters, *Crassostrea virginica* (Gmelin), in Pensacola estuary, Florida. (Florida Marine Research Institute, St. Petersburg).
161. Woodburn K (1962) Clams and oysters in Charlotte county and vicinity. Florida State Board of Conservation Marine Laboratory Report 62-12.
162. Futch C (1967) A Survey of the oyster resources of Brevard county, Florida. (Florida Board of Conservation Research Department, St. Petersburg).
163. Baker P (1995) Review of the ecology and fishery of the Olympia oyster, *Ostrea lurida* with annotated bibliography. *Journal of Shellfish Research* 14:501-518.
164. Groth S & Rumrill S (in press) History of native oysters (*Ostrea conchaphila*) in Oregon estuaries, and a description of recovering populations in Coos Bay. *Journal of Shellfish Research*.
165. Quayle D (1988) Pacific oyster culture in British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 218.
166. Gillespie GE (1999) Status of the Olympia oyster, *Ostrea conchaphila*, in Canada. Canadian Stock Assessment Secretariat Research Document ed DFO (Canadian Stock Assessment Secretariat, Ottawa).
167. Ellis D & Swan L (1981) Teachings of the tides: uses of marine invertebrates by the Manhousat people (Theytus Books, Nanaimo).
168. Moss ML & Erlandson JM (1995) An evaluation, survey, and dating program for archaeological sites on state lands of the northern Oregon coast. (Oregon State Historic Preservation Office, Salem).
169. Dall W (1897) Editorial Correspondence: Marshfield, Oregon (Coos Bay). *The Nautilus* 11:66.
170. Marriage L (1954) The bay clams of Oregon: their economic importance, relative abundance, and general distribution. (Fish Commission of Oregon).
171. Fasten N (1931) The Yaquina oyster beds of Oregon. *American Naturalist* 65:434-468.
172. Baker P, Richmond N, & Terwilliger N (2000) in Marine Bioinvasions: Proceedings of a conference January 24-27, 1999, ed Pederson J (MIT Sea Grant College Program 00(2), Boston), pp 221-231.
173. Gillespie G (in press) Status of the Olympia oyster, *Ostrea conchaphila*, in British Columbia, Canada. *Journal of Shellfish Research*.
174. Kraeg R (1979) Natural resources of Netarts Bay. Estuary Inventory Report (Oregon Department of Fish and Wildlife).
175. Stout H (1976) The natural resources and human utilization of Netarts Bay, Oregon (Oregon State Univesity, Corvallis).
176. Lindsay C & Simons D (1997) in The history, present condition, and future of the molluscan fisheries of North and Central America and Europe: Volume 2: Pacific Coast, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle), pp 89-113.
177. Cook A, Shaffer J, Dumbauld B, & Kauffman B (2000) A plan for rebuilding stocks of Olympia oysters (*Ostreola conchaphila* Carpenter 1857) in Washington state. *Journal of Shellfish Research* 19:409-412.
178. Kinkaid T (1928) Development of the oyster industry in the Pacific. *Transactions of the American Fisheries Society* 58:17-122.
179. Peter-Contesse T & Peabody B (2005) Reestablishing olympia oyster populations in Puget Sound, Washington (University of Washington, Washington Sea Grant, Seattle).
180. Washburn F (1899) Eastern oyster culture in Oregon. *Popular Science Monthly* 56.
181. Washburn F (1901) Present condition of the eastern oyster experiment and the native oyster industry. First Biennial Report of the State Biologist of the State of Oregon (Oregon State Biologist).

182. Robinson A (1997) in The history, present condition, and future of the molluscan fisheries of North and Central America and Europe, Vol. 2 Pacific Coast eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (U.S. Department of Commerce,, Seattle).
183. Steele E (1957) The Rise and Fall of the Olympia Oyster (Fulco Publications, Elma, Washington).
184. McKernan D, Tartar V, & Tollefson R (1949) An investigation of the decline of the native oyster industry of the state of Washington, with special reference to the effects of sulfite pulp mill waste on the Olympia oyster (*Ostrea lurida*). (Washington Department of Fisheries, Olympia).
185. White J, Burhle E, Ruesink J, & Trimble A (in press) Evaluation of native oyster (*Ostreola conchaphila*) status and restoration techniques in Puget Sound, Washington, USA. Journal of Shellfish Research.
186. Carranza A & Rodríguez M (2007) On the benthic molluscs of Banco Inglés (Río de la Plata, Uruguay). Animal Biodiversity and Conservation 30:161-168.
187. Scarabino F, Zaffaroni JC, Clavijo C, Carranza A, & Nin M (2006) in Bases para la conservación y el manejo de la costa uruguaya eds Menafra R, Rodríguez-Gallego L, Scarabino F, & Conde D (Vida Silvestre Montevideo), pp 157-169.
188. Shepherd SA (1986) in A land transformed: environmental change in South Australia, eds Nance C & Speight DL (Longman Cheshire, Adelaide), pp 182-199.
189. Hone P (1996) Summary of existing data collected for the shellfish environmental monitoring program (SEMP) 1992 to 1994. (South Australian Research and Development Institute, Adelaide).
190. Wallace-Carter E (1987) For they were fishers: the history of the fishing industry in South Australia (Amphitrite Publishing House, Adelaide).
191. Gouletquer P & Heral M (1997) in The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3, Europe, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle).
192. Caceres-Martinez J & Figueras A (1997) in The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3, Europe, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle).
193. Ruano FDL (1997) in The history, present condition and future of the molluscan fisheries of North and Central America and Europe: Volume 3, Europe, eds MacKenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle).
194. Forcelini H, Kolm HE, & Absher TM (2007) Microbiological analysis and condition index of oysters sold in Guaratuba- Parana, Brazil. (XII Congresso Latino-Americano de Ciências do Mar - XII COLACMAR).
195. Pereira OM, Machado IC, Henriques MB, Galvão MSN, & Yamanaka N (2001) Stock evaluation of the oyster *Crassostrea brasiliana* in mangroves of rivers and tidal creeks ("gamboas") in Cananéia lagoon estuarine system (São Paulo State, Brazil). Boletim do Instituto de Pesca, São Paulo 27:85-95.
196. Pereira OM, Henriques MB, & Machado IC (2003) Estimations of growth rates of the oyster *Crassostrea brasiliana* in mangroves and a proposal for their sustainable exploitation in Cananéia estuary, SP, Brasil. Boletim do Instituto de Pesca, São Paulo 29(18-19) (in Spanish).
197. Campolim MB & Machado IC (1997) Proposal for the sustainable exploitation of the mangrove oyster *Crassostrea brasiliana* in Cananéia-SP. Instituto Oceanográfico USP e Associação Latino-Americana de Investigadores em Ciências do Mar 1:135-137 (in Spanish).
198. FAO (1994) Management and sustainable use of coastal lagoons in Latin America and the Caribbean Sea. (AQUILA).
199. Rodríguez J & Rojas-Suárez F (1999) Red list of the Venezuelan fauna (Provita-Fundación Polar, Caracas) (in Spanish).
200. Baquero E (1997) in The history, present condition, and future of the molluscan fisheries of North and Central America and Europe: Volume 1, Atlantic and Gulf Coasts, eds Mackenzie CL, Burrell Jr. VG, Rosenfeld A, & Hobart WL (NOAA, Seattle), pp 1-17.
201. Mackenzie C & Wakida-Kusunoki A (1997) The oyster industry of eastern Mexico. Marine Fisheries Review 59:1-13.
202. Doonan IJ, Cranfield HJ, & Michael KP (1994) Catastrophic reduction of the oyster, *Tiostrea chilensis* (Bivalvia:Ostreidae), in Foveaux Strait, New Zealand, due to infestation by the protistan *Bonamia* sp. New Zealand Journal of Marine and Freshwater Research 28:335-344.
203. Sequeira K (2002) Development of artisanal fishery in Rama Cay community, Atlantic coast of Nicaragua. Master Thesis of International Fisheries Management (University of Tromsø-Norway).
204. Valero Lopera A & Caballero Quintero Y (2003) A practitioner´s guide for the culture of marine bivalves in the Colombian Caribbean sea: pearly oysters, oysters, and scallops. Serie de Documentos Generales No. 10 Invermar (Cargraphics, Bogota).
205. Borthagaray A & Carranza A (2007) Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. Acta Oecologica 31:243-250.
206. Eastern Oyster Biological Review Team (2007) Status review of the eastern oyster (*Crassostrea virginica*). Report to the National Marine Fisheries Service (Report to the National Marine Fisheries Service).
207. Rothschild B, Ault J, Gouletquer P, & Heral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Marine Ecology Progress Series 111:29-39.
208. Virginia Marine Resource Commission (2007) Report and recommendations of the blue ribbon oyster panel. (Virginia Marine Resources Commission).
209. Dent RJ (1995) Chesapeake prehistory: old traditions, new directions (Plenum Press, New York).
210. Wharton J (1957) in The Jamestown 350th Anniversary historical booklets, ed Swem EG (Williamsburg, Virginia 350th Anniversary Celebration Corp.; Garrett and Massie, Sales Agent, Richmond, Richmond), Vol 13.
211. McCay BJ (1998) Oyster Wars and the Public Trust (University of Arizona Press, Tucson).
212. Pearson J (1942) The fish and fisheries of colonial Virginia. William and Mary College Quarterly Historical Magazine 22:213-220.
213. Stevenson CH (1894) The oyster industry of Maryland. Bulletin of the United States Fish Commission 12:203-297.

Appendix 1 References

214. Strachey W (1849) *Historie of travaille into Virginia Britannia* (Hakluyt Society, London).
215. Churchill E (1920) *The oyster and the oyster industry of the Atlantic and Gulf coast*. (U.S. Bureau of Fisheries).
216. Heral M, Rothschild B, & Gouletquer P (1990) Decline of oyster production in the Maryland portion of the Chesapeake Bay: Causes and perspectives. (International Council for the Exploration of the Sea).
217. Ingersoll E (1887) in *The fisheries and fishery industry of the United States*, ed Goode GB, Vol Section 2, pp 507-626.
218. Kellog J (1910) *Shell-fish Industries* (H. Holt and Co., New York).
219. Ford S (1997) *History and present status of molluscan shellfisheries from Barnegat Bay to Delaware Bay*. NOAA Technical Report 127 (National Marine Fisheries Service, Washington, D. C.).
220. Hall A (1894) in *Report of the U.S. Commissioner of Fish and Fisheries for 1892*, (U.S. Government Printing Office, Washington, D.C.), pp 463-528.
221. Johnson A (1925) *Geographia Americae with an account of the Delawyre Indians based on surveys and notes made in 1654-1656 by Peter Lindstrom* (The Swedish Colonial Society, Philadelphia).
222. Miller M (1962) *The Delaware oyster industry, past and present*. Ph.D. Dissertation (Boston University).
223. Miller M (1971) *The Delaware oyster industry*. Delaware History 14:238-254.
224. Moore HF (1911) in *Report to the Commissioner of Fisheries for the fiscal year 1910*, (U.S. Government Printing Office, Washington, D. C.), pp 1-29.
225. Watson JF (1868) *Annals of Philadelphia and Pennsylvania, In the Olden Time; Being a Collection of Memoirs, Anecdotes, and Incidents of the City and its Inhabitants and of the Earliest Settlements of the Inland Part of Pennsylvania From the Days of the Founders* (J.B. Lippincott & Co., Philadelphia).
226. NY/NJ Baykeeper (2005) *Oyster restoration in the Hudson-Raritan estuary*. <http://www.nynjbaykeeper.org/pdffiles/finalsdoc.pdf>.
227. Kurlansky M (2006) *The big oyster: history on the half-shell* (Random House, New York).
228. Bain M, et al. (2007) *Target ecosystem characteristics for the Hudson Raritan estuary: technical guidance for developing a comprehensive ecosystem restoration plan*. (Port Authority of NY/NJ., New York).
229. Oviatt C, et al. (2003) *A century of fishing and fish in Narragansett Bay*. Reviews in Fishery Science 11:221-242.
230. Desbonnet A & Lee V (1991) in *Proceedings of the First Rhode Island Shellfisheries Conference*, eds Rice M, Grady M, & Schwartz M (Rhode Island Sea Grant, University of Rhode Island, Narragansett), pp 11-16.
231. Desbonnet A & Lee V (1991) *Historical trends: water quality and fisheries, Narragansett Bay*. (National Sea Grant Publications, Washington, DC).
232. Boyd J (1991) in *Proceedings of the First Rhode Island Shellfisheries Conference*, eds Rice M, Grady M, & Schwartz M (Rhode Island Sea Grant, University of Rhode Island, Narragansett, Rhode Island), pp 2-10.
233. Goode G (1887) *The fisheries and fishery industry of the United States*. (U.S. Government, Washington, D.C.).
234. Kockiss J (1974) *Oystering from New York to Boston* (Wesleyan University Press, Middleton, Connecticut).
235. Rice M, Valliere A, & Caporelli A (2000) *A review of shellfish restoration and management projects in Rhode Island*. Journal of Shellfish Research 19:401-408.
236. Lenihan H & Peterson C (1998) *How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs*. Ecological Applications 8:128-140.
237. Brickell J (1737) *The natural history of North Carolina with an account of the trade, manners, and customs of christians and indian inhabitants* (J. Carson, Dublin).
238. Catesby M (1996) *The natural history of Carolina, Florida, and the Bahama Islands 1731-1743* (Alecto Historical Editions, London).
239. Lawson JD (1712) *A new voyage to Carolina. Accounts from 1700-1701 journey* (University of North Carolina Press, Chapel Hill).
240. Grave C (1905) *Investigations for the promotion of the oyster industry of North Carolina*. (United States Fisheries Commission).
241. Lenihan H (1999) *Physical-biological coupling on oyster reefs: how habitat form influences individual performance*. Ecological Monographs 69:251-275.
242. Lenihan H, Micheli F, Shelton S, & Peterson C (1999) *The influence of multiple environmental stressors on susceptibility to parasites: An experimental determination with oysters*. Limnology and Oceanography 44:910-924.
243. Finet Y & Olive C (2004) *Marine mollusca in the Gallic-Roman diet in Gaul (Gallia Transalpina)*. Preistoria Alpina 40(1):107-114 (in Italian).
244. Diaz-Almela E, Boudry S, Launey FB, & Lape`gue S (2004) *Reduced female gene flow in the European flat oyster Ostrea edulis*. Journal of Heredity 95(6):510-516.
245. Cano J, Rosique MJ, & Rocamora J (1997) *Influence of environmental parameters on reproduction of the European flat oyster (Ostrea edulis L) in a coastal lagoon (Mar Menor, southeastern Spain)*. Journal of Molluscan Studies 63:187-196.
246. Gonzalez-Wanguemert M, Perez-Ruzafa A, Rosique MJ, & Ortiz A (2004) *Genetic differentiation in two cryptic species of Ostreidae, Ostrea edulis (Linnaeus, 1758) and Ostreola stentina (Payraudeau, 1826) in Mar Menor Lagoon, southwestern Mediterranean Sea*. Nautilus 118(3):103-111.
247. Deng J & Jin X (2000) *Study on fishery biodiversity and its conservation in Laizhou Bay and Yellow River estuary*. Zoological Research (in Chinese). 21:76-82.
248. Geng X, Fu M, Xu X, & Li P (1991) *The evolution of modern oyster bioherms and their ecological character with significance of paleo-environment*. Science in China (Series B, in Chinese) 8:867-875.
249. Fang E, Li W, & Yu J (2007) *Sustainable use of live oyster reef in Bohai Gulf*. Modern Fisheries Information (in Chinese) 22:12-14.
250. Yan F (2003) *Causes of zero flow of the Yellow River and humanistic consideration*. Journal of Catastrophology (in Chinese) 18(2):91-96.
251. Gu Y, D. Qi, Y. Ge, R. Yu and R. Zhang (2005) *Ecological evaluation and of oyster reefs in Xiaomiaohong tidal channel in Jiangsu coast*. Marine Sciences (In Chinese) 29(3):42-47.



FSC
INFO



FOR MORE INFORMATION, PLEASE VISIT
WWW.NATURE.ORG/SHELLFISH