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FOR SUSTAINABLE
BIVALVE MARICULTURE



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ECOSYSTEM CONCEPTS FOR SUSTAINABLE BIVALVE MARICULTURE

Committee on Best Practices for Shellfish Mariculture and the
Effects of Commercial Activities in Drakes Estero,
Pt. Reyes National Seashore, California

Ocean Studies Board

Division on Earth and Life Studies

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This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise, in accordance with procedures approved by the NRC's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following individuals for their participation in the review of this report:

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Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations nor did they see the final draft of the report before its release. The review of this report was overseen by Judith E. McDowell, Woods Hole Oceanographic Institution, appointed by the Division on Earth and Life Studies, and Michael C. Kavanaugh, Malcolm Pirnie, Inc., appointed by the Report Review Committee, who were responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution.

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Summary

Almost 50% of all seafood eaten worldwide today is farm raised, compared to only 9% in 1980, primarily from the expansion of aquaculture in China (Food and Agriculture Organization of the United Nations, 2006). In the United States in 2007, mariculture—the cultivation of organisms in the marine environment—produced approximately 15,000 metric tons (meat weight) of bivalve molluscs, mostly oysters, clams, and mussels (National Oceanic and Atmospheric Administration, 2009a). Mariculture production of bivalve molluscs in the United States has roughly doubled over the past 25 years.

Increasing domestic seafood production in the United States in an environmentally and socially responsible way will likely require the use of policy tools, such as best management practices (BMPs) and performance standards. These policy tools are commonly utilized to reduce effects associated with the use of natural resources in commercial activities like mariculture. Although mariculture operations may expand the production of seafood without additional exploitation of wild populations, they still depend upon and affect natural ecosystems and ecosystem services. BMPs and performance standards are useful for protecting the environment while increasing mariculture production.

Bivalve mariculture can have both positive and negative ecological impacts on the marine environment. For instance, culture operations and the associated gear can alter water flow, composition of the sediment, and rate of sedimentation and in some cases can disturb the benthic flora, including seagrass, which provide habitat for fish and

invertebrates. However, bivalve mariculture can enhance production in seagrass beds by increasing water clarity through filtration and by fertilizing the beds through biodeposition. Mariculture gear increases the availability of hard substrates, thereby supporting higher densities of fish and invertebrates that associate with structured habitat, but the presence of artificial hard substrates can also promote colonization and spread of introduced species, such as nonnative tunicates. Such a mix of beneficial and negative effects illustrates the complexity of ecosystem responses to mariculture operations.

Many laws and regulations currently govern bivalve mariculture. At the federal level, the U.S. Army Corps of Engineers issued a nationwide permit for existing mariculture under the Clean Water Act. Implementation is subject to regional conditions to address regional concerns and protect important resources. Because most bivalve operations occur in coastal waters, mariculture also falls under state jurisdiction, with details of regulatory requirements varying from state to state. Inconsistent and confusing laws from multiple layers of local, county, state, and federal jurisdictions can produce an uncertain legal environment for the mariculture industry. In some cases, regulators may be in the conflicted position of promoting the development of the industry, preventing conflicts with other uses, and maintaining terrestrial and marine environments.

The National Park Service asked the National Research Council to investigate the potential ecosystem effects of bivalve shellfish mariculture and recommend best practices to maintain ecosystem integrity. This report examines how ecological effects vary in magnitude and type with the environment, the species cultured, and the habitat type and describes the uncertainties that characterize our current understanding of mariculture's effects. The report reviews how bivalve mariculture can affect wild stocks and what socioeconomic factors influence mariculture operations, and it identifies the most important topics for future research to minimize negative and maximize beneficial environmental impacts (see Appendix A for the full statement of task). The committee acknowledges and draws from many efforts by industry, government, nongovernmental organizations, and academia from around the world to identify best practices and establish ecologically sustainable policies for bivalve shellfish mariculture. The report provides an overview of the scientific issues that should be considered in assessing the effects of bivalve mariculture on estuarine and coastal ocean ecosystems and builds on recent efforts, such as those initiated by the Food and Agriculture Organization of the United Nations, to develop an ecosystem-based approach to management of bivalve shellfish mariculture. Ecosystem-based management considers the web of direct and indirect interactions among the living and non-living elements of an ecosystem, including human

activities. The committee's review of the science is intended, therefore, to inform policy makers about this web of ecosystem consequences so that the implications of alternative policies and management goals will be more transparent.

From organism to ecosystem, there is no free lunch—every additional animal has an incremental effect arising from food extraction and waste excretion. The scope of impacts of cultured bivalves is a function of the scale and location of mariculture operations, a fact that needs to be recognized and quantified. Some effects may be beneficial to the ecosystem, while others may be detrimental, depending on the scale and location of the bivalve farm. All impacts need to be considered in a policy context that appropriately weighs the values of seafood production and of changing ecosystem state so that the costs and benefits of choices about mariculture can be compared.

BEST MANAGEMENT PRACTICES AND PERFORMANCE STANDARDS

BMPs represent one approach to protecting against undesirable consequences of mariculture. Most BMPs for bivalve mariculture have been prepared by industry groups, nongovernmental organizations, and governments with the common goal of sustainability. Industry guidelines mostly address ways to sustain production, but this may not be sufficient to sustain other ecosystem components or to safeguard other societal goals.

An alternative approach to voluntary or mandatory BMPs is the establishment of performance standards for mariculture. Variability in environmental conditions makes it difficult to develop BMPs that are sufficiently flexible and adaptable to protect ecosystem integrity across a broad range of locations and conditions. An alternative that measures performance in sustaining key indicators of ecosystem state and function may be more effective. Because BMPs address mariculture methods rather than monitoring actual ecosystem responses, they do not guarantee that detrimental ecosystem impacts will be controlled or that unacceptable impact will be avoided. Fixed BMPs can also result in a stifling of innovation. By contrast, adoption of performance standards is likely to encourage innovation among growers. With performance standards, mariculture operations are managed adaptively to maintain key indicators within acceptable bounds, through direct monitoring of ecosystem indicators rather than tracking compliance with specific management practices. However, the monitoring required for implementing performance standards is costly, and this additional expense could serve as a disincentive to the expansion of bivalve mariculture in the United States.

Finding: Performance standards are generally more efficient than BMPs because they allow for innovation and track ecosystem responses. However, implementation of performance standards usually involves additional, and potentially costly, requirements for monitoring and enforcement. Many of the issues surrounding bivalve shellfish mariculture are location specific and may not be addressed effectively by broad national standards. Technically oriented BMPs have in some cases been shown to increase efficiency and hence profitability, while reducing environmental impacts. However, no single BMP or standard can address the many contingencies raised by different mariculture techniques, the species in culture, and the environmental conditions that are unique to various regions or sites.

Recommendation: Performance standards that set parameters based on carrying capacity (size of population or biomass that the environment can support; see definition in Chapter 5) should be developed and implemented at the ecosystem level because they can be applied to bivalve mariculture more generally with adjustments for the specific conditions of each mariculture operation, species, and culture technique.

Recommendation: Management of bivalve mariculture should employ performance standards to address carrying capacity concerns at the scale of the water basin but may find the use of BMPs to be more practical and efficient at the local scale, especially where the industry consists of large numbers of small growers.

Because BMPs tend to be specific to the type of mariculture operation and the environmental conditions on site, it is not practical for this report to recommend a set of BMPs to suit all circumstances. Instead the report identifies general principles for best practices and performance standards. In the cases where there are best practices or standards that apply across the range of cultured species and conditions, the committee provides recommendations for managers and practitioners (Table S.1).

ECOLOGICAL EFFECTS OF BIVALVE MARICULTURE

Culturing of suspension-feeding bivalves has effects on the plants, animals, biogeochemical processes, food webs, and habitats of estuarine and coastal ocean ecosystems. Suspension-feeding bivalves gain nourishment by filtering suspended particles, including phytoplankton, organic detritus, and inorganic particles, from the water column. By-products of suspension feeding include excreted, dissolved ammonium and biodeposits of feces and pseudofeces. This filtration and excretion-deposition process affects the food web and the biogeochemical cycling. Further-

more, this filtration and deposition activity has impacts on the physical and chemical environment, modifying various habitats and their ecological functioning.

Submerged aquatic vegetation (SAV) and other benthic plant production can be enhanced by greater penetration of light through reductions in turbidity from suspension feeding and also by fertilization of the bottom through biodeposition by the bivalves. Structures associated with mariculture typically suppress SAV beneath them by shading, and human disturbance associated with mariculture operations, such as foot and boat traffic, can degrade SAV habitat. Impacts on the benthos can occur if mariculture structures substantially modify deposition patterns by altering currents or the cultured organisms transfer organic materials to the bottom through biodeposition, which can either enhance food supplies for some deposit-feeding benthic invertebrates in soft sediments or induce mortality of benthic invertebrates under conditions of limited flow and high-stocking densities.

The structures used by bivalve mariculturists to hold and protect molluscs during grow-out provide novel hard substrates for epibiotic attachment and can attract fish and crustaceans to the structural habitat and to the attached epibiota. Many of these mobile organisms have been shown to feed upon structure-produced prey, but there is no definitive conclusion on whether or not the “artificial reef” effect reflects simple attraction of fish and crustaceans or actual enhancement of their production. Nonetheless, widespread recognition has emerged that such structures enhance production of benthic prey and provide hiding places for fish and crustaceans that feed on these prey. Information on the potential effects of mariculture on birds, marine mammals, and marine turtles is largely based upon a general understanding of wildlife ecology and the relationships of these species to the physical and biological environment rather than on studies to test explicitly the effects of mariculture operations. Potential positive impacts include increased food availability for birds attracted to the fouling organisms on mariculture gear. Some potential negative impacts include entanglement and drowning in nets and other gear and disturbance, removal, or displacement of wildlife whose breeding or foraging habitats occur near mariculture operations.

Historically, bivalve mariculture, especially of oysters, led to numerous examples of both intentional and inadvertent introductions of non-native species. The intentional importation of nonnative species, such as oysters, used in mariculture represents a species introduction, and historically several of these bivalves reproduced and established self-sustaining populations. The imported bivalves often carried unintended “hitchhiker” species, some of which established self-sustaining populations that spread out from the mariculture facilities. However, the development

TABLE S.1 Best Practices and Standards That Can Be Applied Across Bivalve Species and Conditions

Potential Problem	Impact	Best Management Practice
Excessive localized organic loading to sediments via biodeposits from bivalve mariculture	Low oxygen (hypoxia) in sediments and loss of benthic biota	Site selection (e.g., tidal flushing rate, currents) and limiting bivalve biomass to levels below carrying capacity for biodeposits Integrate bivalve mariculture with seaweed culture
Decreased planktonic biomass by overstocking	Shift planktonic composition; reduce turbidity allowing greater light penetration and hence more benthic plant production; deprive native suspension feeders of food	Site selection (highly productive area) Manage stocking density based on carrying capacity for filtration
Loss of carbonate shell from coastal waters	Less habitat for larval settlement and oyster reef biota; reduced buffering capacity for maintaining pH	Recycle shell from shucking operations and restaurants, taking precautions to prevent spread of nonnative species
Introduction and transmission of disease organisms	Large losses of cultured bivalves; transmission of disease to native species with possible biodiversity losses and reduction in wild stocks of bivalves	Largely limit transfer to eyed larvae screened for disease; minimize transfer of adults and only after screening
Establishment of breeding populations of nonnative bivalves introduced through culture	Loss of native biodiversity resulting from competition, predation, and habitat modification	Culture sterile triploids Regulate transport and processing of live animals
Spread of nonnative species associated with mariculture	Loss of biodiversity resulting from competition, predation, and habitat modification	Limit stocking to clean seed or eyed larvae (no adults) Regular cleaning and land-based or other appropriate disposal of fouling organisms

Performance Standard Approach	Desired Outcome
Monitoring for hypoxia in sediments	Limit organic accumulation in sediments, yet fertilize submerged aquatic vegetation (SAV)
Carrying capacity model for estimating stocking density	Maintain or restore biodiversity and natural food web structure; enhance water clarity via filtration and improve SAV habitat
Monitor for change in plankton composition and performance of native suspension feeders	Maintain baseline shell-based habitat and carbonate balance of estuaries and coastal lagoons; compensate for shell removed by harvesting wild bivalve stocks
Monitor for disease organisms	Avoid spread of disease; maintain health of cultured and native bivalves
Monitor for nonnatives in areas near mariculture operations	Protect native species and ecosystem structure
Monitor for nonnatives at mariculture operations and in areas near operations	Protect native species and ecosystem structure

continued

TABLE S.1 Continued

Potential Problem	Impact	Best Management Practice
Overfishing, depleted stocks, and habitat degradation and loss	Reduction in seafood supply	Use mariculture to create habitat and build up brood-stock sources; restore filtering capacity and water clarity; enhance SAV; increase seafood supply
	Food web changes and biodiversity loss	
Displacement of native species and/or predation on cultured stock	Disturbance of birds, marine mammals, and marine turtles	Site selection (avoid areas near breeding and feeding areas)
		Confine activities to less sensitive time periods
Visual impact	Social discord	Employ submerged culture structures

and adoption of industry and intergovernmental codes of practice have greatly reduced threats of new unintentional introductions. In addition, artificial hard substrate habitat (e.g., cages, racks, lines, netting) facilitates the spread and high abundance of nonnative epibiotic organisms in soft-sediment environments.

Disease organisms can still be transferred with bivalve seed used in mariculture, but International Council for the Exploration of the Sea protocols for the transport of eyed larvae from hatcheries with rigorous disease inspection programs and producing seed in quarantine greatly reduce the potential for disease transmission. Diseases that occur at low levels within wild populations can flourish in mariculture populations because of altered conditions, such as crowding and temperature fluctuations. Lastly, the introduction of nonnative bivalve species for the purposes of mariculture can affect the genetics of native populations through the interbreeding of wild and cultured organisms.

Finding: Research that takes a broader landscape-scale and ecosystem-based approach would provide a better understanding of how the scale and intensity of bivalve mariculture influence the natural ecosystem structure and processes. To achieve this goal, methods for accurate estimation of ecosystem carrying capacity will be vital. In addition, further study of the impacts of high-density (intensive)

Performance Standard Approach	Desired Outcome
Monitor prices and demand for wild and cultured bivalves	<p>Recreate some of the historic habitat and nutrient cycling functions of oysters and other bivalves</p> <p>Potentially reduce fishing pressure on wild stocks</p>
Assess sensitivity to disturbance and population resilience of native species	<p>Minimize negative interactions between mariculture and protected species</p> <p>Provide more effective environmental water-quality regulations to prevent microbial contamination of bivalves and wild waters</p>
Establish visual design standards	<p>Increase compatible uses of coastal areas</p> <p>Enhance social acceptance</p>

mariculture on local biodiversity would help decision makers and managers anticipate changes in the ecosystem that could influence social attitudes and public acceptance.

Recommendation: Efforts should be directed at studying effects of bivalve mariculture at appropriate landscape and ecosystem scales that would facilitate managing mariculture at these scales instead of current management scales, which often focus on the scale of the individual lease or even the individual potentially impacted species. Future research efforts should assess how modification of habitat by bivalve mariculture affects aquatic vegetation and mobile fish and invertebrates at larger spatial and longer temporal scales, especially life stages of the guild(s) of fish and crustaceans known to associate with structure and hard substrates. Additionally, mariculture structures, such as racks, lines, bags, and the cultured shellfish should be studied to determine whether they act only as attractants or also enhance productivity of species known to aggregate around structures.

Finding: Continued research efforts could develop appropriate culturing techniques for native bivalve species, as well as enhance ways of restoring and then sustainably managing depleted native stocks. It is important to develop a better understanding of the potential of nonnative bivalve molluscs used in mariculture to become natural-

ized under changing environmental, climatic, and other conditions. Additionally, there is a general lack of information on community- and ecosystem-level responses to mollusc introductions and how those responses compare to native species.

Recommendation: To prevent unintentional and probably irreversible establishment of breeding populations of introduced species, mariculture operators should use sterile triploids as much as possible when they grow nonnative bivalves in areas where the cultured species either has not been introduced or has not established a reproductive population. More attention should be directed toward the eradication of undesirable nonnative species, and a greater emphasis should be placed on studies of ecosystem-level effects of nonnative bivalve introductions.

Finding: Assessments of the impacts of disturbance from bivalve mariculture on birds, marine mammals, and marine turtles are constrained by insufficient baseline data on habitat use by these species and further, by a lack of data both on spatio-temporal variation in disturbance events and on the longer-term consequences of these disturbances on populations of these species.

Recommendation: Managers should recognize that previous studies have limited power to detect adverse effects of disturbance and that a precautionary approach should be taken in order to minimize potential disturbance. Future decision making would benefit from targeted research that incorporates spatially explicit studies of the activities of mariculturists; the individual behavioral responses of birds, marine mammals, and marine turtles using these coastal habitats; and the population consequences of any observed behavioral changes.

BIVALVE MARICULTURE CONTRASTED WITH WILD FISHERIES

Many ecological effects of bivalve mariculture closely parallel the corresponding ecological effects of wild-stock harvests. The similarity is greatest when comparing wild harvest to mariculture operations that raise bivalves in or on natural bottom habitats because similar or identical harvesting methods are typically used. Impacts of dredge-harvest gear on the benthic communities are greater than for any other bottom-disturbing fishing gear, and the intensity and duration of such impacts of harvest disturbance vary with bottom type. Mariculture conducted on lines, racks, or cages does not require dredging and is thus less damaging to the ecosystem than wild-stock harvesting. In a bivalve mariculture operation, the shell habitat is largely maintained by replacing harvested bivalves with new juveniles. In contrast, the exploitation of wild stocks of oysters has

caused the degradation and loss of oyster-reef habitat over time. Hence, fisheries that target species, such as oysters, which create biogenic habitat, can have and have had net negative impacts on habitat quality and quantity. Wild-stock harvests tend to be more frequent and more dispersed, thus causing greater damage to the ecosystem than the less frequent, more localized, and managed harvest of cultured bivalves.

Basic economics suggests that increasing supply through mariculture will reduce seafood prices if other factors remain unchanged. Lower prices will tend to reduce economic incentives to harvest the wild population, thereby reducing fishing pressure on the wild stock. However, this effect can be masked in practice if wild-harvest fisheries remain profitable even at lower prices, if overall demand for the product increases, or if a strong niche market develops for the wild-harvest product. Increasing imports of cultured salmon into the United States since the mid-1990s correlate with falling prices for wild-stock salmon, and a similar pattern of price decline followed the increased domestic production of cultured hard clams.

Finding: Although the effects of disturbance to benthic communities caused by bivalve mariculture activities and those from wild harvest are relatively well understood at local scales, there are few direct comparisons, and less is known about cumulative effects at larger spatial and longer temporal scales.

Recommendation: Direct comparisons of the effects of bivalve mariculture and wild harvest should be conducted in systems with both activities to better understand their effects in comparable environments. Studies at larger spatial scales and over longer periods of time should also be undertaken.

Finding: Economic theory suggests that mariculture production will tend to increase supply and reduce the price of the cultured species, thereby reducing economic incentives to harvest wild populations. The effect of lower prices on fishing pressure depends on the condition and management of the wild fishery. Empirical evidence for these effects is largely limited to observations of price trends with increases in supply, but there has been little formal analysis of responses of either markets or wild fisheries to the expansion of mariculture.

Recommendation: Policy makers and marine resource managers should anticipate possible linkages between wild harvest and mariculture production in shellfish markets when developing forecasts. Managers should monitor changes in market prices to assess the effects of mariculture on supply, product quality and availability, and the response of wild-harvest fisheries to these changes in market conditions.

CARRYING CAPACITY AND BIVALVE MARICULTURE

Carrying capacity as it applies to bivalve mariculture can be defined as the maximum population or biomass that an area will support sustainably, as set by available space, food, and other potentially limiting resources but within the limits set by the capacity of the ecosystem to process biological wastes and by social tolerance for the change in environmental attributes. The concept of carrying capacity is increasingly and appropriately invoked as a quantitative guide to identify limits to stocking densities of bivalves in mariculture operations. Suspension-feeding bivalves remove phytoplankton and suspended detrital and inorganic particles while producing and releasing nutrients in dissolved and biodeposited forms. These biogeochemical functions provide the ecological basis for scaling impacts of different biomass loadings of the cultured bivalves.

Application of a carrying capacity concept to setting mariculture stocking limits requires a determination on what represents acceptable versus unacceptable impacts. In many estuaries, the historical baseline abundances of oysters and other bivalve molluscs, and hence their collective filtration capacity, was dramatically higher before harvesting reduced these stocks. If cultured bivalves were used to help restore baseline conditions of filtration, there could be substantial improvements in the ecosystem state through enhanced water clarity and reductions in algal blooms and hypoxia.

Carrying capacity models can be used to optimize production of the cultured bivalves; reduce the ecological impacts on the food web; or maintain societal values, such as scenic amenity or recreational opportunity. All carrying capacity approaches require models of the mariculture activity and its interactions with living and non-living components of the ecosystem. Although several carrying capacity models have been developed for bivalve mariculture, the uncertainties associated with ecosystem-based models remain large. Monitoring to test model predictions and adaptive modification of the models and of management decisions are thus critical components of implementing site-specific limits to bivalve stocking.

Finding: Assessment of bivalve mariculture has occurred mostly at the local scale by measuring the “footprint” of the shellfish farm. Scaling up these effects to whole systems has been limited by the difficulty in identifying a signal attributable solely to mariculture and by the capacity and resources to make meaningful measurements over larger areas. Similarly, most of the potential measures of ecological carrying capacity consider only a single or a few ecosystem components. Our understanding of factors that affect ecological carrying capacity will evolve as scientists learn more about the functioning of marine ecosystems.

Recommendation: Managers should utilize models based on empirical data that can estimate carrying capacity relative to bivalve production, ecosystem, and social constraints. The models provide an approach for addressing many of the issues that are associated with understanding multiple farm interactions and cumulative effects of other coastal zone activities at a scale relevant to coastal ecosystems.

Recommendation: Further development and refinement of models for estimating carrying capacity should be encouraged. This will require a coordinated and sustained measurement effort to provide the empirical data necessary for iterative modification of these models and to validate projections produced by the models. Models should be designed to address the needs of managers and mariculturists alike. In addition, model parameters and general model outputs should be presented in clear and concise terms that are understandable and acceptable to all users.

ECONOMIC AND POLICY FACTORS AFFECTING BIVALVE MARICULTURE

A complex set of laws, regulations, and policies governs bivalve mariculture in the United States and affects jurisdictional areas, including (a) leasing and tenure policy; (b) land use, zoning, and tax policies; (c) interstate transport policies; and (d) offshore mariculture policy. The estuarine and nearshore coastal waters most appropriate for bivalve mariculture are typically regulated at the state, county, or town level. In most states, the intertidal or shallow subtidal bottom and overlying waters in which mariculture operations are located are owned by the public with the state acting as trustee. A federal permit may be required if mariculture gear could represent an obstruction to navigation or if the operation is located in federal waters. Because mariculture operators in most coastal states do not own the bottom they use in their businesses, uncertainty over leasing and tenure in the long term represents an impediment to investment and may reduce opportunities to obtain financing.

At least 120 federal laws and more than 1,200 state statutes across 32 states, plus local regulations, affect mariculture. Some states have identified a lead agency or established an interagency coordinating committee to help guide prospective culturists through the complex permitting process. Some states exempt mariculture from sales or use taxes or encourage mariculture by special zoning or waterfront revitalization programs. Other states have enacted legislation or constructed regulations to reduce interference with commercial fishing often by restricting potential leasing to areas outside of productive mariculture grounds.

Rules governing the interstate importation of bivalve seed vary widely among states, creating confusion, misinformation, and often non-compliance. The lack of a comprehensive national policy has contributed to the spread of bivalve diseases, along with variability in the capacity of states to test for diseases. To avoid nearshore pollution and use conflicts, mariculturists have become interested in offshore mariculture in federal waters, beyond the jurisdiction of the states. Despite growing interest in offshore mariculture, regulation remains unsettled, and the lack of a settled and transparent regulatory framework and uncertainty over legal tenure inhibits this enterprise. Most mariculture operators in the United States target high-price regional and local markets for specialty, value-added products. Passage of laws to require labeling of bivalves by country of origin may increase demand locally for home-grown products, including cultured bivalves.

Local traditions and nearshore use conflicts often play an important role in bivalve mariculture. Recreational activities, such as boating and swimming, and aesthetic considerations regarding ocean and bay views often affect public acceptance of existing operations and the permitting of new mariculture operations. Bivalve growers can increase societal acceptance and reduce political opposition to mariculture leases by engaging constructively with the local community and by designing their operations to minimize visual impacts. Mariculture operations that restrict foot or boat traffic in nearshore waters or tidal areas face issues of public use and access rights. In some states, mariculture is given lower priority in the resolution of use conflicts. Education of the local community about the ecological benefits of bivalve mariculture may increase public acceptance, particularly in locations where excess nutrient input has caused eutrophication problems, where wild stocks have been depleted, or where seagrass has declined greatly from historical baselines.

Finding: While some laws and regulations may constrain bivalve mariculture development, others can serve to advance its growth. Local traditions and use conflicts can have this dual effect as well.

Recommendation: States should streamline the permitting process for bivalve mariculture in state waters and identify areas within state waters where such activities are encouraged. Shellfish growers should engage the local community and design their operations to minimize conflicts.

ECOSYSTEM SERVICES OF BIVALVES

Suspension-feeding bivalves have the ability to reduce turbidity through their filtration, fertilize benthic habitats through biodeposition,

induce denitrification, counteract some detrimental effects of eutrophication in shallow waters, sequester carbon, provide structural habitats for other marine organisms, and stabilize habitats and shorelines. These ecosystem services of bivalves, along with recognition that oysters, clams, and scallops have been depleted dramatically below historical baselines in many estuaries, explain why bivalve mollusc restoration has become an important component of many programs for restoring impaired estuaries and some coastal waters.

Finding: There is a need for improved quantifying of ecosystem service values so that markets for these ecosystem services could be further explored. Through a market-based approach, the present practice of externalizing the lost value could be changed to a system that assesses the true costs to those who contribute to the deterioration of natural estuarine and coastal marine ecosystems services.

Recommendation: Research at the interface of biology and natural resource economics should be aggressively supported to explore the various proposed ecosystem services of bivalve molluscs and to develop rigorous economic methods of putting values on those services. This could include methods that specify market values for those services that yield to this approach and methods involving “willingness to pay” and other public preference approaches where markets do not exist. This research should then be utilized by policy makers to achieve social equity in putting costs of service losses on those responsible and using fees paid for lost services to restore those ecosystem services and thereby preserve them for the general public trust.

Finding: Many estuaries suffer from eutrophication and potentially could benefit from increasing the biomass of suspension-feeding bivalves to provide resilience to eutrophication and reduce the symptoms of excessive nutrient and sediment loading. In addition to limiting effects of eutrophication and sedimentation, restoring the beneficial biogeochemical functioning of suspension-feeding bivalves, especially oysters, could provide additional ecosystem services associated with filtration of phytoplankton and inorganic particles from the water column and deposition of organic biodeposits. These effects will be greatest in shallow and well-mixed water bodies, such as those typically found in estuaries, coastal bays, and lagoons.

Recommendation: Policies should be developed to encourage restoration of the biogeochemical filtration functions associated with suspension-feeding bivalves in estuaries. Such policies should consider both recovery of wild stocks and mariculture of (preferably

native) suspension-feeding bivalves to restore the filtration functions and associated ecosystem services. For restoration purposes, particular attention should be given to (1) establishing genetic husbandry guidelines to prevent loss of genetic diversity; (2) avoiding negative effects of disturbance of vertebrates and other valued species; (3) controlling spread of nonnative fouling organisms, especially certain tunicates; (4) regulating bivalve stocking to require use of eyed larvae from certified hatcheries with an effective and comprehensive disease inspection or to first-generation seed spawned from adult bivalves under quarantine conditions in order to minimize species introductions and disease spread; (5) insuring that bivalve shellfish loading does not exceed levels that have unacceptable negative impacts on the benthos through excessive organic loading or on other components of the ecosystem through clearance of planktonic foods and organic particles from the water column; (6) preventing unacceptable damage to bottom habitat by harvest gear; and (7) assessing the social tolerance for mariculture on a site-specific basis.

1

Introduction

FRAMING THE ISSUE

As the total worldwide fisheries yield from exploitation of wild stocks has declined, the production from mariculture, defined as the cultivation of organisms in their natural marine environment, has increased (Food and Agriculture Organization of the United Nations, 2009). This pattern is especially evident for bivalve molluscs, which are the focus of this report. The recognition that, even in developed countries with professional fisheries managers, wild-stock fish, shellfish, and bivalve molluscs have not always been sustainably harvested (e.g., Jackson et al., 2001a; Lotze et al., 2006) leads to concerns over how coastal policies can facilitate expanding mariculture to meet rising demand while management is conducted in a way to preserve ecosystem integrity and sustainability. Relative to the global pattern, the growth of bivalve mariculture has lagged in the United States. Consequently, there may be the opportunity and perhaps growing incentives for growth in this sector of the fishing industry in the United States, making a review of best management practices (BMPs) for sustainability a timely contribution.

The development of living natural resource management has followed a progression from its virtual absence, when the intensity of exploitation was low, to an approach based upon attempts to model and limit harvest of individual species stocks to levels that are sustainable. Then more recently, resource management has evolved to an ideal of sustainability of the integrity of the broader ecosystem responsible for producing the targeted stocks (Food and Agriculture Organization of the United Nations,

2008a). An analogous progression in molluscan mariculture management approaches appears to be developing (Secretariat of the Convention on Biological Diversity, 2004). Critical questions regarding impacts of bivalve mariculture on the natural ecosystem need to be addressed in order to preserve natural populations of fish and wildlife and to sustain ecosystem services of the ocean. In brief, molluscan mariculture can be included within comprehensive, spatially explicit, ecosystem-based management (EBM) of ocean and estuarine systems. Despite broad consensus for development of EBM of the oceans (Pew Oceans Commission, 2003; U.S. Commission on Ocean Policy, 2004) and seminal conceptual characterizations of the principles to be included in EBM (e.g., Grumbine, 1994; Christensen et al., 2006), practical implementation of EBM, especially for the oceans, has been slow and difficult (Arkema et al., 2006).

A recent workshop report by the Food and Agriculture Organization of the United Nations (2008b) includes contributions from many experts to answer the question of how an EBM scheme for aquaculture could be developed to preserve and sustain natural ecosystem integrity. This committee used the concepts in this workshop report to make additional progress in identifying the issues involved in achieving sustainable mariculture of suspension-feeding bivalves. This committee's report was written to provide a blueprint for development of EBM for molluscan mariculture. As such, it was prepared in response to the committee's statement of task to "develop recommendations for BMPs for shellfish [i.e., bivalve molluscan] mariculture to maintain ecosystem integrity." Several specific questions were included in the complete task to the committee (Appendix A), the answers to which required inclusion of the following contributions. The committee conducted a review to characterize the various types of bivalve mariculture operations and the processes through which they have potential to affect the structure and function of the natural ecosystem. The uncertainties associated with these potential ecosystem impacts are identified, along with suggestions on research needs that could help reduce uncertainty and lead toward development and implementation of spatially explicit ecosystem-based mariculture planning that could enhance benefits and minimize negative impacts. Such an approach required consideration of the ways in which molluscan mariculture and wild-stock fisheries are related. Because cultured molluscs often include nonnative species, this report explicitly addresses the risks and the BMPs and performance standards associated with nonnative bivalve culture. The discussion of BMPs and standards, and the subsequent findings and recommendations, are intended for regulators, resource managers, and the mariculture industry. In addition, this report provides a framework for socioeconomic assessment of bivalve mariculture, thereby acknowledging that humans are an integral part of the ecosystem and that food

production from the ocean plays an important role in its use and represents one valuable ecosystem service.

COMMUNITY STRUCTURE AND FOOD WEBS

Ecologists study ecosystems because exploring the interplay between the physicochemical environment and living organisms is critical to developing a holistic understanding of the organizational processes that control species abundances and dynamics. Yet, ecosystems seldom, if ever, have discrete boundaries. Even large lakes can trickle into adjacent systems and exchange nutrients with terrestrial ecosystems (Power, 2001). To complicate the analytical challenge further, plant and animal populations vary in space and through time. Among the types of temporal variation, most critical to management is long-term change driven by human intervention. Few had recognized or acknowledged the phenomenon of shifting ecological baselines until high-profile reports alerted scientists, resource and environmental managers, and the public (Pauly, 1995; Jackson et al., 2001a; Lotze et al., 2006) because humans have modified ecosystems progressively over many generations. Our perceptions of what is natural are typically based on our own recollection of the ecosystem state in the past and thus fail to reflect the long history of human intervention that shift those baselines over time, often effectively disguising the pristine state (Pauly, 1995; see Box 1.1). Reconstruction of the past is made especially challenging in the estuaries, lagoons, coastal bays, and shallow coves favored for mariculture because multiple human interventions have combined to move these ecosystems away from their post-Pleistocene glaciation state. This caveat is necessary because humans have been exploiting marine invertebrates for millennia—in Mexico, for example, shell deposits from the Chantuto people created mounds as high as 11 m (Rick and Erlandson, 2009). Centuries of exploitation and pollution continue to influence the individual resident species directly and also the food web in which they are imbedded.

The conceptual basis of ecological understanding and prediction of how organisms affect one another, directly by consumption or indirectly by consuming interacting species one or more steps away, is the food web (broadened to be an interaction web so as to include impacts beyond those of consumption). Elton (1927) introduced the concept of food webs (“food cycles” in his terminology), Tansley (1935) invented and applied the term “ecosystem,” and Paine (1980) discriminated among types of food webs, developing a “taxonomy” that has withstood the test of time. Of Paine’s three basic web categories, descriptive food webs and energy flow webs are essentially illustrative of structure. Only interaction webs focus on how particular linkages within the web’s topology drive or

BOX 1.1 Shellfish in Drakes Estero

The committee's first report, *Shellfish Mariculture in Drakes Estero, Point Reyes National Seashore, California*, discusses the historic ecological baseline of estuarine and lagoonal ecosystems in terms of ecosystem services provided by oysters. Oysters are one of several species of bivalve whose feeding activity maintains water clarity by filtering suspended materials and transferring organic material to the sediment in the form of feces and pseudofeces, a process known as biodeposition. In addition to oysters, other suspension-feeding bivalve species historically harvested for food in California—such as the Pacific gaper clam (*Tresus nuttalli*), cockle (*Clinocardium nuttalli*), littleneck clam (*Protothaca staminea*), and butter or Washington clam (*Saxidomus nuttalli*)—contribute similar biogeochemical functional attributes. Although there are considerable uncertainties about the historical abundance of native Olympia oysters in Drakes Estero, the cultured non-native oysters to some extent replicate the biogeochemical functions of several species of native bivalves, including Olympia oysters. The habitat services provided by mariculture of Pacific oysters may differ from those provided by native Olympia oysters because the native oyster does not form extensive tall reefs, even where abundant, whereas the rack structures holding strings of cultured Pacific oysters extend about 1 m upwards from the bottom and provide hard-substrate habitat for a nonnative tunicate that covers a substantial portion of the rack and oyster surfaces. The biogeochemical effects of the cultured nonnative oysters, as distinguished from the impacts of mariculturists' activities, are likely to be small as long as the level of production is low relative to the ecological carrying capacity of the ecosystem. However, this is only one of the issues to be evaluated in developing appropriate management practices for a bivalve mariculture operation and determining whether a site is appropriate. For Drakes Estero, the committee's first report notes several other considerations, such as the potential for mariculturists' disturbance of harbor seals and water fowl, as well as policy constraints in an area congressionally designated as Potential Wilderness.

modify changes in species populations and thereby create community patterns (see National Research Council, 2006).

Some of the underlying interspecific interactions in these webs are grounded in classic observational, comparative studies (e.g., Brooks and Dodson, 1965; Estes and Palmisano, 1974), others in experimental manipulation (e.g., Paine, 1966; Power et al., 1985), and still more in studies that blend these techniques (e.g., Myers et al., 2007). Studies involving interaction webs have generated a vocabulary of their own—top-down organization (predator control of the system's basic processes) versus bottom-up organization (control by primary productivity)—and have progressed to rejuvenate interest in trophically transmitted (Wootton, 1993; Menge, 1995) and behaviorally mediated (Peacor and Werner, 2001;

Grabowski, 2004) indirect effects. Appreciation of these processes that act on species within a community is necessary in developing the important applied concepts of *system* carrying capacity and EBM.

The evidence that natural ecosystems, because they are composed of networks of dynamically interacting populations, respond to perturbations comes primarily from experimental manipulations conducted at small spatial scales (e.g., Paine, 1966; Dayton, 1971; Sutherland, 1974; Carpenter and Kitchell, 1992). Menge (1997) asks whether those done in marine intertidal systems were of sufficient duration both to detect the anticipated direct effects but also to generate the indirect ones. Both categories of effects generally appeared simultaneously and became statistically significant within the initial 20–40% of the experimental duration. However, a question more relevant to the expanded spatial scales characteristic of most mariculture operations is whether the interactions defined and demonstrated at smaller scales can be scaled up and also applied at the level of an estuary or even an open ecosystem.

Two primary lessons derived from the outcomes of these experimental studies can be applied to the management of bivalve mariculture. First, many of the resident species are dynamically connected, as reflected in the concept of an interaction web, and these interactions have both direct and indirect consequences. Second, the most effective means of identifying the fundamental dynamics is by intervening in the system. Bivalve mariculture itself is an intervention, as is the addition, or depletion, of a higher, consuming trophic level, or successful establishment (in abundance) of an invasive species. Box 1.2 presents three examples¹ to illustrate that species population dynamics are linked and that ecological “surprises” can arise in the form of unanticipated indirect effects of suspension-feeding bivalves.

The denominator common to these three studies is that ecosystems at large spatial scales can have their primary productivity substantially redirected by large populations of suspension-feeding bivalves, which is most clearly demonstrated by the unintended ecosystem intervention of successful establishment and proliferation of a set of nonnative suspension-feeding bivalves. While U.S. molluscan mariculture has not reached the levels provided in the examples above, it is important to understand the potential impacts of high-density culture of both native and nonnative species. Dumbauld et al. (2009) review in detail the nuances

¹ These examples are not intended to suggest any global generality to the identified patterns, although they do relate directly to the challenge of assessing ecosystem carrying capacity. Collectively, they imply some guidance in what to include in best management practices and how to assess the optimal carrying capacity for a focal species in a multi-species system.

BOX 1.2 The Ecosystem Impact of Selected Invasive Bivalves

Zebra mussel (*Dreissena* spp.)

This benthic invertebrate is an iconic invasive species that was first identified in North American waters in 1988 and has since spread broadly (Johnson et al., 2006). Zebra mussels are suspension feeders—hence their relevance to the bivalves used in molluscan mariculture—and often occur as dense populations. The community impact of their entry, establishment, and proliferation is best documented from Lake Erie and especially the Hudson River estuary (Strayer et al., 2004; Strayer and Malcom, 2007; Strayer, 2009). They were initially recognized in the Hudson River in May 1991, and 17 months later, their biomass “...exceeded that of all other heterotrophs in the freshwater tidal Hudson...” (Strayer et al., 1999). Measured filtration rates translate to a theoretical turnover of the entire water column in 1.2–3.6 days for this tidally well-mixed estuary. Figure 1.1 identifies the sweeping consequences of this invasion. Phytoplankton and small zooplankton have declined precipitously (-80% and -71%, respectively), as have pelagic fish (-28%), reflecting a dramatic impact on the pelagic food web. On the other hand, the benthic food web has flourished, in large part because of clearer water, enhanced growth of submerged macrophytes, and increased densities of both nearshore invertebrates and fish. Indirect effects are apparent. Bacterial populations have increased, and some bivalve-consuming ducks have benefited, yet some native bivalves may be nearing local extinction, and crayfish are heavily and detrimentally fouled.

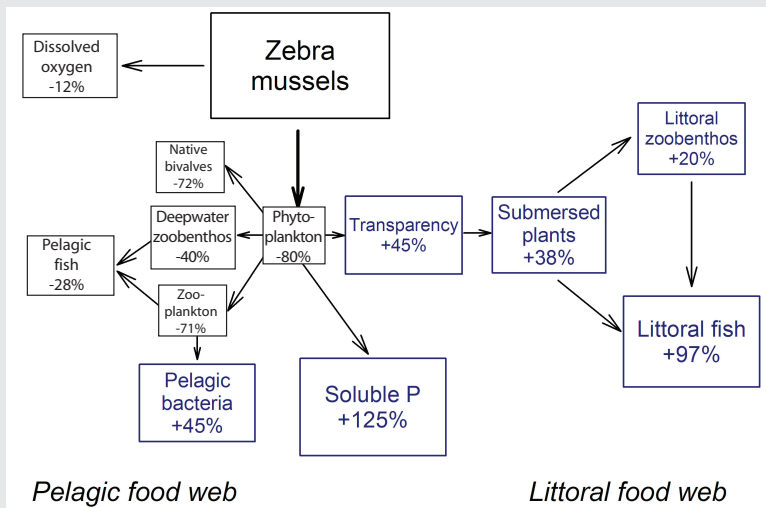


FIGURE 1.1 Summary of the effects of the zebra mussel invasion on the Hudson River ecosystem (copyright by the Ecological Society of America; Strayer, 2009).

***Corbicula fluminea* in the Potomac River**

This introduced Asiatic bivalve was recognized in the tidal, but basically fresh-water, Potomac River in 1977 (Cohen et al., 1984). Prior studies had shown a downstream gradient in phytoplankton abundance. Clam density, about 1,500 per m², peaked in 1980 and 1981, just prior to a population crash and correlated spatially with a substantial drop in phytoplankton presence along a 16 km stretch of the river. Estimates of the clam filtering rate suggest that 30% of the river's chlorophyll *a* along this stretch could be pumped through the *C. fluminea* in three to four days. The decline in phytoplankton presence appears consistent with the clam's filtering ability. The bivalves appear to have substantially influenced the nutrient resources common to other suspension feeders. (Indirect effects were not identified.)

***Potamocorbula amurensis* in San Francisco Bay**

The capacity of suspension-feeding bivalves to alter community structure is clearly illustrated in the largest estuary on the U.S. Pacific coast, the San Francisco Bay estuary. The presence of *P. amurensis* was recognized by 1986 (Carlton et al., 1990). An individual adult can filter about 4 liters of water per day. That per capita rate, combined with a density of about 16,000 per m² (Chauvaud et al., 2003), was sufficient to account for the observed suppression of an annual phytoplankton bloom lasting from late spring to fall (Alpine and Cloern, 1992). Associated with this suppression was an approximate 80% decrease in copepod density, presumably due to reduced phytoplankton availability (Nichols et al., 1990). Copepods are a major prey for endangered and federally listed smelt species. The relationship between water rights law, California agriculture, Chinook salmon production, and the Endangered Species Act represents a regulatory quagmire. While bivalve mariculture is not involved, the sweeping consequences to a diverse stakeholder assemblage attributed to a dominant and introduced suspension feeder are obvious. One indirect effect is on diving ducks. These introduced bivalves are readily consumed by Greater Scaup, but because the introduced species has a thicker shell than their normal prey, the per clam food value is reduced, and the duck's dispersal and over-wintering habits have been altered (Poulton et al., 2002).

underlying potential shifts in community structure. In general, nutrient availability, the identity of the phytoplankton species, per capita prey growth and predator consumption rates, and respective densities of all major participants are needed at minimum to model the potential for change. Thus, modeling will be an essential component of research to identify the carrying capacity of suspension-feeding bivalves (see Chapter 5), and this is dependent on meeting the challenge of estimating the various rate functions.

Do commercially farmed bivalves, generally capable of filtering a broad size spectrum of prey (even including some invertebrate larvae), influence the local community by simultaneously being a competitor and a predator? All communities in nature are ensembles of dynamically interacting species. Enough detail is now known to be able to predict change following the addition of dense suspension-feeding bivalve populations; however, knowledge is insufficient to predict with confidence the consequences for particular species. The implications for intensive, local development of bivalve mariculture seem obvious—ecosystem impacts can be anticipated although many of them may not be immediately apparent and cannot be predicted with the certainty that stakeholders often demand from resource managers and decision makers. Assessing whether anticipated modifications of the estuarine ecosystem are beneficial or detrimental depends in part on knowledge of historical baselines of bivalve abundance and a synthesis of the net value of direct and indirect impacts. As detailed in the scientific literature and some high-profile reviews (e.g., Lotze et al., 2006), estuaries are largely degraded worldwide. This implies that managing for a return toward historical baselines represents a beneficial change, especially where abundant wild populations of suspension-feeding bivalves played an historical role of providing resilience against eutrophication symptoms (Jackson et al., 2001a).

KEY CONCEPTS

Ecological integrity—the capacity of an ecosystem to support and maintain a balanced, integrated, adaptive community of organisms having an indigenous species composition, diversity, and functional organization comparable to that of similar undisturbed ecosystems in the region (Carignan and Villard, 2002).

Resilience—the capacity of an ecosystem to maintain its characteristic patterns, structures, function, and rates of processes in the face of disturbance or perturbation (Leslie and Kinzig, 2009).

SPECIES CONSIDERED IN THIS REPORT

The bivalve molluscs currently or historically cultured in the United States to market as food include oysters of several species (*Crassostrea virginica*, *C. gigas*, *C. ariakensis*, *C. sikamea*, *Ostrea lurida*, and *O. edulis*), mussels (*Mytilus edulis*, *M. trossulus*, and *M. galloprovincialis*), several venerid (family Veneridae) clams (*Mercenaria mercenaria*, *Protothaca staminea*, and *Venerupis philippinarum*), scallops (*Argopecten irradians*), geoducks (*Panopea generosa*), soft-shell clams (*Mya arenaria*), cockles (*Clinocardium nuttallii*), rock scallops (*Hinnites giganteus*), arks (*Anadara transversa* and *A. ovalis*), and razor clams (*Siliqua alta*, *S. costata*, and *S. patula*). Although not a bivalve mollusc but rather a marine gastropod mollusc, this report also discusses abalone (*Haliotis* spp.) because they are commonly cultured on the U.S. Pacific coast and provide insight into disease issues shared with bivalve molluscs. Culturing of bivalves includes many experimental trials that resulted in failure, such that this list of bivalve types does not imply that bioeconomically feasible culturing has been demonstrated for each group or each species.

These cultured molluscs and the methods of growing them differ in discrete ways. The bivalve species can be subdivided by aquatic environmental regime in which they live (ocean versus estuary versus marine lagoon), relationship to substrate (epifauna on the surface of the hard substrate versus infauna buried within the soft substrate), and major predators (e.g., seaducks for mussels, gastropods for oysters). Likewise, culture techniques fall into clearly distinguishable categories. Culture can be conducted in floating containers, suspended containers or lines, or on the bottom. The jargon of molluscan mariculture also separates the intensity of methods (e.g., use of external inputs, which also translates to density of animals per unit area of culture) from extensive methods (e.g., cast out on the bottom, with or without protective mesh or netting) to semi-intensive (with some external control) to intensive culture within a hatchery where food, aeration, and seawater are provided. Clearly, the method and location of culturing can dictate the kinds and intensities of impacts on other species and the broader ecosystem.

GENERAL APPROACHES TO DEFINING CARRYING CAPACITY

The generic concept of carrying capacity in ecology has been developed to refer to the Malthusian notion that resources in the environment are limited such that no population can grow without limit. Formal definitions of carrying capacity for a population of a given species have emerged from mathematical representations of single-species population growth. The most well known of which is the logistic curve where the rate of population growth approaches exponential as abundance nears zero

and resources do not constrain population growth and then approaches zero as the population size (N) nears some value (K) defined as the carrying capacity of the environment. This simple logistic growth curve is represented as:

$$\frac{dN}{dt} = rN \frac{(K - N)}{K}$$

where r is the maximum intrinsic rate of natural increase. This logistic growth curve has played and continues to play an important role in formalizing theory in population and community ecology. Species interactions are included by inserting parameters relating to competing species and/or predators and expressing interactions among species through coefficients that reflect the nature and strength of those between-species relationships. The fundamental basis of this type of representation is so deeply engrained in ecology and environmental sciences and has sufficient parallels in economics that the general notion of a single-species carrying capacity is widespread and used in conceptual and mathematical models by resource managers and environmental organizations.

Although the concept of carrying capacity is generally understood, there are numerous alternative bases on which to set the carrying capacity for molluscan mariculture, each with different implications for management. The strict application of the logistic growth curve to stocking of suspension-feeding bivalves would lead to a hydrographically defined water body in which individual bivalve seed would become stunted in growth because of exhaustion of the resources required for growth. This situation would be unacceptable to the growers because when food demands of the bivalves cannot be met and growth is stunted, the culture operations would cease to remain financially viable. Furthermore, the impacts of high-bivalve density can be expressed on several different spatial scales, dependent upon renewal processes and rates for suspended foods. Growth rates of individual suspension-feeding bivalves decline with local density on scales as fine as 1 m^2 (Peterson, 1982; Peterson and Black, 1987) and within individual mariculture operations (Newell et al., 1998; Drapeau et al., 2006). These sorts of consequences probably have more relevance to management decisions of the individual grower, but such localized depletion of suspended foods would also affect natural populations of suspension feeders of all sorts, including zooplankton as well as benthic invertebrates.

As alternatives to estimating carrying capacity based on maintaining adequate supplies of suspended foods for the cultured bivalves, carrying capacity can instead be based on sustaining ecosystem needs or on social acceptance of mariculture. Determining the ecosystem needs of other suspension feeders in the water column and on the bottom and assessing

the ecosystem capacity to process the release of dissolved nutrients and the biodeposits of feces and pseudofeces represents a scientific challenge but moves management of bivalve mariculture closer to an EBM ideal of sustaining ecological integrity. There is precedent within the management regimes of some wild-stock bivalve fisheries. For example, mussel production in the Netherlands is allocated to fishermen only after inferred demand from mollusc-eating birds is satisfied (see Wadden Sea box in Chapter 4). Newly developing approaches to this challenge are even producing methods of comparing benefits of fishery production to declines in important species in the ecosystem that are indirectly affected through the food web impacts (Richerson et al., 2009). Setting a carrying capacity for bivalve mariculture sensitive to the resource demands of non-commercial species would lead to a lower carrying capacity than one based on the cultured mollusc production alone. The social carrying capacity reflects the local public attitudes toward use of waters for a variety of alternative, largely incompatible purposes. Because the social carrying capacity is likely to vary widely from place to place determined by multiple user conflicts, in large part dependent upon the rising human population density along the coasts (Diana, 2009), less-populated regions are expected to be more tolerant of bivalve mariculture interventions as a “new” coastal use. Social carrying capacity probably requires some form of a survey tool to determine prevalent local attitudes because of its place-specific nature. Carrying capacity based on social considerations will generally be a lower, often far lower, number of cultured molluscs than the level that could still supply ecosystem needs and thus sustain ecological integrity. In addition, these different types of carrying capacity are not independent. Many stakeholders will provide social input that reflects an environmentalist commitment to sustaining ecological integrity, such that this consideration will contribute to determining social carrying capacity.

REPORT ORGANIZATION

This report is organized to review the challenges, constraints, and benefits of maintaining or restoring ecosystem integrity in the presence of bivalve mariculture. Chapter 2 describes BMPs and performance standards for bivalve mariculture. Chapter 3 identifies the ecological effects of bivalve mariculture. Chapter 4 discusses the relationship between bivalve mariculture and wild-stock harvest. Chapter 5 analyzes carrying capacity as it relates to bivalve mariculture. Chapter 6 focuses on the economic and policy factors affecting bivalve mariculture activities, and finally Chapter 7 provides some concluding synthetic perspectives on ecosystem services of bivalves. Appendix A includes the committee’s verbatim statement of task, and Appendix B presents the committee and staff biographies.

2

Best Management Practices and Performance Standards

It is widely accepted that most human activities in the marine environment will have some effect on marine species and habitats. The scale of these impacts depends on the nature of the activity, its intensity, and the sensitivity of the receiving environment. The degree of change that is considered permissible depends on a number of factors, not the least of which is public perception. Empirical data demonstrating change or impact is the most obvious basis on which to justify management actions or inactions. Equally important is linking the change observed directly to the process under consideration (e.g., bivalve mariculture). Best management practices (BMPs) and other standards have been adopted as means of mitigating against unacceptable environmental interactions. The major categories of BMPs and standards include the following:

- BMPs (or design standards or specifications) for growers, mariculture regulators, and managers
- Regulatory standards governing bivalve mariculture
- Certification standards for bivalve products (e.g., organic, sustainable, fair trade, domestically or even locally grown)

BMPs often are developed by the industry group (e.g., growers) to which they apply. Adoption of and adherence to these codes is usually voluntary. Regulatory standards usually are imposed by a public authority (i.e., federal, state, or local agencies responsible for permitting and oversight of mariculture); compliance is often required by law as a

condition of the permit. Certification standards are developed by buyers, public agencies, nongovernmental organizations, or marketing groups as a means of providing consumers with information about a product with the goal of influencing growers through the leverage of consumer choice and market forces. Pursuit of certification is voluntary for growers.

All these practices and standards may have multiple objectives including, for example, reducing the likelihood that mollusc farming will have unacceptable ecological effects. When designing and formulating a BMP or performance standard, the following are some of the major decisions to be made (Breyer, 1982):

- Targets of the regulation—What specific ecological goals are to be achieved or ecological harm(s) are to be guarded against?
- Scope of the regulation—Does the standard address specific forms of mollusc farming or the broad spectrum?
- Performance or design specification—Does the standard specify what level of effects are acceptable, or, alternatively, how to do the farming?
- Technology forcing—Should the standard set objectives not achievable with current practice and technology?

A performance standard may set targets for a parameter (e.g., ambient phytoplankton concentrations should not be reduced by more than X% below baseline levels) that is a proxy or surrogate for the ultimate objective (e.g., maintenance of suitable conditions for health of native filter-feeder populations). The choice of the specific parameters targeted by the code or regulation has to take into account its relationship to the ultimate objectives and the cost of monitoring and enforcement.

In settings where bivalve mariculture is carried out by a number of small, independent operators (none of whom individually approaches carrying capacity limits), it makes sense for the mariculture regulator(s) to focus on system-wide carrying capacity questions, taking into account the cumulative effects of all farming operations. BMPs or standards that target parameters related to ecological and social carrying capacity (see Chapter 5) can be focused on bivalve mariculture broadly and may not have to address each location, species, and culture technique separately. However, given that the ability to quantify and measure ecological carrying capacity remains limited (see Chapter 5), adopting this approach will require careful consideration of the risks, the acceptable level of ecological change, and the appropriate parameters to monitor.

The choice between performance and design specifications embodies a fundamental tension between flexibility and enforceability (Helfand, 1991; Montero, 2002; Bruneau, 2004). Design standards are easier to

enforce but limit the farmer's flexibility in the choice of approach and innovation; adoption of such standards may restrict the development and application of technological advances. Performance specifications are more likely to promote innovation because they leave the choice of how to meet the objective to the individual grower (Downing and White, 1986; Malueg, 1989). Performance standards are likely to be more efficient (in economic terms) in the long run because they provide incentives for farmers to optimize their technology and processes, but they may be more expensive because they require more extensive ongoing monitoring and documentation of environmental and ecological parameters in order to document compliance (Breyer, 1982; Besanko, 1987). In the context of bivalve mariculture, it may be most productive in many settings for the public managers to focus on carrying capacity issues (in the broad sense) at an appropriate ecosystem scale and from a performance standard perspective but to cast rules and regulations for growers in concrete, design-standard terms, especially where individual growers' production is small relative to local carrying capacity.

ESTABLISHED PRACTICES AND STANDARDS FOR MOLLUSC FARMING

BMPs dealing with environmental interactions seem to have been derived primarily from forestry and agricultural practices in response to concerns raised about soil erosion, nutrient loading, and waste outputs from feedlot operations. Likewise, BMPs for mariculture have generally been developed in order to minimize various potential interactions between the mariculture operation and environmental or ecological conditions, as well as interactions with the general public. Examples of the earliest versions of BMPs might be outreach brochures on husbandry techniques (e.g., Washington Sea Grant, 2002; Alaska Sea Grant, 2009; University of Maryland, 2009) to identify the optimal ways to culture bivalve molluscs. While many publications have focused primarily on methods to maximize production, they can be considered important precursors to current BMPs, in that they required a good understanding of local environmental or ecological conditions, as well as an understanding of the interaction of specific culture methods with environmental conditions (e.g., productivity, predation minimization, shelter).

A variety of BMPs and standards have been developed by non-governmental organizations (e.g., the World Wildlife Fund), regulatory authorities (state and federal), and producer organizations to address issues in mollusc farming (Table 2.1). BMPs for bivalve mariculture range from dealing with general principles to local issues. Broader BMPs are developed with a view to serving national or international audiences.

TABLE 2.1 Examples of Best Management Practices and Performance Standards for the Farming of Bivalve Molluscs Produced by a Range of Organizations, Demonstrating the Range of Topics and the Variety of Subjects Covered

Author	Affiliation
U.S. Agency for International Development	Regulator, nongovernmental organization, and academia
World Wildlife Fund	Nongovernmental organization
U.S. Department of Agriculture	Regulator
State of Virginia	Advisory agency, regulator, and industry
Pacific Coast Shellfish Growers Association	Industry
Seafish (UK)	Regulator, industry, and advisory agency
State of Massachusetts	Industry, regulatory, and advisory agency
Maryland Aquaculture Coordinating Council	Industry, regulatory, and advisory agency
Ireland	Industry and advisory agency
Florida Department of Agriculture and Consumer Services	Regulator
International Council for the Exploration of the Sea	International convention
Maine Aquaculture Association	Industry
National Oceanic and Atmospheric Administration	Regulatory
Creswell and McNevin (2008)	Academia

Scope	Scale	Reference
Generic guidelines and environmental interactions	International	Boyd et al., 2008
Environmental interactions	International	World Wildlife Fund, 2008; 2009
Policy on organic certification and environmental interactions	National	Belle et al., 2008
Environmental interactions and permitting	State	Oesterling and Luckenbach, 2008
Policy and environmental interactions	Regional	Pacific Coast Shellfish Growers Association, 2001
Alien species interactions	National	Syvret et al., 2008
Environmental interactions, permitting, and husbandry	State (local)	Leavitt, 2004
Environmental interactions, permitting, and husbandry advice	State	Maryland Aquaculture Coordinating Council, 2007
Generic environmental interactions	National	Irish Seas Fisheries Board, 2003
Permitting and environmental interactions	State	Bronson, 2007
Alien species interactions	International	International Council for the Exploration of the Sea, 2005
Environmental interactions and permitting	State	Maine Aquaculture Association, 2006
Environmental interactions and policy	National	National Oceanic and Atmospheric Administration, 1998; Shumway and Kraeuter, 2000
Generic guidelines, environmental interactions, and husbandry	International	Creswell and McNevin, 2008

By their nature, these broader BMPs are usually non-technical and general in orientation, identifying a range of broad environmental goals or principles. As such, they are unlikely to address effectively the specific issues that present themselves to regulatory agencies and the producers, particularly when these are local in origin and context and have to be considered on a much smaller scale. Consequently, these are best seen as generic guidelines that highlight a range of general principles and present a suite of possible solutions to universal and common issues (i.e., the toolbox approach). Other BMPs deal with more regional issues, and yet others specifically consider the day-to-day operations at farms and their interactions. These locally oriented guidelines can provide important advice on pertinent laws and ordinances and focus on important local issues (e.g., environmental interactions, stakeholder interactions, community relationships). In summary, all of the BMPs serve some purpose, and while the origins of BMPs are varied, they are almost all driven by the ultimate goal of producing molluscs under the broader umbrella of sustainability. They can identify solutions that range from farm- or small-scale measures to broader societal solutions focusing upon competing uses and values.

While the focus and goals of BMPs in the mariculture of bivalve molluscs are varied, there are some general characteristics that they share. Many of them are fluid and subject to constant review and adjustment to arrive at more sustainable, effective, and acceptable conditions. Further, it is important to note that BMPs are not a proxy for performance (Clay, 2008); just because they are adhered to does not mean that they necessarily meet goals for reducing impacts on the ecosystem. As previously indicated, many of the concerns presented by bivalve mariculture are local in origin, and although management plans or husbandry practices may be derived from empirical field measurements, the adoption of broad-scale, general BMPs may have little or no impact in terms of measureable environmental improvements. This is especially true given the variety of methods used to culture bivalve molluscs and the range of environmental conditions under which the culture operations are carried out. The implementation of a BMP or a code of practice is no guarantee of success (i.e., to maintain or improve environmental conditions) and informs little in the absence of meaningful monitoring information to assess its efficacy. At the same time, the implementation of some BMPs will increase costs associated with the culture of molluscs. This can affect the price competitiveness of molluscs grown under restrictive BMPs that are costly to implement relative to molluscs grown without BMPs, especially in markets accessible to international trade.

Importantly, most existing BMP approaches are more of a design standard (“do things this way”) than a performance standard (“achieve the following environmental objective”). It is worth noting that neither type

of standard is inherently more compatible with maintaining ecological integrity but that performance standards speak more directly to ecological integrity objectives. Because it is usually easier to verify a practice than to verify an effect, BMPs have the advantage of lower administrative burden for demonstrating compliance but have the drawback that there is no guarantee of environmental benefit. Clay (2008) suggests that BMPs in isolation are perhaps on the way out as management strategies with a move toward performance standards, which focus less attention upon how the objectives are achieved and more on the end result (e.g., acceptable level of environmental impacts as a condition for continuing the culture operation). Examples of performance standards for mollusc farming include minimum and maximum permissible levels of nutrients in the water, turbidity, or changes in abundance of local native species. (Other examples of such standards can be found in Schulze [1999].) Nevertheless, the value of a BMP as a marketing tool is likely to remain. For example, the Marine Stewardship Council (MSC) utilizes an “environmental standard” to certify fisheries (Marine Stewardship Council, 2002) as sustainable by specifying a combination of management practices, performance goals, and general design standards. MSC certification and labeling serve to educate the public on the importance of sustainable seafood practices and purchasing and are seen as marketing tools by seafood producers. In addition, some BMPs have been proven to maintain efficiency and hence profitability, while reducing environmental impacts (e.g., the use of triploid oysters in order to mitigate against successful reproduction and spread in areas where the oyster is nonnative) (Nell, 2002; Syvret et al., 2008). However, it must be acknowledged that no one BMP would be sufficient to cover the spectrum of issues that are place specific or address the variety of bivalve mariculture practices and technologies.

USEFUL CHARACTERISTICS OF BEST MANAGEMENT PRACTICES AND STANDARDS

BMPs or performance standards are intended to limit the risk of undesirable ecological effects to an acceptable level. BMPs are often general and can be cast as design standards, which may or may not be enforceable by legal or regulatory means. BMPs alone can be useful in promoting sound practices and as marketing tools, but they are of limited use in the pursuit of specific ecological objectives. Performance standards are likely to be more efficient (in economic terms) in the long run because they provide incentives for mollusc farmers to optimize their technology and processes, but they may be more expensive to comply with and enforce because they require more extensive monitoring and documentation of environmental and ecological parameters in order to document

compliance. Both performance standards and BMPs have an appropriate role in the context of bivalve mariculture. In many settings, the local or regional public managers are best positioned to consider the effects of mariculture at the relevant ecosystem level and can focus on carrying capacity issues at that scale from a performance standard perspective to ensure that ecological effects remain within acceptable limits. They can then translate these ecosystem-scale performance standards into concrete design-standard terms akin to BMPs for growers, especially where individual growers' production is small relative to ecosystem carrying capacity. The central objective of avoiding undesirable ecological effects through standards and practices requires a detailed understanding of these effects, and much of this report deals with what is known about them and where the remaining uncertainties lie. A useful concept in considering the effects in aggregate is that of carrying capacity, a measure of the level of mollusc farming that a given area can sustain before certain limits on effects are breached. In many cases, it will be useful for those designing future practices and standards to think in terms of carrying capacity. As discussed in Chapter 5, carrying capacity concepts extend to social and economic as well as ecological considerations, and they require dealing with trade-offs, risk, and uncertainty. Managing for carrying capacity therefore requires a political process that is informed by science and that ensures the balanced representation of stakeholder views. A focus on carrying capacity strikes at the heart of the issue of ecosystem impacts and can clarify to regulators and the public the explicit trade-offs that are being made in regulatory decisions. Increasing transparency in environmental management has the benefit of enabling broader stakeholder and public participation and thereby insuring that the industry is not left to regulate itself because they alone possess the power of knowledge.

Estimates of carrying capacity are likely to be uncertain, and carrying capacity is subject to change over time as ecosystem and socioeconomic circumstances change (see Chapter 5). BMPs and regulations that are linked to carrying capacity must take this into account, and that can be done by framing the standards and their application within a context of adaptive management (Holling, 1978; Williams et al., 2007). Adaptive management is a structured, iterative process of making resource management decisions (in this case, the decision to permit a certain level of change in environmental parameters related to carrying capacity or to permit a certain level of bivalve production) when there is uncertainty about the nature or extent of the ecosystem response. For example, a BMP might call for mariculture to be permitted initially so as to produce what is anticipated to be a modest harvest volume relative to carrying capacity and for the volume of permitted mariculture to be increased over time as

uncertainty about ecological effects is reduced. This approach requires ecological monitoring programs to be designed to collect information that will systematically reduce uncertainty.

FINDINGS AND RECOMMENDATIONS

Finding: Performance standards are generally more efficient than BMPs because they allow for innovation and track ecosystem responses. However, implementation of performance standards usually involves additional, and potentially costly, requirements for monitoring and enforcement. Many of the issues surrounding bivalve shellfish mariculture are location specific and may not be addressed effectively by broad national standards. Technically oriented BMPs have in some cases been shown to increase efficiency and hence profitability, while reducing environmental impacts. However, no single BMP or standard can address the many contingencies raised by different mariculture techniques, the species in culture, and the environmental conditions that are unique to various regions or sites.

Recommendation: Performance standards that set parameters based on carrying capacity (size of population or biomass that the environment can support; see definition in Chapter 5) should be developed and implemented at the ecosystem level because they can be applied to bivalve mariculture more generally with adjustments for the specific conditions of each mariculture operation, species, and culture technique.

Recommendation: Management of bivalve mariculture should employ performance standards to address carrying capacity concerns at the scale of the water basin but may find the use of BMPs to be more practical and efficient at the local scale, especially where the industry consists of large numbers of small growers.

Finding: Estimates of carrying capacity are likely to be uncertain, and carrying capacity is subject to change over time as ecosystems and socioeconomic circumstances change.

Recommendation: BMPs and regulations that are linked to carrying capacity must take uncertainty and change into account, which can be done by framing the standards and their implementation within a context of adaptive management, reviewing them at regular intervals, and changing them as additional information becomes available.

3

Ecological Effects of Bivalve Mariculture

The role of suspension-feeding bivalves in estuarine and marine ecosystems has been extensively documented through research in ecology, physiology, biogeochemistry, mariculture, interdisciplinary marine science, and fisheries science. Suspension-feeding bivalve molluscs consume at the lowest trophic level, feeding largely as herbivores (Duarte et al., 2009). This chapter is divided into three sections to characterize: (1) the biological activities of molluscs (whether wild or cultured) and the effects of their biogeochemical modifications and habitat provision; (2) the incidental impacts of bivalve mariculture operations on multiple components of the ecosystem caused by mariculture structures and activities and by the biological activities of the molluscs; and (3) consequences of actions taken by culturists to alter ecological interactions purposely to manage the effects of pests, competitors, and predators on mariculture systems. The purpose of these sections is to illustrate issues that have been or could be addressed in best management practices—a complete description of the ecosystem services provided by molluscs in both natural systems and in mariculture is provided in Chapter 7 (also see National Research Council, 2009). The last section of the chapter (Uncertainties, Unknowns, and Recommended Research) summarizes issues where additional research will be necessary to determine ecosystem impacts and develop effective mitigation approaches.

BIOLOGICAL EFFECTS OF MOLLUSCS: BIOGEOCHEMICAL CYCLING AND HABITAT PROVISION

Benthic suspension feeders, such as many species of bivalve molluscs, influence the nutrient and organic coupling of benthic and pelagic systems (Dame, 1996) through their ability to filter a wide size range of particles and deposit organic wastes that sink to the bottom (biodeposition). Suspension-feeding bivalves perform this function in a range of habitats and physiographic conditions (e.g., estuaries, lagoons, coastal oceanic systems) where they filter out and deposit significant amounts of suspended material, as well as excrete dissolved nutrients. In estuarine systems, the influence of benthic suspension-feeding bivalves on benthic-pelagic coupling, turbidity, nutrient remineralization, primary production, deposition, and habitat complexity has been well documented (reviewed in Dame and Olenin, 2005). Kaiser (2001) reviews the effects of molluscan cultivation on the ecology of systems, identifying a similar set of mechanisms of influence, and concludes that such processes have a generally positive influence on the overall water quality of a system. Suspension-feeding bivalves also drive many other biogeochemical processes and cycles, which are well described for intertidal oysters by Dame (2005).

Nutrient Dynamics

Molluscs influence nutrient dynamics through direct excretion and indirectly through microbially mediated remineralization of their organic deposits in the sediments (McKindsey et al., 2006a). Therefore, nutrient regeneration is related to the abundance and location (shallow versus deep water) of bivalves in a system. The extent to which this affects overall nutrient budgets and thus primary production is related to the system flushing rate and residence time (Dame, 1996; Newell et al., 2005). The subsequent proportions of elements in the system will influence the levels of recycling and possibly result in one or more being limited (Dame, 1996).

The majority of studies of bivalve effects on nutrient recycling have focused on nitrogen because this is the most common nutrient-limiting biological production in marine and estuarine systems (Parsons et al., 1983; Howarth, 1988; National Research Council, 2000). Benthic bivalves are important contributors of nitrogen (usually in the form of ammonium, NH_4^+) to both subtidal and intertidal systems. Nixon et al. (1976) conclude that nitrogen flux across oyster reefs is highly variable and is heavily influenced by tidal flow. Dame (1986) reviews a body of work relating to nutrient fluxes involving *Crassostrea gigas* in northern France and concludes that 15–40% of nitrogen in the system was derived from the oysters. In addition, measured values were always higher than the estimated values, likely due to remineralization occurring in adjacent

sediments. The suggestion that macroalgal cover of mussel beds will intercept nitrogen (Asmus and Asmus, 1991), thereby making it unavailable for phytoplankton production, has also been proposed for other systems (Mazouni et al., 1998; Lin et al., 2005; see Wadden Sea box in Chapter 4). In contrast, nitrogen is retained within some systems through direct recycling of nitrogen from bivalves (e.g., *Crassostrea virginica*) to phytoplankton (Dame and Libes, 1993; Newell et al., 2005). Numerous studies have demonstrated that nutrients derived from biodeposits and/or excreted nitrogen serve to enhance growth of eelgrass and other submerged aquatic vegetation (see below).

In the Marennes-Oléron culture region in France, Leguerrier et al. (2004) show that higher oyster production increased benthic-pelagic coupling, which in turn increased secondary production (in the form of meiofauna), providing food for juveniles of predatory nektonic species. Also, Mazouni (2004) and Newell et al. (2005) demonstrate that other planktonic organisms (bacteria, ciliates, and flagellates) can act as sources of nitrogen for bivalve molluscs in the absence of suitable autotrophic phytoplankton.

Phosphorus is important to biological systems, and phosphorous budgets constructed in and around mollusc assemblages show considerable removal of this nutrient from the system through biodeposition. Asmus et al. (1990) demonstrate that mussel beds with large macroalgal populations released less phosphate than beds without a large macroalgal component. Silicon is an important element for diatoms and can be limiting in systems dominated by diatoms. Bivalve molluscs contribute to recycling of silicate through transfer of this nutrient from the water column to the sediment with little being sourced from the bivalves (Prins and Smaal, 1994). Molluscs, such as mussels, may also selectively feed on components of particulate matter and thereby concentrate certain metals like copper in their pseudofeces (Allison et al., 1998).

The production of pseudofeces in large quantities is an important mechanism by which bivalves couple the water column to the bottom (see review in Dame, 1996). Epifaunal bivalves (oysters and mussels) have a plastic response to increasing levels of plankton and detritus in the water column with ever-increasing filtration capacity and production of pseudofeces. However, this response is not observed in infaunal bivalves (clams and cockles), which regulate ingestion rates at high-sediment concentrations by adjusting clearance rates rather than by increasing production of pseudofeces (e.g., Foster-Smith, 1975; Bricelj and Malouf, 1984; Bricelj et al., 1984; Prins et al., 1991; Iglesias et al., 1996). Oysters and mussels are also known to tolerate relatively high levels of suspended inorganic particles and continue to filter and produce higher levels of biodeposits.

The positive and negative feedback mechanisms observed in aquatic systems as a consequence of nutrient dynamics mediated by molluscs

have been the subject of numerous studies (Dame, 1996; Prins et al., 1998; Newell et al., 2005). Their high filtration capacity, rapid response to high levels of food (e.g., plankton), and relative permanence in aquatic systems give bivalves the ability to stabilize systems and enhance resilience to perturbations (Jackson et al., 2001a; Newell, 2004). Large bivalve assemblages can regulate the abundance of phytoplankton in shallow seas (see Newell et al. [2005] and McKindsey et al. [2006a] for list of relevant studies), and intense filtering can reduce phytoplankton bloom intensity while extending the duration of less intense blooms (Herman and Scholten, 1990). Filtration and biodeposition of phytoplankton and other suspended materials by extensive beds of bivalves also reduce downstream transport, thereby moderating effects of excess nutrients or sedimentation in outlying waters. Thus, bivalves provide the system with a capacity to buffer against sudden perturbations (DeAngelis et al., 1986; Jackson et al., 2001a; Lotze et al., 2006). The large-scale removal of bivalves from a system has resulted in some well-documented shifts in system processes and has contributed to general degradation of water quality or, more appropriately, a reduction in the resilience of the system to perturbations like nutrient loading and sedimentation (e.g., oysters in Chesapeake Bay; see Newell et al. [2005, 2007] and Pomeroy et al. [2006]).

Many estuaries, such as Chesapeake Bay, and coastal oceans suffer from eutrophication, in which excess nutrients enter waterways from land-based sources and atmospheric deposition (e.g., sewage treatment plants, farm animal wastes, agricultural use of fertilizers, industrial releases of nitrogen oxides or ammonia) and trigger massive blooms of phytoplankton and other algae. Phytoplankton blooms reduce water clarity and deplete the water of oxygen as they die and decompose. Bivalves can reduce excessive growth of phytoplankton and, at high density, can counteract symptoms of eutrophication, thereby improving local, and in some cases downstream, water quality. Yet many bivalve molluscs have been depleted by overfishing, especially oysters (Jackson et al., 2001a; Kirby, 2004; Lotze et al., 2006; Beck et al. 2009), but also clams (Peterson, 2002; Krauter et al., 2008) and scallops (Peterson et al., 2008). Consequently, augmenting suspension-feeding bivalves, preferably native, through restoration and mariculture has the potential to enhance suspension-feeding activity and controls in systems where natural populations have been depleted (Jackson et al., 2001a).

Biom mineralization

In addition to nutrient cycling, molluscs contribute to biogeochemical processes through shell formation, which captures carbon in the form of calcium carbonate and can lead to sequestration of carbon in marine

sediments after natural mortality of wild molluscs or terrestrial burial of shells after consumption of wild-caught or cultured molluscs. The shells of molluscs (living and dead) accumulate in various types of structures in estuarine, coastal, and oceanic systems (Shumway and Kraeuter, 2000). Surface shell accumulations provide a range of ecosystem services, primary among which are structural habitat (e.g., refuge, complexity) and erosion reduction (Coen and Grizzle, 2007).

Shell is also an important source of sedimentary carbonate content. The carbonate budget of estuarine and coastal waters is now of concern because of extensive shell extraction (through mollusc harvesting and mining for construction), the prohibitive cost of long-term continuous substrate provisioning to support fisheries, and the loss of shell via reduced bivalve populations resulting from fishing and disease processes (Mann and Powell, 2007). Moreover, growing ocean acidification caused by increasing concentrations of atmospheric CO₂ has serious implications for seawater carbonate chemistry (Brewer, 1997; Caldeira and Wickett, 2003; Feely et al., 2004; Doney et al., 2009). Recent studies have shown that bivalve growth, development, and survival are negatively affected by decreased pH (e.g., Berge et al., 2006; Fabry et al., 2008; Kurihara, 2008). The change in carbonate water chemistry and concomitant decrease in viability of bivalve molluscs potentially will reduce both the provisioning and persistence of shell in coastal and estuarine systems, particularly those in high-latitude areas with low alkalinity seawater (Feely et al., 2004; Lee et al., 2006). Availability of abundant mollusc shells in the surface sediments can provide local buffering against increasing acidity.

The importance of the interactions between ecological communities and sedimentary carbonate content was articulated in a conceptual model that described a positive feedback process between benthic molluscs and carbonate addition to the sediments. The taphonomic (process of fossilization) feedback hypothesis underlying this conceptual model (Kidwell and Jablonski, 1983) states that increasing shell content encourages settlement of calcifying organisms, and their deaths increase the rate of carbonate addition, forming a positive feedback process. Recent studies have shown that the interaction between carbonate content and community dynamics is critical to ecosystem dynamics in estuarine systems (Gutierrez et al., 2003; Powell et al., 2006; Powell and Klinck, 2007). The species benefiting most are the carbonate producers, particularly bivalves that, through their own deaths, provide a critical sedimentary constituent promoting the long-term survival of their species.

Shell is an essential component of present-day estuarine and coastal ecosystems; however, it is not a stable resource (Powell et al., 2006). Shell must be continually renewed and will disappear rapidly if the processes that support this renewal are slowed or stopped. Carbonate loss possibly

exceeds gain in shallow-water marine ecosystems today (see discussion in Powell et al. [2006]). It is likely that current environmental conditions and commercial mariculture practices, when coupled with predicted changes, such as ocean acidification, will facilitate and accelerate carbonate loss in estuarine and coastal systems. Thus, management of shell-producing commercial species must also include management of the habitat that will maximize production of carbonate. Long-term sustainability of mollusc stocks depends upon the maintenance of a positive shell budget for carbonate, as well as provision of habitat that supports recruitment, growth, and survival of bivalves. Mariculture of bivalve molluscs can contribute favorably to shell production and preservation in coastal ecosystems if the operators return the shell resource to the environment after harvest. However, regulations requiring the return of shells to the estuarine, lagoonal, or coastal bottom after shucking may be required to achieve this goal.

Habitat Creation and Maintenance

Shell adds hard substrate and habitat complexity to soft substrates, thereby increasing species diversity (Wells, 1961; Larsen, 1985; Coen et al., 1999; Harding and Mann, 2000; 2001; Mann, 2000; Gutierrez et al., 2003) and enhancing recruitment and survival of bivalves (Haven and Whitcomb, 1983; Abbe, 1988; Kraeuter et al., 2003; Bushek et al., 2004; Green et al., 2004; Soniat and Burton, 2005). When present in significant amounts, shell adds bottom-habitat complexity to the ecosystem (Haven and Whitcomb, 1983; DeAlteris, 1988; Grizzle, 1990; Powell et al., 1995; Allen et al., 2005). Fish have been shown to associate with both biogenic and artificial structures on the bottom, such as eelgrass, bivalve reefs, and the legs of oil platforms, as a consequence of attraction to structured habitat for protection or feeding (Franks, 2000; Heck et al., 2003; Peterson et al., 2003; Coen and Grizzle, 2007; Horinouchi, 2007; Jablonski, 2008).

Seagrasses are often considered to be an extremely important plant in estuaries and lagoons where they form emergent structural habitat for fish and invertebrates in these soft-sediment systems (Jackson et al., 2001b; Williams and Heck, 2001; Heck et al., 2003; Bostrom et al., 2006). Local improvements in water clarity induced by filter-feeding bivalves can promote the spread of eelgrass, especially to depths where light would otherwise be limiting (Dennison et al., 1993). Augmentation of nutrient concentrations in sediments can also stimulate eelgrass growth, as has been shown to occur for eelgrass growing alongside mussels in Europe, Florida, and southern California (Reusch et al., 1994, Reusch and Williams, 1998; Peterson and Heck, 1999; 2001a, b). Many estuaries on the west coast of the United States are flushed with relatively nutrient-rich ocean waters, and under these circumstances, eelgrass may not benefit as

much from the additional nutrients released by bivalves (Dumbauld et al., 2009). Both the reduction of turbidity and fertilizing effects of bivalve molluscs have been demonstrated experimentally for modest densities (16 per m²) of hard clams (*Mercenaria mercenaria*) in a relatively oligotrophic Long Island estuary (Carroll et al., 2008). Positive effects of a modest number of suspension-feeding bivalves are more likely to benefit eelgrass in relatively oligotrophic water bodies, where functional enhancement of water clarity may be achieved without a huge increase in filtering capacity (Carroll et al., 2008).

IMPACTS OF MARICULTURE OPERATIONS ON ECOSYSTEMS

Organic Loading by Cultured Bivalve Biodeposits

Several factors contribute to the rate of production of biodeposits, including the distribution, density, and the species of bivalves coupled with environmental conditions, such as food concentrations, water temperature, turbidity, and feeding rates of the bivalves (Jaramillo et al., 1992; Dame, 1996). Rates of accumulation or dispersion of the biodeposits also depend on water movements close to the seafloor (Widdows et al., 1998; Callier et al., 2008). Generally, mariculture activities in well-flushed intertidal areas are likely to result in dispersal of the organic biodeposits, whereas subtidal mariculture in quiescent areas has the potential of producing a greater accumulation of biodeposits and consequently a greater localized impact on the benthos. The vast majority of the literature pertaining to organic enrichment has focused on mussel farming. Most studies have concluded that the effect of bivalve mollusc farming is relatively small and much less than that caused by finfish farming where organic matter is added to the system as food (e.g., Baudinet et al., 1990; Grant et al., 1995; Buschmann et al., 1996; Cranford et al., 2007; Zhang et al., 2009). Only a few studies have characterized organic loading from mollusc farms as high (e.g., Dahlbäck and Gunnarsson, 1981; Mattsson and Linden, 1983; Metzger et al., 2007), and these are cases in which cultured mussel densities are high and/or tidal circulation is low.

Bivalve Mariculture Effects on Aquatic Plant Life

Culture operations for bivalves interact with aquatic plants through displacement of seagrass by the cultured bivalves and associated culture structures, through disturbance caused by shellfish planting and harvesting, through provision of unnatural hard substrates involved in culturing, through physical modification of flows regimes and sediments, and through water clarification and nutrient delivery to the bottom. Facili-

tation of benthic plants can occur when bivalve molluscs or associated culture structures provide attachment sites for macroalgae, the growth of which provides ecosystem services (habitat and nutrient sequestration; DeAlteris et al., 2004; Luckenbach and Birch, 2009). Eelgrass and other submerged aquatic vegetation (SAV) species can benefit from increased light penetration that expands the range of suitable bottom for occupation by SAV and from fertilization of the plants with biodeposits, as discussed earlier. In addition, bivalve mariculture activities can have negative effects on SAV. In Willapa Bay, total production of eelgrass was lower in areas with oyster mariculture (Tallis et al., 2009). The relative growth rate of eelgrass was unaffected by the presence of oysters or geoducks in Willapa Bay and Totten Inlet, respectively. However, in these examples, shoot size varied and may have been responding to increased porewater ammonium or reduced intraspecific competition when molluscs were present (Dumbauld et al., 2009; Tallis et al., 2009). Augmentation of sediment nutrient concentrations is known to stimulate eelgrass growth in some locations (see earlier section, Habitat Creation and Maintenance). Theoretically, high levels of biodeposits could lead to toxic sulfide concentrations, but this has only been shown to occur when conditions were already eutrophic (Vinther et al., 2008). Finally, bivalve culture can stimulate growth of several species of macroalgae (DeCasabianca et al., 1997; Vinther et al., 2008), which can in turn negatively affect seagrasses (Hauxwell et al., 2001).

Seagrasses are subject to multiple anthropogenic disturbances, which have been shown to be at least partly responsible for a general worldwide decline in their abundance (Orth et al., 2006; Waycott et al., 2009). Seagrasses are highly susceptible to rapid changes in their environment because of their requirement for high-incident light levels and their restriction to relatively shallow nearshore coastal waters (Dennison and Alberte, 1985; Orth et al., 2006). Eelgrass, *Zostera marina*, is one of the more common species studied in relation to bivalve mariculture because of its worldwide distribution in temperate seas. The upper distributional limit of *Z. marina* is determined primarily by desiccation (Boese et al., 2005) and the lower limit determined by light penetration, which is affected by turbidity in the estuary. *Z. marina* distribution overlaps directly with the area where most bivalve culture occurs, extending to almost -10 m where water clarity is high on both coasts of the United States (Phillips, 1984; Moore et al., 1996; Thom et al., 2003; Kemp et al., 2004). The enhancement of water clarity by suspension-feeding bivalves thus relieves an intrinsic limitation to the spread of eelgrass.

In some areas, mollusc culture operations and aquatic vegetation compete for space. However, this relationship is not one-to-one. In Willapa Bay, Washington, an apparent threshold has been detected above which

eelgrass declined by more than the area covered by ground-cultured oysters, while at lower levels of oyster cover, eelgrass was more abundant than predicted from simply the amount of space available (Dumbauld et al., 2009). Part of the threshold effect has been attributed to the severing of eelgrass blades by the sharp tips of the oyster shells (Schreffler and Griffen, 2000), reducing its percent cover and possibly reproductive capacity. Shading from overwater structures is another form of negative interaction. Work conducted by Everett et al. (1995) in Coos Bay, Oregon, found 100% loss of eelgrass directly under oyster racks, presumably resulting from shading and sediment erosion (10–15 cm at the base of the structure). Smaller reductions in eelgrass cover and density have been documented with other forms of off-bottom culture, such as long-lines and stakes, but losses tended to scale with density or spacing and were restricted primarily to the area beneath lines and stakes where shading or sedimentation occurred (Everett et al., 1995; Rumrill and Poulton, 2004; Tallis et al., 2009). In one of the few landscape-scale studies that monitored changes for a long period of time, eelgrasses in Bahia de San Quentin, Mexico, did not decline as might be expected from shading by oyster culture racks (Ward et al., 2003).

Benthic Invertebrates

The degree to which benthic invertebrate populations and communities are impacted by bivalve mariculture is typically related to the scale of operation, the species and culture techniques being used, and the physical and hydrodynamic characteristics of the culture site. As a result, scientific studies demonstrate a broad range of responses of benthic infauna to mariculture, ranging from no or moderate negative effects to positive effects. In addition to the relatively complex nature of the impacts of bivalve culture on benthic invertebrate populations and communities, many of the studies have focused only on the grow-out phase of cultivation rather than assessing all aspects of the cultivation process (Kaiser et al., 1998). For instance, although collection of wild mussel seed for most commercial cultivation is done by the use of spat collectors, in a few locations (e.g., Maine in the United States, the Wadden Sea in Germany and the Netherlands, the Irish Sea) seed is harvested by bottom dredging in subtidal areas (see Box 4.2 on the Wadden Sea), resulting in greater impacts on benthic habitat. Lastly, disturbances to benthic habitats associated with routine maintenance, harvesting, and handling of the molluscs are also not normally evaluated in published studies. Much of the research regarding the effects of bivalve mariculture on benthic invertebrate populations has focused on the following two areas: (1) effects of increased organic loading to the sediments from bivalve biodeposits and (2) habitat

modification associated with the off- and on-bottom mariculture gear (e.g., racks, cages, bags) and the replacement, reduction, or enhancement of the local fauna by the cultivated bivalve species. The relative influence of each of these on benthic habitats varies depending upon the factors previously mentioned.

Habitat Modification and Alteration of Benthic Communities

Bivalve culture can modify benthic habitats in a number of positive and negative ways. For example, growing a species on the seafloor (e.g., oysters) increases habitat structure and enhances local biodiversity relative to soft-sediment landscapes (e.g., Ferraro and Cole, 2007). Folke and Kautsky (1989) suggest that large-scale mussel culture can result in structural changes in marine ecosystems by indirectly affecting the recruitment of other commercially important species. In addition, adult bivalves can remove larvae of some invertebrate species through their filtering activities. Pechenik et al. (2004) demonstrate that adult Pacific and European flat oysters were capable of filtering the larvae of the slipper shell snail, *Crepidula fornicata*, although ample numbers of *C. fornicata* larvae survived through settlement and metamorphosis. Similarly, Troost et al. (2008) show that an escape response was elicited when Pacific oyster and blue mussel larvae were subjected to suction currents similar to those of adult Pacific oyster feeding currents. However, both studies acknowledge that experimental conditions were not necessarily reflective of natural conditions where many other factors come into play. Thus, the potential for high-density bivalve culture to impact recruitment of benthic species with planktonic larvae requires further study.

Structures used in some types of mariculture operations, such as racks, bags, and ropes, can increase biodiversity by providing more habitat for fouling species (e.g., Powers et al., 2007) but also can alter the hydrodynamics of an area to some degree (see review by Kaiser et al. [1998]). These structures can redirect water flow and produce either scouring or accretion of sediment around the structures, depending on the local hydrodynamic regime (Hecht and Britz, 1992; Everett et al., 1995). At an intertidal Pacific oyster farm in Dungarvan Bay, Ireland, tides and strong currents around the farm site prevented organic enrichment beneath oyster trestles by dissipating biodeposits, but in access lanes that were subject to compaction and dispersal of the sediment by boat traffic, the species composition and abundance of certain epibenthos and infauna differed significantly when compared with those parameters at a distant control site (de Grave et al., 1998). Castel et al. (1989) note that Pacific oyster culture on suspended racks in Arcachon Bay, France, increased sedimentation and enhanced the accumulation of debris (e.g., shells, macroalgae). An investi-

gation of the effects of two types of oyster mariculture on sediment surface topography by Everett et al. (1995) found that stake culture resulted in a significant increase in sediment deposition, whereas rack culture resulted in more erosion compared with reference sites.

Re-seeding large areas of the seabed with cultured or wild-collected bivalve seed stock and then harvesting market-sized individuals by dredging is common culture practice in many parts of the world (e.g., United States, France, the Netherlands, Ireland, Japan). Dredging has been widely reported to cause significant habitat and community changes (Dayton et al., 1995; Jennings and Kaiser, 1998; National Research Council, 2002). Dankers and Zuidema (1995) found that the most obvious impact of mussel culture on the Dutch Wadden Sea environment was dredging of seed mussels, which reduced the food supply for several bird species (see Chapter 4 for a more detailed discussion of harvest effects and Box 4.2 on the Wadden Sea as a case study). In some regions, the culture area is also mechanically worked to remove predators and prepare the substrate for re-seeding. For example, in Japan, re-seeded scallop beds are scraped with a “mop” to remove predators. Relatively large areas (e.g., square kilometers) can be affected, and the mopping activity can substantially alter the benthic epifaunal community structure.

Fish and Mobile Crustaceans

Studies of bivalve mariculture operations, mostly off-bottom, have shown higher abundances of some fish and crustaceans in areas with mariculture structures in comparison to nearby areas with unstructured open mudflats, eelgrasses, or even nearby oyster reefs and rocky substrates, although eelgrass generally harbors more unique species (DeAlteris et al., 2004; Clynick et al., 2008; Erbland and Ozbay, 2008). A study of flatfish behavior showed that juvenile sole utilized oyster trestles for protection during the day and foraged over adjacent sand flats at night (Laffargue et al., 2006). A number of studies have documented the positive influence of suspended mussel mariculture on food resources and therefore abundance of large macroinvertebrates and fish (Freire and Gonzalez-Gurriaran, 1995; D'Amours et al., 2008). A study in Narragansett Bay, Rhode Island, found that scup (*Stenotomus chrysops*) grew slightly faster on adjacent rocky habitats than in oyster mariculture bottom cages; tagging suggested that they had greater fidelity to the oyster cages (Tallman and Forrester, 2007).

Powers et al. (2007) demonstrate that densities of fish and free-swimming invertebrates in North Carolina are as high over cultured clams in plastic bottom net bags (and associated fouling epibiota) as in eelgrass beds, with much lower fish and invertebrate densities over

unvegetated bottoms. However, abundance estimates are not necessarily an indication of how structured habitats benefit fish because structures can attract fish without enhancing their productivity (e.g., reproduction, growth, survival). This is the classic “production versus aggregation” debate. Nevertheless, experimental research has shown that artificial reef structures provide nektonic organisms with protection against predation, thereby offering a survival advantage, especially to more vulnerable juvenile life stages (Dempster and Taquet, 2004). Also, gut contents reveal that demersal fish associated with structures are consuming organisms found on and enhanced by the availability of the hard substrates (Posey et al., 1999; Peterson et al., 2003).

Studies of fish around bivalve mariculture operations in U.S. west coast estuaries provide useful insights into the interactive processes that may occur between mariculture structures associated with bivalve mariculture and mobile species. In Humboldt Bay, California, oyster long lines were found to harbor more fish than either eelgrass or open mudflats (Pinnix et al., 2004). In Willapa Bay, Washington, few statistically significant density differences were found among the more than 20 species of fish and crabs collected at intertidal locations when oyster bottom culture, eelgrass, and open mudflats were compared (Hosack et al., 2006). In both studies, some individual species like tube-snouts (*Aulorhynchus flavidus*) were more abundant in structured habitats. In a preliminary study submitted as a project report to the National Park Service (Elliott-Fisk et al., 2005), Wechsler (2004) examined the potential effects of oyster mariculture on fish communities in Drakes Estero, California. No significant differences in fish abundances or species richness were detected among three sampling sites; however, there was an indication that fish assemblages were modified near oyster racks by enhanced numbers of the guild characterized as “structure-associated fishes.” This pattern was driven primarily by increases in one species (kelp surfperch, *Brachyistius frenatus*), typically associated with hard substrate (Wechsler, 2004; Elliott-Fisk et al., 2005).

Larger mobile invertebrates have also been shown to display modified species-specific and even life-stage-specific behaviors around structure. In one study, juvenile Dungeness crabs (*Cancer magister*) utilized artificial structures, but older individuals utilized open mudflats, whereas red rock crabs (*Cancer productus*) preferred on-bottom oyster culture structures (Holsman et al., 2006).

Genetics of Bivalve Molluscs

The following are three areas in which bivalve genetics are pertinent to the development of best practices for mariculture: (1) domestication

and genetic improvement of molluscs for mariculture; (2) genetic impacts of translocations or introductions of molluscs; and (3) genetic impacts of interbreeding between hatchery stocks and wild populations, such as might arise in either bivalve restoration programs or commercial mariculture.

Bivalve mariculture is faced with the dual challenge of becoming more efficient (producing more from less area) and of adapting to a changing ocean. Genetic improvement and domestication are proven routes to increase the efficiency of agricultural production across a range of environments, but research toward these ends in bivalve mariculture is in a primitive state. Unique challenges are, moreover, presented by the high fecundity of these animals.

Though cultivated since Roman times (Günther, 1897), bivalve molluscs are in a proto-domestication phase (Harris and Hilman, 1989): diverse species are no more than exploited captives (Clutton-Brock, 1981; Duarte et al., 2007). Obvious candidates for concerted domestication efforts are the seven bivalve molluscs among the top-40 species of global aquaculture (*C. gigas*, *Ruditapes philippinarum*, *Patinopecten yessoensis*, *Sinonovacula constricta*, *Mytillidae*, *Anadara granosa*, and *Perna viridis*), yet the knowledge base for domesticating and improving these top-producing bivalves is shockingly narrow. A principal limitation to assessing genetic improvement and domestication is a lack of basic, detailed, mariculture statistics. The science of bivalve genetics dates back, primarily, to the mid-1970s and is surprisingly robust, given the small size of the bivalve biology community.

Work on bivalve population genetics to date has focused primarily on geographic subdivision and the causes of marker-associated heterosis (superiority of marker heterozygotes to homozygotes with respect to growth, survival, and other fitness traits) in natural populations (e.g., Zouros et al., 1980; Fujio, 1982; Buroker, 1983; Gaffney, 1994; Zouros and Pogson, 1994; Bierne et al., 1998; David, 1998; Launey and Hedgecock, 2001); heterosis in yield—the product of growth and survival—in experimental populations (Hedgecock et al., 1995; Hedgecock and Davis, 2007); the heritability of production characteristics, mostly in oysters (Lannan, 1980; Newkirk, 1980; Sheridan, 1997; Langdon et al., 2003; Dégremont et al., 2007); and the development of genomic approaches to understanding complex traits and physiological ecology, mostly in oysters and mussels (Hedgecock et al., 2005; Saavedra and Bachere, 2006; Hedgecock et al., 2007a; Gaffney, 2008; Gracey et al., 2008; Tanguy et al., 2008).

Most bivalve genetic diversity resides in natural populations, from which mariculture stocks are derived continuously. As demonstrated by early allozyme studies and reinforced now by numerous DNA studies, bivalves are among the most genetically variable animals. This diversity extends to additive genetic variance in quantitative traits, such as

response to selection, as has been recorded in studies of disease resistance (Hershberger et al., 1984; Haskin and Ford, 1987; Dégremont et al., 2007) and yield (Langdon et al., 2003). Non-additive genetic variance is also important in highly fecund bivalves, as evidenced by yield heterosis (hybrid vigor) in the Pacific oyster that is as dramatic as that in maize (Shull, 1908; Crow, 1998), even in crosses among inbred lines derived from the same wild population (Hedgcock and Davis, 2007). Yield heterosis is associated with equally dramatic inbreeding depression (Evans et al., 2004), attributed to a remarkably large load of deleterious recessive mutations (Bierne et al., 1998; Launey and Hedgcock, 2001). Inbreeding depression can easily eliminate or reverse gains from selection. A large mutational load in bivalves was predicted by Williams (1975), in the Elm-Oyster model for the advantages of sexual reproduction in species with high fecundity and high early mortality. Since high fecundity and high early mortality are the dominant life history features among marine fish (Winemiller and Rose, 1992) and invertebrates (Thorson, 1950), considerable scope for genetic improvement likely lies in crossbreeding of inbred lines.

The best practice for bivalve breeding is to take advantage of both additive genetic variance, through selection, and non-additive genetic variance, by identification of selected inbred lines for crossbreeding. Development of genomic resources promises to accelerate discovery of phenotypic-genotypic associations, the genes underlying economically important traits, and methods for determining the breeding or crossbreeding values of broodstock at early life stages (Pace et al., 2006; Hedgcock et al., 2007a).

Since the oyster and other bivalve industries have shifted heavily toward use of triploids because non-reproductive oysters enhance production (Nell, 2002)—also a welcome trend for minimizing impacts on natural populations, as discussed below—breeding programs seek to improve triploid, as well as diploid, seed. Triploid seed is currently produced by fertilizing diploid eggs with sperm from tetraploid males (Guo et al., 1996; National Research Council, 2004). Existing tetraploid stocks of the Pacific oyster were derived haphazardly from a rather narrow genetic base of wild diploid oysters. To take full advantage of additive and non-additive genetic variance for yield, breeders will need to build new tetraploid lines that incorporate good genes and genetic combinations from diploid lines. Biosecurity of reproductively competent tetraploid stocks in the environment is an issue that is just beginning to be addressed (Piferrer et al., 2009); early experience with tetraploid Pacific oysters suggests that they are not robust enough, at present, to have a negative impact on reproductive success of diploid stocks.

Even when native molluscs are used in mariculture, the natural genetic structure can be disrupted via interbreeding between wild and cultured

genotypes, potentially jeopardizing wild populations by decreasing their adaptive potential (Lynch, 1991; Allendorf et al., 2001). The risks depend on the amount of genetic divergence between the wild and cultured populations. Marine molluscs, with widely dispersing planktonic larvae, typically show minimal genetic divergence over broad scales (Hedgecock et al., 2007b). The Eastern oyster (*C. virginica*) is a notable exception, with a major genetic discontinuity between Gulf of Mexico and Atlantic populations (Buroker, 1983; Reeb and Avise, 1990; Karl and Avise, 1992; Cunningham and Collins, 1994; McDonald et al., 1996). A regional sub-population divide along the mid-Atlantic coast has, further, been identified with molecular markers (Hoover and Gaffney, 2005; Gaffney, 2006) and may correspond with the races identified earlier on physiological grounds (Loosanoff and Nomejko, 1951; Barber et al., 1991). Although genetic impacts from historical translocations of Eastern oysters have yet to be reported, the precautionary approach dictates that proposed translocations ought to be preceded, at least, by a determination of the population genetic structure of the target species (Bell et al., 2005; Ward, 2006) and, ideally, also by quantitative analysis of local adaptation.

The majority of marine bivalve molluscs share a suite of life-history traits—relatively late maturation, high fecundity, small eggs, long-lived plankton-feeding larvae with relatively high-dispersal potential, and broad geographic ranges (Winemiller and Rose, 1992)—that renders them more vulnerable to loss of variation and extinction than might be expected from their sheer abundance (Palumbi and Hedgecock, 2005). Reproductive success, because it involves a complex chain of events for molluscs, may vary dramatically among individuals, perhaps even among individuals adjacent to one another in space but spawning at slightly different times. Consequently, reproductive success in marine organisms is hypothesized to resemble, at times, a sweepstakes lottery, in which there are a few big winners and many losers (Hedgecock, 1994). Support for this hypothesis has come from both empirical (e.g., Li and Hedgecock, 1998; Hauser et al., 2002; Turner et al., 2002; Hedgecock et al., 2007c; Lee and Boulding, 2007; 2009) and theoretical (Waples, 2002; Hedrick, 2005; Eldon and Wakeley, 2006; Sargsyan and Wakeley, 2008) studies. The conservation implication is that even abundant bivalve stocks may have effective population sizes (as reflected in genetic diversity) that are orders of magnitude smaller than census sizes and, thus, rates of genetic drift and inbreeding that can erode biodiversity on ecological time scales.

Adverse interactions of wild and hatchery-propagated stocks are growing with the global expansion of mariculture for finfish, such as salmon (McGinnity et al., 2003; Hindar et al., 2006), and stock enhancement programs, including shellfish restoration efforts (Born et al., 2004; Gaffney, 2006). High fecundity and large variance in reproductive suc-

cess in hatchery stocks (Gaffney et al., 1993; Boudry et al., 2002) create a risk of diluting the genetic diversity of wild populations with hatchery-propagated bivalves (Allen and Hilbish, 2000; Gaffney, 2006).

One way to eliminate the risk of interaction between wild and hatchery stocks is to render farmed stocks sterile. Triploidy is commonly induced in bivalves to reduce reproductive effort, divert energy to growth, and improve meat quality during the normal spawning season (Allen and Downing, 1986; Nell, 2002). Because triploids are effectively sterile, their use in bivalve mariculture dramatically reduces but does not eliminate the risk of spawning and mixing with local native or naturalized stocks. If an introduced or farmed species is a nonnative, however, triploidy may offer only a short-term reduction in the risk of an introduction (National Research Council, 2004). Gene knockout offers another means of sterilization (Grewe et al., 2007; Wong and van Eenennaam, 2008), but public resistance to genetically modified organisms makes this a less attractive strategy.

Introduced Species

To augment or replace depleted natural stocks or to diversify the number of species used in mariculture operations, managers of molluscs in the past have employed translocations of native species and introductions of nonnative species. No new nonnative bivalves have been introduced for mariculture purposes for several decades (Naylor et al., 2001), although introduction of the nonnative Asian oyster (*Crassostrea ariakensis*) was proposed by Virginia and Maryland as a strategy for replenishing the oyster population in Chesapeake Bay (National Research Council, 2004). Virginia and Maryland have since decided not to move forward with the introduction of the Asian oyster following the U.S. Army Corps of Engineers' preferred alternative for the use of native Eastern oysters over the nonnative Asian oyster in restoration activities (U.S. Army Corps of Engineers, 2009). The introduction of nonnative species in mariculture has also been responsible for the unintentional importation of other nonnative species (i.e., "hitchhikers"). In most cases, current bivalve mariculture best management practices prevent the unintentional introduction of hitchhiking species.

There are several reviews on the importation of nonnative molluscs for mariculture (e.g., Andrews, 1980; Chew, 1990), particularly Pacific oysters (*C. gigas*) (Coleman, 1996; Shatkin et al., 1997; Ruesink et al., 2005). In some instances, these importations have resulted in the establishment of naturalized (breeding) populations of the nonnative molluscs that has affected resident oyster species. For example, there is evidence that naturalized populations of *C. gigas* have become a significant competitor of

native oyster species in France (Gouletquer and Heral, 1991), Australia (Ayles, 1991), New Zealand (Dinamani, 1991), and the western United States (Trimble et al., 2009). While it should be noted that not all nonnative shellfish introductions have led to negative consequences on the native species, nonnative species often exhibit faster growth rates than equivalent native species (e.g., *C. gigas*; Ruesink et al., 2005) and thus are apt to be superior competitors for resources. However, some faster growers, such as the triploid Asian oyster (*C. ariakensis*), allocate fewer resources to shell thickness and are thus more susceptible to predation by crabs and perhaps other predators (Bishop and Peterson, 2006).

In addition to affecting native, economically important species, culturing of nonnative bivalve species may influence native biodiversity, have direct and indirect influences on local community composition, and influence the performance of ecosystems with resultant economic impacts. Although there is a burgeoning literature cataloging and assessing the impacts of introduced species in coastal waters (e.g., reviews of Carlton, 1985; 1987; 1989; Ruiz et al., 1997; 1999; 2000; Grosholz, 2002), Ruesink et al. (2005) note there is a surprising lack of information on the effects of nonnative oyster introductions on community- and ecosystem-level structure and function and on how similar the ecosystem services provided by nonnative species are to native species. There also appears to be a similar general lack of knowledge regarding the impacts of other nonnative bivalve species (e.g., clams and scallops) that are commonly used in mariculture operations (Whiteley and Bendell-Young, 2007). The National Research Council (2009) details the impacts and risks of nonnative species introductions, focusing on Pacific oysters.

Several practices are used to reduce the risk of the establishment of naturalized populations from nonnative cultured bivalves, including the use of triploid seed or the culture of bivalves in areas with low potential for the establishment of a wild population. To date, the use of triploid nonnative bivalves on a commercial basis has largely been restricted to *C. gigas*, and in 2002, about one-third of the “eyed larvae” (i.e., larvae that have an eye spot and a foot, which indicate readiness to set on a growing surface) produced by U.S. west-coast hatcheries were triploids (Nell, 2002). Interest in mariculture of the nonnative oyster *C. ariakensis* in Chesapeake Bay led to considerable research for improving techniques to reduce the percentage of reversion of triploid oysters toward diploidy, as well as screening procedures to reduce the risk of inadvertent introduction of reproductive *C. ariakensis* (Allen and Bureson, 2002). As discussed in an earlier report on nonnative oysters (National Research Council, 2004), there is no federal statute establishing criteria for deliberate, nonnative marine species introductions. States have the authority to set criteria for introductions, but “the existing regulatory and institutional frame-

work is not adequate for monitoring or overseeing the interjurisdictional aspects" of nonnative marine species introductions (National Research Council, 2004). As mentioned above, Virginia and Maryland have decided to forego the use of *C. ariakensis* in mariculture to focus instead on the restoration of the native *C. virginica* oyster.

Intentional introductions of nonnative molluscs have also resulted in the unintentional transfer of a wide variety of other nonnative plants and animals that "hitchhiked" with the introduced shellfish (Carlton, 1992a, b). For instance, it has been estimated that about 20% of the nonnative species found in San Francisco Bay are the result of shipments of Eastern (*C. virginica*) and Pacific (*C. gigas*) oysters, particularly during the early 19th century. Some of these species have become important predators and competitors of the resident fauna and flora, as well as pests in mariculture operations.

In recent years, tighter controls have been invoked for the importation and transfer of nonnative shellfish species around the world. A Code of Practice for the introduction of nonnative species, developed by the International Council for the Exploration of the Seas (ICES), has been adopted in many countries (Sinderman et al., 1992). The Code requires that the species being considered for introduction be studied in its native habitat for known pests, predators, and diseases, as well as for its biological characteristics, such as genetic makeup. Only broodstock of the nonnative species may be brought into the recipient country and only into quarantine facilities for breeding so that only first-generation offspring can be released into open waters after testing to ensure that no diseases or pests are present.

In response to the past decade's rich scientific literature on the negative impacts of nonnative "hitchhikers" on shellfish production and on the altering of structure and function of the native populations and communities (see review of Ruesink et al. [2005] for the Pacific oyster), bivalve mariculture industry practices have been adopted to reduce the potential spread of nonnative species. For instance, the use of hatchery-reared seed on the U.S. west coast, coupled with the application of the ICES protocols, can greatly reduce the risk of co-introductions.

Molluscan Diseases

When nonnative oysters were brought to the U.S. west coast in the early 20th century, regulatory agencies and the shellfish industry were not fully aware of the threat posed by diseases carried by the imported bivalve mollusc stock (Sinderman, 1984). The resulting introductions of exotic diseases created a number of persistent problems that still have not been solved (e.g., Andrews and Frierman, 1974; Naylor et al., 2001; Bower, 2006).

Current industry practices are designed to prevent the spread of molluscan diseases associated with the use of nonnative species (e.g., Elston, 2004; Office Internationale des Epizooties, 2006). The culture of native species is frequently recommended as an alternative to reduce or avoid harmful interactions among cultured nonnatives and wild species (e.g., Naylor et al., 2001). This strategy does not, however, preclude epidemiological and genetic impacts on the resident populations of conspecifics. Diseases naturally present at low densities in wild populations can achieve epidemic status in culture (e.g., Multinucleated Spore X [MSX] disease in oysters [*C. virginica*; Ewart and Ford, 1993], Quahog Parasite X [QPX] disease in northern quahogs [*M. mercenaria*; Lyons et al., 2007]).

The importance of disease management and prevention is well recognized in the mariculture community (see Office Internationale des Epizooties, 2006). Typically regional and or national guidelines and policies exist to reduce the potential introduction or transfer of a disease agent or parasite to a new location. In addition to these policies, the World Organization for Animal Health via representatives from member countries develops health management plans, policies, and diagnostic methods for known (and also novel) disease agents.

Numerous examples of disease transfer via movement of infected stocks have been documented (Harvell et al., 1999; Burreson et al., 2000; Naylor et al., 2001). In the majority of these cases, the fact that the translocated animals harbored a disease agent was unknown, as a consequence of either a lack of basic knowledge of the diseases themselves or inadequate testing and monitoring before translocation. Approaches to successful health management of any species, wild or cultured, is predicated on prior knowledge of typical symbiotic, commensal, and pathogenic organisms associated with that species. The consensus among human and animal health experts is that such baseline health data are lacking for most species impacted by a disease (Haaker et al., 1992; Harvell et al., 1999). Without this information, it is difficult to predict potential health problems, such as disease outbreaks, or to determine the source of emerging epidemic infections. For instance, no baseline data were available for abalone (a gastropod not a bivalve, yet relevant to this problem) in California prior to the outbreak of withering syndrome in 1985 (Haaker et al., 1992). Because of the complexity of the host–parasite relationships and the variability among abalone species, it was difficult to establish which among several newly observed parasites was the causative agent of the withering syndrome outbreak (Haaker et al., 1992; VanBlaricom et al., 1993; Friedman et al., 1993; 1997; 2000; 2007; Gardner et al., 1995; Moore et al., 2000; 2001). In addition, the identification and understanding of new or emerging diseases is dependent on baseline data; emergent disease has been frequently associated with both climatic change and anthropogenic

activities, including animal movements associated with molluscan mariculture (Friedman and Perkins, 1994; Harvell et al., 1999; Burrenson et al., 2000; Daszak et al., 2001; Naylor et al., 2001).

Clearly, adequate baseline information on the presence or absence of particular pathogens is crucial to the management of both wild and cultured stocks because it allows us to identify both potentially problematic pathogens and the locales in which they occur. When Pacific oysters were brought to the U.S. east coast after successful culture on the west coast, the oysters failed to thrive, but a parasite that infects Pacific oysters, *Haplosporidium nelsoni* (MSX), came with them and became established in the native Eastern oysters, *C. virginica* (Burrenson et al., 2000). Because MSX appears to cause little disease and mortality in adult Pacific oysters, it had not been detected in the Pacific oyster. However, the same parasite causes a fatal disease in the Eastern oyster that has contributed to the population decline in many areas of the east coast, such as Chesapeake Bay and Delaware Bay (Andrews, 1976; Ford and Haskin, 1982; Friedman et al., 1991; Ford, 1992; Friedman, 1996; Burrenson et al., 2000). In Australia, a recently observed (December 2005 to present) herpes-like virus has caused severe losses of wild abalones, and a lack of baseline health information has made it impossible to determine whether the pathogen emerged from native stocks or was introduced (Hooper et al., 2007; Carolyn Friedman, personal observation). Similar deficiencies in background information have been observed in many marine species (Harvell et al., 1999).

In the aquatic environment, invertebrate hosts and pathogens are subject to many abiotic stressors, such as thermal shifts related to climate (Harvell et al., 1999; 2002; Daszak et al., 2001). A thermal shift as small as 1°C can alter the dynamics of a disease from causing minor infections and little disease to population-wide epidemics (Harvell et al., 2002; Burge et al., 2006; 2007; Travers et al., 2008a). For example, significant alterations in host–parasite dynamics have been observed in recent years associated with climatic changes and small thermal increases in several species of marine gastropods (abalones: *Haliotis* spp.) with bacterial pathogens, such as *Vibrio* spp. (Travers et al., 2008b), rickettsia-like organisms (e.g., Moore et al., 2000), and viruses (Burge et al., 2006; 2007). Alternatively, thermal increases may reduce the pathogenicity and associated disease load if the ambient temperature is beyond the tolerable range of the parasite (Lafferty, 1997).

Birds, Marine Mammals, and Marine Turtles

Mariculture can have both positive and negative effects upon populations of large marine vertebrates, such as birds, marine mammals, and marine turtles. Almost all research on these interactions has focused on

finfish farming and the economic and ecological impacts that result from depredation (e.g., Nash et al., 2000). Of the limited research on the impact of bivalve mariculture on wildlife populations, most relate to bird populations. Three published studies explore impacts on marine mammals (Markowitz et al., 2004; Watson-Capps and Mann, 2005; Becker et al., 2009), but they were not designed specifically to detect ecological impacts on these species, and only Becker et al. (2009) relate to bivalve mariculture methods currently used within the United States. No published studies on potential interactions with marine or estuarine turtles were identified.

Drawing upon a broader understanding of the ecology of these species, potential impacts of bivalve mariculture upon these wildlife populations have been identified in one published review (Kemper et al., 2003). In addition, a National Oceanic and Atmospheric Administration workshop (Moore and Wieting, 1999) explored broader interactions between mariculture and marine mammals and marine turtles, and a discussion paper on the potential effects of mussel farming on marine mammals and seabirds was produced by the New Zealand Department of Conservation (Lloyd, 2003). The potential impacts identified from these sources are summarized in Table 3.1. It should be noted that direct demonstrations of these impacts are rare, and in most cases, potential effects are therefore predicted from the best existing information.

Entanglement in fishing gear and marine debris is a major cause of mortality for seabirds, marine mammals, and marine and estuarine turtles (Lewison et al., 2004; Read et al., 2006). Entanglement in mariculture gear appears to be rare, but two Bryde's whales have reportedly died in separate incidents after entanglement in mussel spat collection ropes in New Zealand (Lloyd, 2003), and marine turtles have also been entangled in ropes (Godley et al., 1998; Kemper et al., 2003). The introduction of any lines or netting, for example to exclude predators, may therefore pose a risk of entanglement to birds, marine mammals, and marine and estuarine turtles. Where bivalve mariculture operations expand into offshore areas, this may increase the likelihood of interactions with large whales and sea turtles, which are protected in the United States under the Endangered Species Act. Based on experience with other types of mariculture and fishing operations, the risks of entanglement can be reduced by using heavier lines and ensuring that lines and anti-predator nets are kept taut.

Ingestion of marine litter is also known to cause mortality in birds, marine mammals, and marine turtles (Derraik, 2002). Mariculture operations are recognized as a major source of marine litter (Johnson, 2008). For example, young Australian gannets in New Zealand's Marlborough Sound have been found entangled in rope ties from mussel farms that have been incorporated into their nests (Lloyd, 2003).

Mariculture activity may also influence prey availability for birds,

TABLE 3.1 Summary of Potential Impacts of Bivalve Mariculture on Birds, Marine Mammals, and Marine Turtles (Modified from Lloyd, 2003)

Impact Type	Impact Source
Entanglement	Farm structures Litter from farms
Ingestion	Litter from farms
Changed prey abundance	Phytoplankton depletion Biofouling of farm structures
Habitat exclusion	Farm structures Disturbance from workers or boat traffic
Creation of shelter or resting places	Farm structures

marine mammals, and marine and estuarine turtles in several ways. As discussed earlier, the presence of culture bags will alter the structure of benthic communities and the extent of eelgrass beds, indirectly affecting prey availability. Also, Manila clam cultivation in bags negatively affects the use of favored foraging areas by oystercatchers (Godet et al., 2009). Alternatively, farm structures may increase food availability by providing a substrate for biofouling organisms suitable as prey, such as mussels. In British Columbia, for example, densities of Surf Scoter (*Melanitta perspicillata*) and Barrow's Goldeneye (*Bucephala islandica*) were positively associated with the presence of oyster farms (Žydelis et al., 2009). Because these species do not feed upon oysters, this association appeared to be driven by the high densities of mussels recorded on mariculture structures (Kirk et al., 2007). In this case, seaduck predation on wild mussels was not perceived as negative by shellfish farmers (Žydelis et al., 2009). However, experiments on natural mussel beds have shown that predation by eiders can reduce mussel biomass by 50% (Hamilton, 2000), demonstrating the impact that seaducks can have upon commercial mussel farms in some areas.

In intertidal areas, the presence of culture bags may directly exclude shorebirds that probe in the sediment from foraging habitat (Kelly et al., 1996). Würsig and Gailey (2002) also highlight the need to consider potential loss of feeding and breeding habitat for cetaceans due to the physical presence of bivalve mollusc farms, particularly given predicted increases in these facilities in inshore environments. Subsequent studies in Western Australia and New Zealand (Markowitz et al., 2004; Watson-Capps and Mann, 2005) indicate that bottlenose dolphins (*Tursiops* spp.) and dusky

dolphins (*Lagenorhynchus obscurus*) avoid farmed areas where oyster and mussel cultivation hanging lines are present.

Displacement from key areas may also result from disturbances attributable to the activities of mariculture workers (Becker et al., 2009). This disturbance may be caused directly by the presence of workers on intertidal areas or by boats associated with mariculture activity. In addition, marine mammals may respond to noise from mariculture-related boat traffic.

Mariculture structures can provide shelter, roost, or haul-out sites for birds and seals. This is unlikely to have negative effects on bird or seal populations, but it may increase the likelihood that these species cause fecal contamination of mollusc beds. It has also been noted that the presence of mariculture structures could attract juvenile marine turtles, which usually aggregate under patches of floating weed, thereby disrupting natural dispersal behavior (National Oceanic and Atmospheric Administration, 1999).

Information on the potential effects of mariculture outlined above is largely based upon a general understanding of wildlife ecology and the relationships of these species to the physical and biological environment rather than based upon directed studies built around mariculture operations. Even where studies have been carried out around shellfish farms, uncertainty over spatial and temporal variation in both the location of structures (Watson-Capps and Mann, 2005) and levels of disturbance (Becker et al., 2009) constrain the conclusions that can be drawn about the impacts of mariculture. However, there is less uncertainty about the general effects of “disturbance.” The tending of any mariculture operation requires a human presence, and many studies have used avoidance distances to establish buffer zones to minimize disturbance from other human activities (e.g., Rodgers and Smith, 1997; Blumstein et al., 2003). However, it is important to recognize that some species may not show marked avoidance if they lack suitable alternative habitat, even where the fitness costs are high, and disturbance costs may therefore be underestimated or unrecognized (Gill et al., 2001). Consequently, assessing whether disturbance has a population consequence, estimated as increased mortality or decreased fecundity, is a much more difficult proposition (Stillman et al., 2007). In addition, limited understanding of the foraging distribution of birds, marine mammals, and marine turtles from spatially localized breeding colonies also makes it extremely challenging to assess population-level impacts of disturbance, entanglement, or habitat loss resulting from bivalve mariculture. Thus, if there is increased mortality around a culture site, there could be consequences for breeding colonies hundreds of kilometers away.

PREDATOR, COMPETITOR, AND PEST CONTROL MANAGEMENT

Bivalve molluscs are cultured in the marine or estuarine environment, which exposes them to competitors associated with biofouling (i.e., undesirable sedentary organisms that settle on shells and mariculture structures, such as racks, stakes, lines, and bags) and to mobile competitors and predators, including other invertebrates, finfish, birds, and marine mammals. Growers have responded by developing control and management practices, including placing the bivalve molluscs on or under protective structures (i.e., racks, cages, bags, or under netting), physical removal of pests and predators, chemical control, and in some cases biological control.

Fouling Organisms

Biofouling is a common and potentially increasing problem for growers. Epifaunal mussels and oysters are especially vulnerable because their shells and culture structures provide hard substrate for settlement of fouling organisms, and such hard surfaces are often rare in soft-bottom estuarine and coastal systems. The fouling organisms, mostly filter feeders, reduce water flow and can compete with the cultured animals for food (Michael and Chew, 1976; Claereboudt et al., 1994; Taylor et al., 1997), although the magnitude of the effects, if any, will depend on location and species (Arakawa, 1990; Lesser et al., 1992; Ross et al., 2002; LeBlanc et al., 2003; Mallet et al., 2009). Several fouling organisms are nonnative species that came as hitchhikers with the introduction of the cultured bivalves (reviewed by McKindsey et al., 2007). Although current international protocols, typically enforced at the state level in the United States, have reduced unintentional species introductions associated with culture of nonnative bivalve molluscs, fouled hulls and ballast water releases associated with global trade and marine transport have resulted in more introductions of nonnative fouling organisms, including various species of algae and tunicates (e.g., the algae *Sargassum muticum*, *Undaria pinnatifida*, and *Codium fragile* and the tunicates *Didemnum* spp. and *Ciona intestinalis*).

Shellfish culture on the seafloor (e.g., oysters, mussels) or suspended off the bottom (e.g., oysters, mussels, scallops) adds substrate area for the colonization of a variety of native and nonnative fouling species or epibionts (e.g., barnacles, tunicates, sponges, bryozoans, macroalgae). In many benthic habitats, the hard substrate surface area provided by bivalve shells on the seafloor may be equal to or greater than the amount of natural inert hard substrate (Railkin, 2004), and it is well recognized that adding more structure to benthic habitats results in an increase in the overall biodiversity to those habitats (e.g., Dumbauld et al., 2001;

Peterson et al., 2003). In addition, off-bottom mariculture activities typically employ a variety of gear types that have the potential for greatly enhancing the abundance and diversity of species through greater provision of additional substrata for the colonization of fouling species. These include ropes and netting used in mussel culture; racks, trays, and bags used in oyster culture; and nets used in scallop culture.

While the addition of structure may increase overall local biodiversity in a system, as compared to unstructured habitats, there is evidence that the biofouling community structure can differ greatly from that on natural hard substrates (e.g., Karlson, 1978; Anderson and Underwood, 1994; Glasby et al., 2007). In addition, there is some evidence that artificial substrates may disproportionately favor the colonization of nonnative fouling species by increasing local sources of propagules of these species (Tyrrell and Byers, 2007). In some cases, the proliferation of nonnative biofoulers has resulted in reductions in local biodiversity (e.g., Blum et al., 2007), which have the potential to facilitate further invasions (Stachowicz et al., 2002) and to lead to potential alterations in population and community structure in coastal food webs (Byrnes et al., 2007).

While some studies have shown that cultured mollusc growth is unaffected (e.g., Lesser et al., 1992; Lopez et al., 2000) or even enhanced (Ross et al., 2002) by fouling, most studies have found that fouling results in reduced mollusc growth and survival and in increased costs to the industry (Watson et al., 2009). In one especially dire circumstance, the invasive tunicate *Ciona intestinalis* threatens 77% of Canadian mussel farms; at Prince Edward Island, some mariculturists may lose their livelihoods (Edwards and Leung, 2009). Because biofouling by both native and nonnative species increases production costs for the industry, several practices have been developed and implemented to reduce or control it. The general trend is to use techniques that reduce labor costs, ensure product quality, and minimize potential environmental impacts. Techniques include mechanical, chemical, and biological control methods with mechanical and chemical techniques being the most common methods used to remove fouling species from cultured bivalve molluscs and mariculture gear (Watson et al., 2009) (Box 3.1). However, specific applications and their effectiveness typically depend upon the species being cultured, the nature and degree of the biofouling community, and the local environmental conditions. For instance, one-minute exposures to vinegar are 100% effective in mitigating *C. intestinalis* biofouling (Carver et al., 2003).

Biofouling Mitigation Methods

Growers use various methods to control biofouling, most often based on physical removal or inhibition by turning over nets and bags (Mallet et

BOX 3.1 **Removal of Fouling Organisms**

Proliferation of fouling organisms (primarily tunicates) on mariculture gear and on oysters is a major economic issue for shellfish farmers. Many methods have been used in an attempt to control this problem, including chemical treatments with saturated brine, sodium hydroxide, hydrated lime, acetic and citric acids, formalin, detergents, and chlorine, as well as physical treatments using air drying, ultraviolet light, steam, hot water, electricity, smothering, pressure washing, and puncturing (Carver et al., 2003; Coutts and Forrest, 2007; LeBlanc et al., 2007; Locke et al., 2009). Removal of fouling organisms on mariculture gear is done almost universally over the water. The committee is not aware of any published studies on the impacts of the large-scale removal of fouling organisms and of disposal at sea or in the estuary on the marine pelagic or benthic environments near shellfish farms. The level of ecosystem impact would likely depend on the intensity of fouling, the season and spatial scale of removal efforts, and the health and character of the receiving aquatic ecosystem. Experienced bivalve farmers employing divers have reported that the added organic materials are either washed away quickly by tidal flow, are consumed by benthic scavengers, or are quickly dissipated by currents (Robert Rheault, personal communication). Because most of the fouling organisms being removed from mariculture gear are tunicates of a high-saltwater content, the potential for land-based removal for composting is considered small.

al., 2009) but sometimes by using antifouling agents and other chemical treatments (e.g., acetic acid brine) that are typically applied as dips and followed by brief aerial exposure of the affected organisms or structures (Shearer and MacKenzie, 1961; Huguenin and Huguenin, 1982; Carver et al., 2003; Forrest et al., 2007; LeBlanc et al., 2007; Locke et al., 2009). Some growers have experimented with biological control agents, such as crabs, littorinid snails, and even fish, but this method does not appear to have been widely adopted (Hidu et al., 1981; Enright et al., 1983; 1993; Cigarria et al., 1998). Physical removal of fouling organisms has the potential effect of spreading marine invasive species and increasing the bottom deposition of organic material when conducted over water. With proper disposal techniques, both physical and chemical treatments conducted offsite or in separate holding areas would have little additional environmental effects, but this is economically feasible only on the small scale. Impacts of direct application of chemical control agents in the field at larger scales have not been examined (see Shumway et al. [1988] for details on the use of calcium oxide).

Predators on Bivalve Molluscs

Predation on commercially raised bivalve molluscs, particularly small juveniles planted directly in marine or estuarine growing areas, continues to constrain mariculture in many areas. Predators range in size from diminutive flatworms to birds and mammals (Woelke, 1956; Jory et al., 1984). Some predators, such as the Japanese oyster drill (*Ocenebrellis inornatus*), were introduced along with the nonnative bivalves and have remained problematic for both cultured and non-cultured species (Chapman and Banner, 1949; Buhle and Ruesink, 2009). Birds are recognized predators and are often more abundant in areas with mussel culture than nearby controls (Caldow et al., 2004; Roycroft et al., 2004), yet the direct effect of bivalve mariculture operations on their behavior varies by species.

Predator Control Measures

Where depredation of the cultured species is a problem, farmers use a wide range of both passive (Dionne et al., 2006) and active deterrents (Ross et al., 2001; Thompson and Gillis, 2001) to reduce losses (Table 3.2). These practices can in turn influence the distribution patterns and behavior of the species preying upon molluscs in their farms or upon other species coexisting in the area. If the use of anti-predator netting leads to entanglement or if shooting is used to reduce predation, these interactions may also result in a reduction in the abundance of affected predator populations. These interactions can raise both ethical and legal issues, particularly where migrating wildfowl or shorebirds are protected under international treaties. In the United States, turtles and some marine mammals are protected

TABLE 3.2 Techniques Attempted to Mitigate Sea Duck Predation on Bivalves

Technique	Challenge	Effectiveness	Cost
Exclusion nets	Fouling and predator mortality	Effective	Relatively high
Loud sounds	Habituation and battery life	Moderate	Expensive
Chemical deterrents	Effect duration	Effective	Unknown
Boat patrol	Habituation	Effective	Expensive, at large spatial scale
Biological methods (e.g., falcons, eagles)	Habituation	Minimal	Unknown

by the Endangered Species Act, and the Marine Mammal Protection Act prohibits the intentional killing or harassment of all marine mammals.

Shellfish growers have responded to predation threats primarily by providing physical protection measures like raising the bivalves off the bottom to protect them from crawling benthic predators or growing the bivalves in protective bags, under netting, surrounded by fences, in tubes, or by adding gravel and shell fragments to the substrate (Castagna and Kraeuter, 1977; Kraeuter and Castagna, 1985; Beattie, 1992; Thompson, 1995). Protective structures modify water flow; affect sediment deposition; provide attachment sites for fouling organisms; and some structures, such as racks, create shaded spots that inhibit the growth of seagrasses (Everett et al., 1995; Rumrill and Poulton, 2004; Tallis et al., 2009). Clam mariculture conducted in bags has been shown to affect sediment but not water column characteristics. Macroalgae and bryozoans attached to bags were shown to attract mobile invertebrates and fish (Powers et al., 2007). Predator netting can result in slightly enhanced sediment organic content but has little consistent effect on sediment grain size or presence of indigenous bivalves (Munroe and McKinley, 2007; Whiteley and Bendell-Young, 2007). Adding gravel and shell to the substrate in Puget Sound, Washington, appears to have site-specific effects on the benthic community, with a general trend of enhanced gammarid amphipod and nemertean abundance and reduced abundance of glycerid, sabellid, and nereid polychaetes (Simenstad and Fresh, 1995; Thompson, 1995).

Though mussels are sometimes grown under protective covering, they are still highly vulnerable, and thus both visual and acoustic deterrents to disturb birds that prey on mussels have been investigated (Ross et al., 2001) (see Table 3.2). These practices would seem to have little direct environmental impact but could change local predator-prey relationships.

In some cases, predators may be trapped, removed by hand, or mechanically removed. For example, starfish have been removed by towing mops, cotton bundles tied to a metal frame, across the bottom (MacKenzie, 1970). Chemical means of controlling predators on bivalve molluscs were extensively investigated in the 1960s (Loosanoff et al., 1960) and applied on small scales for oyster drills and sea stars (Glude, 1957; Huguenin, 1977; Shumway et al., 1988), but chemicals have been rarely used on large estuary-wide scales.

One exception has been the use of the pesticide carbaryl to control burrowing shrimp on oyster beds in Washington State (Feldman et al., 2000). The shrimp are not direct predators but strong bioturbators, which indirectly cause mortality by burying and smothering the oysters under sediment. Because this practice of poisoning has raised persistent concerns about effects on the resident ecological community, it has been studied reasonably well. Long-term changes in the structure of the com-

munity are driven by the removal of one ecosystem engineer (the shrimp) and replacement with another (oysters and even eelgrass; Dumbauld et al., 2001; Dumbauld and Wyllie-Echeverria, 2003). Bioturbation by shrimp oxygenates sediments, thereby accelerating degradation of organic matter and nutrient cycling (Dewitt et al., 2004; D'Andrea and DeWitt, 2009). Abundances of the commensal bivalve, *Cryptomya californica*, crashed after experimental ghost shrimp removal in a southern California lagoon, whereas recruitment of another bivalve (*Sanguinolaria nuttalli*) was dramatically enhanced (Peterson, 1977; 1984). The scale of ghost shrimp removal programs is small relative to the size of most estuaries where carbaryl is used. For example, <1% of the intertidal in Willapa Bay is treated annually, and the shrimp are abundant in untreated areas (at least 20% of the intertidal area in Willapa Bay; Dumbauld et al., 2008).

UNCERTAINTIES, UNKNOWN, AND RECOMMENDED RESEARCH

Ecological uncertainties associated with managing the environmental consequences of mariculture will depend on the species cultured, the characteristics of the resident ecosystem, and the scale of the culture operation. This section summarizes some of the areas in which additional research would help to address key questions about the ecological effects of molluscan mariculture to improve best management practices.

Nutrient Cycling and Carrying Capacity

The impact of a small mariculture operation (possibly defined by stocking density) on the ecological community in a large, well-flushed system will probably be undetectable relative to the natural “noise” of the system. With an increase in stocking density relative to the supply of food or other resources, the ecological effects could become measurable in at least three aspects. First, there could be direct competition for resources, especially food and space, between the farmed species and the other residents of the system. Second, the biodeposition of organic materials could induce local oxygen depletion and mortality of natural bottom invertebrates where shellfish loading is high and physical flushing low. Third, the cultured suspension-feeding bivalves could conceivably function as predators on the eggs and dispersing larvae of resident species. Knowledge of these effects is critical for evaluating system carrying capacity and addressing concerns about potential impacts on biodiversity.

Finding: Research that takes a broader landscape-scale and ecosystem-based approach would provide a better understanding of how the

scale and intensity of bivalve mariculture influence the natural ecosystem structure and processes. To achieve this goal, methods for accurate estimation of ecosystem carrying capacity will be vital. In addition, further study of the impacts of high-density (intensive) mariculture on local biodiversity would help decision makers and managers anticipate changes in the ecosystem that could influence social attitudes and public acceptance.

Recommendation: Efforts should be directed at studying effects of bivalve mariculture at appropriate landscape and ecosystem scales that would facilitate managing mariculture at these scales instead of current management scales, which often focus on the scale of the individual lease or even individual potentially impacted species.

Finding: Long-term sustainability of bivalve stocks depends upon the maintenance of a positive shell budget for carbonate, as well as provision of habitat that supports recruitment, growth, and survival. Mariculture of bivalves can contribute favorably to shell production and preservation in coastal ecosystems if the operators return the shell resource to the environment after harvest.

Recommendation: Programs should be developed to either encourage or require the return of shells (after shucking) to the estuarine, lagoonal, or coastal bottom to conserve and enhance shell resources, of particular importance as chemical buffers as the ocean acidifies further.

Seagrass Vegetation

Not much is known about the factors that cause seagrasses to alter their reproductive strategy (seed or spore production versus asexual expansion via rhizomes and blade growth); how plants respond to disturbance from bivalve mariculture operations relative to natural disturbances; and how response to disturbance varies by season (plant density varies naturally across seasons), location, environment, and species.

Finding: These effects need to be studied at larger spatial scales, such as an estuarine landscape, and over longer and more relevant temporal scales. This would facilitate spatially explicit management and in some areas might make it practical to manage bivalve mariculture to promote the growth and expansion of adjacent seagrass vegetation.

Recommendation: Future research efforts should assess how modification of habitat by bivalve mariculture affects aquatic vegetation and mobile fish and invertebrates at larger spatial and longer temporal scales, especially life stages of the guild(s) of fish and crustaceans

known to associate with structure and hard substrates. Additionally, mariculture structures, such as racks, lines, bags, and the cultured shellfish should be studied to determine whether they act only as attractants or also enhance productivity of species known to aggregate around structures.

Culture of Nonnative Molluscs

The use of nonnative species in bivalve mariculture is likely to persist in areas, such as the Pacific Northwest, where there is a long history of culturing nonnatives, such as the Pacific oyster and the Manila clam. In some cases, these nonnatives have become naturalized—reproductive populations have become established in ecosystems well removed from the immediate vicinity of the shellfish farms. Even in areas where the cultured species has not established a self-replicating population, there is still the possibility that the cultured nonnative bivalve may become naturalized. The presence of nonnative molluscs may suppress the recovery of native species. For example, Trimble et al. (2009) show conclusively that competent larvae of the native oyster *O. lurida* are lured into settling in unfavorable environments by the presence of shells of the nonnative *C. gigas*. This contributes to the lack of recovery of *O. lurida* populations even though remnant populations in some estuaries and lagoons reproduce annually. There are also risks associated with nonnative molluscs as vectors of invasion for hitchhiking species and disease agents that may affect economically important resident species, as well as having potential impacts on population-, community-, and ecosystem-level structure and function. The implementation of current nonnative bivalve transfer practices, such as the ICES Code of Practice, has greatly reduced the potential introduction of nonnative hitchhiking species. However, there are still concerns about the importation of pathogens and other organisms that may not be detected by normal screening procedures.

Finding: There is a need for the harmonization across states of importation regulations and health requirements prior to movement of animals, including transport involved in the sale of live molluscs. Education of those involved in conducting and regulating animal transfers across biogeographic regions in appropriate methods and concerns would help limit further the inadvertent transmission of disease agents.

Finding: Continued research efforts could develop appropriate culturing techniques for native bivalve species, as well as enhance ways of restoring and then sustainably managing depleted native stocks.

It is important to develop a better understanding of the potential of nonnative bivalve molluscs used in mariculture to become naturalized under changing environmental, climatic, and other conditions. Additionally, there is a general lack of information on community- and ecosystem-level responses to mollusc introductions and how those responses compare to native species.

Recommendation: To prevent unintentional and probably irreversible establishment of breeding populations of introduced species, mariculture operators should use sterile triploids as much as possible when they grow nonnative bivalves in areas where the cultured species either has not been introduced or has not established a reproductive population. More attention should be directed toward the eradication of undesirable nonnative species, and a greater emphasis should be placed on studies of ecosystem-level effects of nonnative bivalve introductions.

Bivalve Diseases and Genetics

Infectious diseases can be key drivers shaping local community structure and biodiversity. Despite this, parasites and pathogens are commonly overlooked or underappreciated elements of the ecology and biodiversity of many systems. Although the general roles of infectious diseases in population regulation are recognized, the roles of specific disease agents are often disregarded or have not been well studied (see review by Thomas et al. [2008]). Characteristics of the host, pathogen, and environment shape the ecology of infectious diseases and may cause dramatic fluctuations in populations. Although parasites and disease agents are natural components of ecosystems, their expression may be magnified or altered in an environment where animals are in high density. Such potential for changing impacts of parasites and diseases can be easily monitored in a bivalve mariculture setting. High densities favor parasite transmission via higher levels of parasite release and/or greater contact between infected and uninfected organisms (e.g., Stiven, 1964; Anderson and May, 1981). Many examples exist in which the introduction or transfer of marine molluscs has resulted in the inadvertent introduction of a pathogen (e.g., Elston et al., 1986; Burreson et al., 2000; Naylor et al., 2001; Friedman and Finley, 2003; Wetchateng, 2008). Should a parasite be introduced into a new environment with new potential hosts, one cannot predict the outcome of such encounters (Lafferty et al., 2004). In addition, with global climate changes, current host–parasite relationships that appear to be in equilibrium may shift in or out of favor for the parasite and result in epidemics or improved health in the host population(s).

Finding: Collection of baseline data on existing diseases and parasites is often lacking and is needed to determine the introduction or change in distribution, incidence, or infestation intensity of a disease or parasite. In addition, continued development of diagnostic methods will enhance our ability to discover new parasites and diseases and to diagnose infected individuals prior to potential movement to a new location.

Finding: Long-term research on developing and improving domesticated mollusc stocks is needed to make mollusc farming more efficient.

Recommendation: Such research should be coupled with research on reducing or eliminating interactions between wild and farmed populations (e.g., by inducing triploidy in hatchery-propagated stocks). Hatchery-based restoration efforts should proceed with caution, using best practices for minimizing genetic differences between planted and wild seed.

Interactions with Wildlife Populations

Information on the potential effects of mariculture outlined above is largely based upon a general understanding of wildlife ecology and the relationships of these species to the physical and biological environment rather than directed studies built around mariculture operations. In addition, limited understanding of the foraging distribution of birds, marine mammals, and marine turtles from spatially localized breeding colonies makes it extremely challenging to assess population-level impacts of disturbance, entanglement, or habitat loss resulting from bivalve mariculture.

Finding: Assessments of the impacts of disturbance from bivalve mariculture on birds, marine mammals, and marine turtles are constrained by insufficient baseline data on habitat use by these species and further, by a lack of data both on spatio-temporal variation in disturbance events and on the longer-term consequences of these disturbances on populations of these species.

Recommendation: Managers should recognize that previous studies have limited power to detect adverse effects of disturbance and that a precautionary approach should be taken in order to minimize potential disturbance. Future decision making would benefit from targeted research that incorporates spatially explicit studies of the activities of mariculturists; the individual behavioral responses of birds, marine

mammals, and marine turtles using these coastal habitats; and the population consequences of any observed behavioral changes.

Finding: Effective integration of bivalve mariculture and wildlife conservation interests into marine spatial planning requires a better broad-scale understanding of the distribution of the birds, marine mammals, and marine turtles. Finer-scale studies are also required to characterize the behavior and ecology of individual birds, marine mammals, and marine and estuarine turtles around mariculture sites and in relation to the activities of mariculture workers.

Recommendation: Opportunities should be identified to assess mariculture impacts on these species through controlled studies that are conducted before and after the development of shellfish farms. Focused studies should be done to identify management approaches that best minimize potential impacts upon birds, marine mammals, and turtles.

Finding: While integrated pest management is the broader goal, it is rarely being implemented, and the ecology and effects of pests, predators, and control practices are rarely evaluated, especially at spatial scales larger than an individual farm or portion thereof (e.g., for burrowing shrimp in west coast oyster mariculture; Dumbauld et al., 2006).

Finding: Despite early progress and much success with protective devices, substantial mortality of cultured molluscs at early life-history stages is still observed, and research is still needed on tools and best management practices for controlling pests and predators. Benthic community changes associated with removing predators are also understudied and largely unknown, and the effects of excluding predators are little studied at the estuarine-landscape scale.

Recommendation: Opportunities to assess the effects of pest and predator control practices on the wider benthic community and implement integrated pest management at this larger spatial scale should be pursued, especially where shellfish farms might be expected to have an effect at this scale.

4

Bivalve Mariculture Contrasted with Wild Fisheries

As understanding has grown of how seriously ocean ecosystems have been degraded by extractive fisheries and as many fisheries have proven unsustainable, attention has turned to mariculture, including bivalve mariculture, as a possible simultaneous solution to both problems. Perhaps bivalve farming can be done without the same levels of disruption of natural ocean and estuarine ecosystems that are associated with exploitative fisheries, and perhaps by wise and informed husbandry, bivalve culture could be sustainable. Testing the hypothesis that bivalve mariculture might have less impact on the natural ecosystem than the exploitation of wild stocks requires synthesis of the environmental consequences of bivalve mariculture as compared to wild-stock exploitation. This chapter examines these issues.

COMPARISON OF ECOLOGICAL EFFECTS OF BIVALVE MARICULTURE AND WILD-STOCK HARVEST

Probably the most serious environmental concern associated with wild-stock fisheries for bivalve molluscs involves the physical and biological impacts of mollusc harvest (Collie et al., 2000; National Research Council, 2002; Kaiser et al., 2006). The effects of harvesting bivalves for mariculture operations on the benthic community are similar to those of wild fisheries harvest in (1) removing target species, which can serve as important biogenic habitat structure, and (2) causing disturbance to the benthos, which operates to reset the community to an early successional

stage and exclude more long-lived species, especially epibiota. The harvest impacts vary with method, habitat type, species and size of response organism(s) being studied, and scale of the harvest activity (National Research Council, 2002; Kaiser et al., 2006). In wild mollusc fisheries, dredges or scrapes are normally used to capture epifaunal species (e.g., oysters, scallops, mussels), whereas hydraulic suction dredges or pumps are used to capture infaunal species (e.g., clams). In a review of fishing impacts, Kaiser et al. (2006) found that initial impacts to biota were small and short-lived; however, recovery was slower in muddy and especially in biogenic habitats (e.g., mollusc reefs, seagrass, coral) than in sandy coarse sediments that were subject to higher frequencies of natural disturbances. This was particularly true for the use of mechanical dredges and rakes versus harvest by hand, as numerous studies have demonstrated the significant habitat and community changes caused by these methods (Dayton et al., 1995; Jennings and Kaiser, 1998; Collie et al., 2000; Cranfield et al., 2001; National Research Council, 2002). The community effects and their persistence for small benthic organisms are generally related to mobility and generation time so prolonged effects are only apparent when the benthic fauna is sessile and/or relatively long-lived or when affected areas are so large as to break connections with the surrounding undisturbed habitat.

In many but not all cases, wild-harvest impacts are not directly comparable to bivalve mariculture because culture occurs in a location (shallow and even intertidal habitats) different from that of wild harvest (often deeper subtidal areas), and culturists often transplant harvested individuals from place to place. Bivalve culture can also occur in a different form (e.g., single oysters planted on a tide flat or mussels growing on a line or rack versus an oyster or mussel reef in a wild-harvest scenario) and is typically more concentrated in local areas favorable for growth than wild-stock molluscs. Impacts to wild oyster and mussel reefs are thus potentially more severe and longer lasting than mariculture harvest impacts, and both clam and oyster harvests from these reefs have been shown to cause reef degradation and more substantial losses to oyster resources than clams (Lenihan and Micheli, 1999; Lenihan and Peterson, 2004). Secondary impacts, especially to birds and the less mobile fish and invertebrates, that use the structured habitat for food and protection are also likely to be greater in wild-stock bivalve fisheries that disturb these reefs.

Because of the importance of aquatic vegetation as habitat for other organisms, the effects of harvest activity on these plants have been most studied (Waddell, 1964; Fonseca et al., 1984; Peterson et al., 1987; Orth et al., 2002; Neckles et al., 2005; Wisehart et al., 2007; Tallis et al., 2009). In general, the disturbance to seagrass habitat by mollusc harvest activities

should vary with seagrass species, disturbance scope, disturbance intensity, seasonal timing of disturbance, and sediment characteristics. Seagrasses can recover via lateral rhizome spread or via sexual reproduction and seed dispersal depending on location and species, and both natural and human disturbances have been shown to enhance sexual reproduction in seagrass (Marba and Duarte, 1995; Peterken and Conacher, 1997; Plus et al., 2003; Olesen et al., 2004).

For clam fisheries, effects of harvest appear related to the extent and depth to which sediment is disturbed. Several hard clam harvest methods have been shown to reduce eelgrass (e.g., *Zostera noltii* and *Z. marina*), including mechanical “clam kicking” with propeller wash (Peterson et al., 1987) with 65% reduction of eelgrass biomass and only limited recovery up to four years after disturbance, raking with seagrass loss varying by implement used but with full recovery in one year (87% loss for a bull rake and 47% loss for a pea digger; Peterson et al., 1983), and even hand digging when rhizomes became extensively fragmented (Cabaco et al., 2005). Intertidal clam harvest in Portugal resulted in two-fold higher seed production and an extended reproductive season for *Z. noltii*, which enabled it to recover from harvest within a year (Alexandre et al., 2005). Effects of recreational clam harvest using rakes on *Z. marina* were undetectable, but digging clams with shovels reduced eelgrass cover and biomass over the short term, although recovery occurred fairly rapidly (months) in Yaquina Bay, Oregon (Boese, 2002). An exceptional case of disturbance may be for geoducks in Puget Sound, Washington, where harvest excavation of these large clams in the wild and in culture operations penetrates to great depths (50–60 cm) using water jets, and these effects are currently being explored (Washington Sea Grant, 2007a; Straus et al., 2008; Box 4.1).

The initial impact and time to recovery have also been shown to be variable in studies of the effects of cultured oyster harvest on eelgrass on the U.S. west coast. Results of experimental harvest with a toothed metal dredge in Willapa Bay, Washington, showed 42% loss of *Z. marina* at a muddy site with relatively slow recovery (four years), while initial decline was only 15% at a sandier site and recovery occurred in one year (Tallis et al., 2009). Waddell (1964) found even more significant loss of eelgrass (up to 96%) with several passes of a suction dredge and a two-year recovery period in Humboldt Bay, California. When harvest occurred by hand, eelgrass production was shown to be higher than that on dredge-harvested beds (Tallis et al., 2009), but eelgrass production per unit area was driven by density and plant size and therefore lower in all harvested oyster mariculture beds than in nearby eelgrass reference areas. For large repeatedly disturbed areas, seed germination or asexual reproduction of remnant adults is required to restore eelgrass. Seed germination was high (>4 per m²), particularly on dredged beds in Willapa Bay, Washington

BOX 4.1 The Geoduck

The geoduck (*Panope abrupta*) is a very large (i.e., up to 25 cm with siphon fully contracted and up to 75 cm when extended) infaunal bivalve that when extracted from the sediment has a very large siphon and foot, which it is incapable of withdrawing into the security of its two valves. Geoducks can burrow to a depth of 1 m, are primarily subtidal in their distribution, and can live up to 150 years. They are viewed as having aphrodisiacal properties in Asia and support an \$80 million a year mariculture industry in Washington State and a \$35 million one in British Columbia. There is a lucrative, illegal subtidal harvest of wild stocks as well.

Geoduck mariculture is largely confined to the intertidal zone in Washington State, although subtidal tracts can also be seeded. The intertidal culture technique involves housing several juvenile or seed geoducks in a PVC pipe (at a seeding density of about 35,000 per acre or 3 pipes per m²) (Figure 4.1) and protecting the young clams from a host of potential predators with an evolving set of additional protective measures like plastic mesh screens. The crop cycle is about six years from planting to harvest. Harvest is achieved by liquefying the sediment with a high-pressure hose and manual extraction of the bivalve. A summary of geoduck biology, carrying capacity, parasites, disease, and possible genetic effects on wild conspecifics is available from Straus et al. (2008).



FIGURE 4.1. Arrays of geoduck culture tubes in 2004 in Case Inlet, Washington (used with permission from Jennifer Ruesink, University of Washington).

It is instructive to examine the minimally resolved public debate characterizing geoduck mariculture in Washington State, where tidelands have been sold into private ownership or, if in the public domain, can be leased from the state. These geoduck culture practices have generated spatial heterogeneity in mariculture development and a substantial not-in-my-backyard (NIMBY) conflict because culture occurs conspicuously in the intertidal zone and produces shoreline debris when the PVC pipes are displaced by storms. (See the section on Local Traditions and Not-in-My-Backyard (NIMBY) Issues in Chapter 6 for further discussion of aesthetics and NIMBY issues.) Because it is a relatively new practice, few data exist on the ecological effects of these PVC plantations, and this exacerbated the public debate to the point that the Washington State Legislature held a symposium and appropriated funds through Washington Sea Grant to study the issue in 2007. While certain scientific studies (e.g., effects of pipes and mesh covers on biodiversity and predator abundance on a local scale [Washington Sea Grant, 2007b], effects of the sediment liquefaction harvest process on sediment structure and the associated vegetation and infauna [Washington Sea Grant, 2007c]) might clarify the issue, the viewscape issues that appear to be at the heart of the upland owners' concerns will likely remain unresolved. These issues are less apparent for traditional commercial fishery activities, which occur out-of-sight in subtidal areas and where commercial catch limits and spatial rotation of harvest sites restrict exploitation to a very small fraction of the stock biomass in Washington and British Columbia.

(Wisehart et al., 2007), although seedling survival was universally low across oyster harvest treatments (1–2%; Wisehart, 2006). Rhizome branching appears to be important for recovery of gaps in eelgrass (up to 16 m²) but only occurs seasonally, and thus gaps created experimentally in mid-summer did not begin to recover from the edges until the following spring and can vary by tidal height and surrounding eelgrass density with slower recovery (Boese et al., 2009; Eric Wagner, unpublished data). Clearly, the amount of sexual versus asexual reproduction that contributes to eelgrass resilience is important and may vary both temporally and spatially, but this has not been examined at broad spatial scales relevant to bivalve mariculture in many estuaries.

The scale and frequency of harvest activity have been shown to be important for both the direct effects on seagrass and associated organ-

BOX 4.2

The Wadden Sea: A Case Study of Bivalve Mariculture, Conflict Resolution, and Ecosystem Restoration

The Wadden Sea, which runs 400 km along the North Sea coast of Denmark, the Netherlands, and Germany, is a large temperate coastal wetland ecosystem with many transitional habitats of tidal channels, sandy shoals, seagrass meadows, mussel beds, sandbars, mudflats, salt marshes, estuaries, beaches, and dunes. It is the staging, molting, and wintering area for up to 12 million birds every year. For 43 bird species, the Wadden Sea supports more than 1% of the entire flyway population, which is the criterion used by the Ramsar Convention for identifying wetlands of international importance. In June 2009, the Dutch-German part of the Wadden Sea became a World Heritage Site.

The most important mariculture and fisheries activities in the Wadden Sea are on-bottom blue mussel, cockle, and shrimp fisheries. In the 1980s and 1990s, the environmental quality of the Wadden Sea was documented to be decreasing with blame placed on the impacts of fisheries, which disrupted the sediment dynamics and composition, and on the continued impoundment of wetlands. Integrated coastal governance and management systems of the complex natural, fisheries, and social and political milieu of the Wadden Sea began with the first Trilateral Governmental Conference in 1978, which led to the Trilateral Wadden Sea Cooperation as the focal point for coordination among governments of the three countries (Olsen and Nickerson, 2003). The common principles and objectives of the Trilateral Cooperation are based on a binding political agreement among the three governments and complement the European Habitats Directive of 1992, which also designated major parts of the Wadden Sea as Special Areas of Conservation. The implementation of the European Union's directive in the Wadden Sea is coordinated by the member states, which cooperate in the Trilateral Wadden Sea Cooperation that made the common principles legally binding (Common Wadden

isms and the secondary impacts of harvest on food for shorebirds and waterfowl. Small-scale harvest of clams by hand in a national park in Spain (Navedo and Masero, 2008) appeared to be sustainable with very little impact, while the impacts of dredge harvesting of wild stocks of mussels and cockles in intertidal areas of the Dutch Wadden Sea at much larger scales are highly debated (Piersma et al., 2001; Verhulst et al., 2004; Kraan et al., 2007; Box 4.2). This mariculture is often either practiced in areas where vegetation is not present, involves harvest by hand in more spatially restricted areas, or harvest is much less frequent (once every two to three years) than in wild-stock harvest situations. Wild-stock harvest occurs at least annually and often more frequently in part because different fishermen each typically conduct trial fishing to determine abundances of the resource.

Sea Secretariat, 2008). Aquaculture and fisheries activities were part of a comprehensive management scheme in line with the European Union's Water Framework Directive and Habitats Directive, both leading to strict regulations and complemented by the establishment of a number of marine no-take protected areas and restoration programs. Zoning of aquaculture and fisheries activities is applied on a permanent or seasonal basis to regulate activities that could disturb birds and seals during critical periods of their life cycle. Decentralized planning and decision making began with a co-management program undertaken by the Dutch Shellfish Fisheries Association in 1993 that provided for shared responsibilities between the government and industry. A steering group composed of government representatives, mollusc farmers, and fishermen drafted a management plan that applied best environmental practices to the harvesting of cockles and mussels, and after three years of implementation, several evaluations concluded that the co-management approach had indeed been a success (Olsen and Nickerson, 2003).

Nonetheless, controversy has persisted. In 2004, the Dutch House of Representatives banned mechanical harvesting of cockles (Swart and van AnDEL, 2008). Analyses of the three-way interaction between mechanical overexploitation of benthic resources, declining food abundance for migratory shorebirds, and population declines in these birds suggested that the loss of 55% of their best foraging areas drove the relationship (Kraan et al., 2009). Further evidence for ecosystem deterioration of the Wadden Sea (de Jong, 2009) has led to legislation that will prohibit all mussel bottom dredging by 2020. Instead, mussels are expected to settle directly on devices suspended in the water column. It remains to be seen whether sustainable mussel mariculture is compatible with the Wadden Sea's designation as a World Heritage Site.

Uncertainties and Unknowns in Ecological Effects of Harvesting

Although the effects of disturbance to benthic communities from bivalve mariculture activities and those of wild harvest are relatively well understood at local scales, there are few direct comparisons, and even less is known about cumulative effects at larger spatial scales (e.g., lease and bed, especially multiple lease and estuarine-landscape levels) and longer temporal scales (e.g., multiple years, harvests). Direct comparisons of the effects of bivalve mariculture and wild-stock harvest in systems where they coexist would be extremely useful for management purposes, particularly if conducted at appropriate temporal and spatial scales.

Carbon Footprint

No published work has addressed the relative carbon footprint (net carbon emissions per kilogram of harvest) or energy use of wild-stock bivalve exploitation versus bivalve culture; however, this comparison has been made for finfish (see Troell et al., 2004; Tyedmers, 2004). The carbon footprint of bivalve production is likely to vary significantly across different culture techniques and locations. Improved information about the carbon footprint of mollusc production will be needed if mollusc carbon markets are to be developed.

Disease Effects of Bivalve Mariculture as Compared with Wild-Stock Harvest

Although documented cases of the introduction of disease agents via transfer of cultured bivalves exist, little documentation of transfer of disease agents via fishing activities has been published. It is conceivable that the use of live wells and bait may introduce exotics or spread existing disease agents that affect fish and some other groups. For example, the importation of frozen bait shrimp from China and other sources into the United States resulted in the introduction of two viral diseases: white spot syndrome (Hasson et al., 2006) and Taura syndrome (Prior et al., 2001). In addition, shrimp packing plants have also been implicated in the movement of shrimp pathogens (Joint Subcommittee on Aquaculture Shrimp Virus Working Group, 1997). More examples exist whereby fishing pressure has been shown to impact host–parasite relationships leading to decreases or increases in clinical disease. For example, fishing of scallops was found to reduce the incidence of trematode parasites of scallops by reducing the host-density threshold needed for successful parasite transmission (Sanders, 1966). Fishing on high trophic-level species has also been shown to increase diseases at lower trophic levels (Jackson et al., 2001a) by reducing numbers of keystone predators resulting in large

increases in their prey species to levels that favor pathogen transmission. A number of examples exist, such as several diseases in sea urchins upon loss of lobsters and other predators (Gilles and Pearse, 1986; Lessios, 1988; Lafferty, 2004) and the rickettsial disease, withering syndrome, in black abalone upon loss of predatory sea otters (Lafferty and Kuris, 1993). Fishing has also been shown to modify habitat, and at least one example exists of increased disease as a result—a haplosporidian disease, bonamiasis, in New Zealand dredge oysters (Cranfield et al., 1999).

EFFECT OF MARICULTURE ON WILD POPULATION FISHING PRESSURE

Defining “Fishing Pressure”

There is no universally accepted definition of “fishing pressure” in fisheries management literature; the term is used in a variety of ways to describe the level of fishing effort or catch (landings) relative to what may be sustainable in the long term. To examine the effects of mariculture on the harvesting of wild populations of the same or comparable species, it is useful to consider “fishing pressure” both in terms of the physical pressure on a fish stock from harvesting and in terms of the economic factors that influence fishing activity.

Physical fishing pressure (FP) on a wild population (stock) of molluscs can be defined as the non-dimensional ratio of the current rate of exploitation of the wild population (harvest or catch, C , usually measured in live [whole] or meat weight per year) to the maximum sustainable yield this population can support at present stock levels ($SY(X)$):

$$FP = \frac{C}{SY(X)}$$

$SY(X)$ is the estimated maximum rate of harvesting that the wild stock can sustain at stock level X without being (further) depleted. In general, this is not the same as the long-term maximum sustainable yield (MSY) as commonly defined in fisheries management (Russell, 1931; Graham, 1935). In particular, $SY(X)$ will be less than MSY for a stock that has been overexploited, where the present stock level (X) is less than X_{MSY} (defined as the stock level associated with maximum sustainable yield). Under this definition, $FP < 1$ indicates a level of fishing pressure that allows the wild population to grow (if $X < X_{MSY}$) or remain stable (if $X > X_{MSY}$), whereas $FP > 1$ indicates a level of fishing pressure that results in depletion of the wild population.

Harvest is related to fishing effort, which is determined by the economic incentives and management constraints facing fishermen. The

economic incentive to fish is related to its profitability—the difference between the market price of the bivalve molluscs and the cost of fishing. A higher differential will lead to a greater incentive to fish and, in the absence of management limits (e.g., an “open access” fishery), can be expected to result in greater fishing effort and increased landings (at least in the short term, other factors remaining unchanged). The market price is a reflection of demand and supply, including wild harvest, mariculture, and net imports. Demand is influenced by the size of the consuming population, by their tastes and preferences, and by the supply (price and availability) of substitutes.

Management of the wild fishery may limit fishing effort or landings, thereby capping physical fishing pressure.¹ As a result, it is possible for the economic factors underlying fishing pressure to change without a change in the fishing pressure exerted on the wild stock. For example, a highly profitable fishery that is operating near MSY, and in which catch and effort are carefully managed, may not see any significant shift in fishing pressure despite an increase in market price (because increased fishing is proscribed by management) or a moderate decrease in market price (so long as profit remains positive). On the other hand, in an open-access fishery without effective management limits on catch or effort, it is more likely that a change in market price will result in a shift in physical fishing pressure.

Links Between Mariculture and Fishing Pressure

Mariculture can affect fishing pressure in two main ways: directly, by affecting market price, which influences the fishing effort; and indirectly, by increasing or decreasing the size of the wild population, and thereby changing sustainable yield. The market price of wild molluscs depends on supply and demand (see above). If demand is constant and mariculture increases the total market supply of the molluscs or of a species that is seen by consumers as a substitute, the market price will typically decline, reducing the economic incentive to fish and tending to reduce fishing pressure over the long term.

Bivalve mariculture may increase sustainable yield if it is employed in the service of restocking, stock enhancement, or sea ranching activities designed to enhance “wild” production (Bell et al., 2008). Other things remaining equal, the addition of cultured molluscs to the wild population increases the stock level and thereby tends to reduce fishing pressure

¹ Management measures may also subsidize fishing, for example through subsidized loans for the purchase of fishing gear or fuel subsidies for fishing boats, effectively reducing fishermen’s cost of harvesting and thereby tending to increase fishing pressure.

(assuming harvest stays the same).² By the same token, if mariculture is practiced in a way that negatively affects the health or abundance of wild populations, it can reduce sustainable yield and therefore increase fishing pressure. (Refer to the genetics section in Chapter 3 for more information on the genetic impacts of interactions between farmed molluscs and wild stocks.)

Although bivalve mariculture generally produces effects that in theory will lead to a decrease in fishing pressure on wild populations, it is possible that no reduction in wild-capture landings or fishing pressure will occur despite increasing mariculture production. If demand is robust and growing (as it is globally for many seafood products; see Food and Agriculture Organization of the United Nations, 2009), the market price may not change sufficiently to affect fishermen's behavior. It is also possible that marketing campaigns to promote a specific product (either wild harvest or cultured) and wider availability of molluscs associated with large-scale mariculture can, over time, influence consumers and increase demand more significantly than it might have without mariculture. The result could be an increase in both supply and demand with little or no net effect on price and, therefore, no associated reduction in fishing pressure.

Empirical Evidence

There has been little formal analysis of the effects of mariculture on wild-stock fishing pressure for molluscs or finfish in the United States, although a few studies have discussed possible evidence of such effects. The most dramatic increase in global mariculture production has taken place for salmon, with an associated decline in U.S. prices for wild salmon. Global mariculture production of salmonids increased from about 100,000 metric tons per year in 1980 to nearly 2 million metric tons per year in 2007; farmed salmon today accounts for more than 65% of global supply. The experience with the profound expansion of the salmon market may provide some insight into what effects a large expansion of bivalve mariculture might have on the fishery for wild stocks.

Salmon imports into the United States accelerated significantly around 1995 (Figure 4.2), reflecting the global increase in salmon aquaculture production. The price of imported, farmed salmon dropped substantially from 1990 to 2005 (Figure 4.3). These developments were followed by a decline in wild-harvest prices, while wild-harvest production remained more or

² It should be noted that the effect on fishing pressure is general, regardless of stock size. Also, what happens in practice in response to pressure from fishermen depends on fisheries management, and if harvest is allowed to rise, pressure may remain constant.

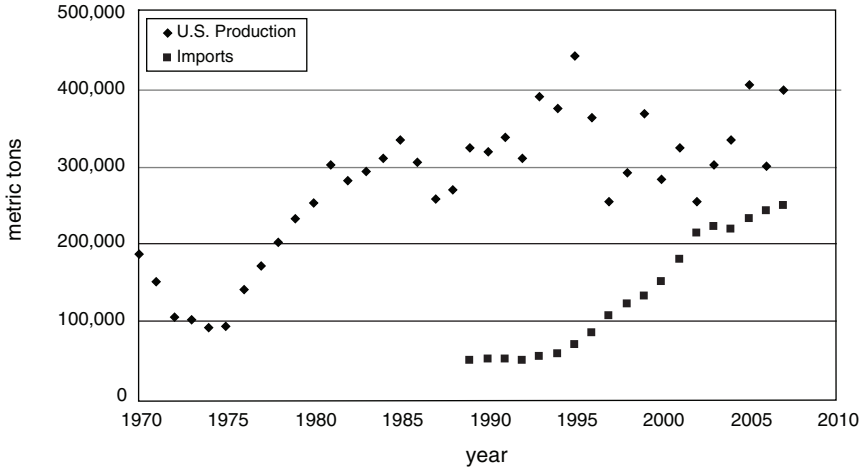


FIGURE 4.2 U.S. salmon landings (1970–2007) and imports (1989–2007). SOURCE: National Oceanic and Atmospheric Administration (2007; 2009b).

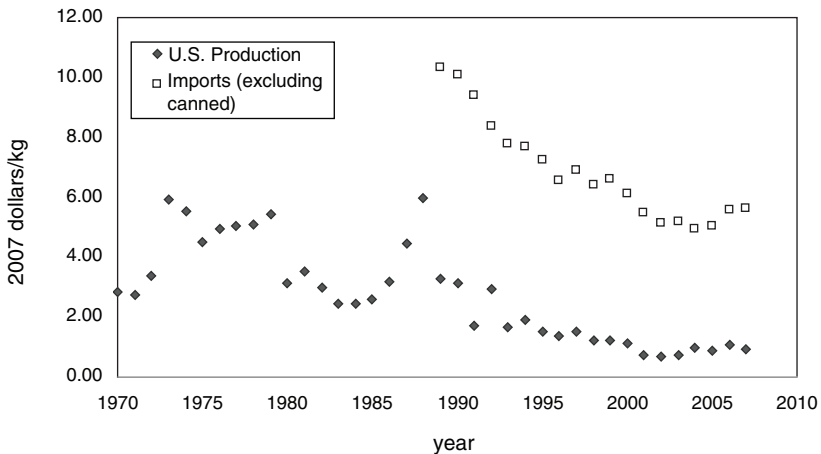


FIGURE 4.3 U.S. salmon prices (1970–2007). U.S. production price is dockside value of whole fish; import price is for fillets. SOURCE: National Oceanic and Atmospheric Administration (2007; 2009b).

less steady (but quite volatile) after 1990. The trends seen in these data suggest that prices decreased in response to the rapid expansion in supply, although association is not causation. In a study of the Japanese salmon market, Asche et al. (2005) examined market integration of farmed and wild salmon and found that the increase in mariculture production was

associated with a decrease in the price of both wild and farmed salmon. The decrease in price reduces the economic incentive to harvest the wild stocks. Effective management of the level of wild-salmon harvest could explain the apparent lack of impact of reduced prices on wild-salmon production, although the price decrease appeared to increase the incentive to reduce fishing capacity in Alaska (Anderson, 2002). Without the supply from farmed salmon, the economic pressure to harvest wild salmon resources might be greater today.

There is anecdotal evidence of similar price effects in bivalve molluscs. For example, cultured production of hard clams increased significantly in Virginia and Florida during the 1990s; the total farm-gate value (i.e., the net value of the product when it leaves the farm) of Florida cultured hard clams rose from \$3.7 million in 1993 to \$15.9 million in 1999 (Philippakos et al., 2001). This increase in mariculture production in Florida was associated with a decline in the average market price of these clams from \$0.23 per clam (Philippakos et al., 2001) to \$0.145 per clam (Adams et al., 2009).

The lack of consistent and meaningful time-series data on mollusc production by species at the national level (see Markets, Prices, and Trade in Chapter 6) makes it difficult to interpret these trends with confidence. According to National Oceanic and Atmospheric Administration (2007; 2009b, d) production and import statistics, oyster imports into the United States rose from about 6,000 metric tons (meat weight) per year in 1995 to about 11,000 metric tons (meat weight) per year in 2007, presently accounting for more than a third of the U.S. oyster market (see Chapter 6 for details). However, most of these imports represent farmed and processed product (smoked and canned) from Korea and China, a sector of the market that is unlikely to compete directly with the U.S. product that is predominantly fresh (shucked or live oysters). Therefore, it is difficult to assess the effect of cultured oyster imports on U.S. market prices, although the inexpensive processed imports would likely discourage investment in a domestic canned or smoked product.

In conclusion, economic theory suggests that mariculture production will tend to increase supply and, if there are no compensatory changes in the market, drive down the price of the cultured species. As a consequence of lower prices, the economic incentives to harvest wild populations will tend to be reduced. The extent to which this change in economic incentives reduces fishing pressure depends on the condition and management of the wild fishery. Empirical evidence of such effects in U.S. fisheries is largely anecdotal and limited to prices. For example, rising imports of cultured salmon since the mid-1990s have been associated with declines in average market price, but there is no clear indication of a corresponding

change in physical fishing pressure on wild stocks. For molluscs, analysis of these changes is complicated by data limitations.

FINDINGS AND RECOMMENDATIONS

Finding: Although the effects of disturbance to benthic communities caused by bivalve mariculture activities and those from wild harvest are relatively well understood at local scales, there are few direct comparisons, and less is known about cumulative effects at larger spatial and longer temporal scales.

Recommendation: Direct comparisons of the effects of bivalve mariculture and wild harvest should be conducted in systems with both activities to better understand their effects in comparable environments. Studies at larger spatial scales and over longer periods of time should also be undertaken.

Finding: Economic theory suggests that mariculture production will tend to increase supply and reduce the price of the cultured species, thereby reducing economic incentives to harvest wild populations. The effect of lower prices on fishing pressure depends on the condition and management of the wild fishery. Empirical evidence for these effects is largely limited to observations of price trends with increases in supply, but there has been little formal analysis of responses of either markets or wild fisheries to the expansion of mariculture.

Recommendation: Policy makers and marine resource managers should anticipate possible linkages between wild harvest and mariculture production in shellfish markets when developing forecasts. Managers should monitor changes in market prices to assess the effects of mariculture on supply, product quality and availability, and the response of wild-harvest fisheries to these changes in market conditions.

5

Carrying Capacity and Bivalve Mariculture

Aquaculture is the fastest growing food-producing sector worldwide and, combined with stock rebuilding programs and improved management, provides a means for filling the growing gap between consumer demand and seafood production from traditional capture fisheries (Duarte et al., 2009). Numerous bivalve species are now farmed; bivalve mariculture is expanding worldwide (Howlett and Rayner, 2004), representing about 27% of total aquaculture production and about 13% of total fish produced for human consumption worldwide in 2006 (Food and Agriculture Organization of the United Nations, 2009). Environmental modifications have been documented in areas where molluscs are farmed (e.g., Raillard and Máneguen, 1994; Christensen et al., 2003; Kurlansky, 2007), most of which result from the ability of cultured bivalve species to filter large volumes and extract phytoplankton, particulate detritus, and inorganic particulates; to excrete large quantities of ammonia; and to deposit large quantities of digested (feces) and undigested (pseudofeces) organic matter on the seabed. Local benthic enrichment and oxygen depletion are the most apparent impacts of bivalve culture and have generally received the most attention.

The expansion of bivalve mariculture and the increase in environmental awareness have encouraged a more ecosystem-based perspective for managing and developing bivalve culture. For example, polyculture or integrated aquaculture is a growing trend that considers the ecosystem as a whole and allows for the culture in one location of multiple species that are presumably synergistically related (Box 5.1). An ecosystem-based

BOX 5.1 Polyculture and Ecosystem-Based Approaches

As with terrestrial agriculture systems, there is a potential for synergy between the co-cultivation of animals and plants in marine polyculture or “integrated aquaculture” systems. Molluscan and fish mariculture produces potentially valuable by-products, which can be recaptured as nutrient support and energy for extractive seaweed aquaculture providing biomitigation and also producing additional, valuable crops within the same leased areas; this has been called “integrated multi-trophic aquaculture” (Chopin et al., 2001). Trophic diversification can be increased by adding lower trophic-level organisms to this mix to balance ecosystem functions and further increase the number of value-added crops.

The Food and Agriculture Organization of the United Nations developed guidelines for an ecosystem-based approach to mariculture (Soto et al., 2008), which can be used to design “aquaculture ecosystems” (Costa-Pierce, 2002). However, of the many iterations of marine integrated aquaculture options reviewed by Costa-Pierce (2008), there are few examples of successful models developed between mollusc crops and commercially important seaweeds, such as *Laminaria saccharina*, *Porphyra purpurea*, and *Palmaria palmata*. Chopin et al. (1999) proposes that integrating *P. purpurea* into mariculture could be an important method for bioremediation and diversification. *P. purpurea* requires a constant availability of high-quality nutrients so cultivation near salmon cages would allow for alleviation of nutrient depletion, and frequent harvesting provides for constant removal of significant quantities of nutrients from coastal waters and for the production of seaweeds of commercial value. Similar advantages of integrating the culture of *P. purpurea* with molluscs would be expected.

The most advanced examples of complex integrated aquaculture being implemented at the commercial level come from Korea and China (Food and Agriculture Organization of the United Nations, 1989; Chung et al., 2008). A wide range of molluscs are grown commercially with fish and invertebrates in Korea, and in China, the two main types of integrated seaweed–mollusc systems involve *L. saccharina* with mussels or with scallops (Food and Agriculture Organization of the

perspective has led to the development of prognostic site-assessment tools and practical ecosystem-performance indicators. The need to understand and predict the response of interlinked ecosystem processes and to determine the consequences of these for management and commercial decisions has resulted in the emergence of ecosystem modeling as an important tool for bivalve mariculture management.

WHAT IS CARRYING CAPACITY?

The following definitions are based on work by others (Inglis, 2000; McKindsey et al., 2006b):

United Nations, 1989). *L. saccharina* is grown on rafts with mussels in both vertical and horizontal systems and provides shade, creates sheltered areas less vulnerable to current flows, releases oxygen as a by-product of photosynthesis, and generally improves water quality. In turn, mussels produce metabolic by-products, especially dissolved N, P, and CO₂, which provide nutrients to the *L. saccharina*. In the simplest method of integrated aquaculture, rafts of alternating seaweed ropes and mussel ropes are suspended vertically from a floating raft rope. This method is also used in China to grow other marine species in conjunction with *L. saccharina*, such as scallops, which are suspended in cylindrical net cages about 40 cm in diameter and 1 m long. *L. saccharina* yields from these integrated systems compared with monoculture were 23–35% higher, and market values were 27–31% higher. *L. saccharina* produced in integrated aquaculture was of higher quality than in monoculture; the proportion of “first-class product” rose from 59% under monoculture to 74% and 80% in the integrated systems. Output and market value of mussels improved by 19% compared with mussel monoculture. Integrated aquaculture systems had a 58% increase in market returns compared with *L. saccharina* monoculture using identical production facilities (Food and Agriculture Organization of the United Nations, 1989).

The challenges from the biological, environmental, economic, technological, engineering, regulatory, and societal perspectives are numerous. Appropriate extractive species need to be selected based on their biology, growing methods, and harvesting technology and adapted to local conditions. High-value markets will have to be found for these species to justify their culture, and seaweed will likely have a lower total value than molluscs (Chopin, 2008). Growing multiple species requires aquatic farmers to develop additional “skill sets” since mollusc and seaweed farming, for example, are completely different activities. There are also issues with permitting and regulatory authorities. Multi-spatial ocean planning and “multi-functional co-management” (Chopin, 2008) are needed in such cases to help define management of multiple uses.

1. **Physical carrying capacity**—the total area of marine farms that can be accommodated in the available physical space.

2. **Production carrying capacity**—the stocking density (that at which production levels are maximized) that provides the maximum economic return (i.e., the economically “optimized” level of production of the target species).

3. **Ecological carrying capacity**—the stocking or farm density above which “unacceptable ecological impacts” begin to manifest. From a practical standpoint, this process begins with the definition of components of interest (e.g., species, habitats) and acceptable levels of change for each of these.

4. **Social carrying capacity**—the level of farm development that causes unacceptable social impacts.

A goal of mariculture management is to estimate the capacity of an area to support the cultured species (i.e., to determine the carrying capacity of a system). The system carrying capacity can be defined in terms of the physical environment, the ecological state of a system, the production yield, or the tolerance of local social and cultural structures (McKindsey et al., 2006b). Estimation of system carrying capacity has largely focused on the identification of production carrying capacity, which is the maximum sustainable economic yield of culture that can be produced within a region (see citations in McKindsey et al., [2006b]). However, estimation of carrying capacity is rapidly evolving from a focus on maximizing mariculture production to an ecosystem-based management (EBM) approach with a focus on ensuring ecological integrity and resilience of the ecosystem in which mariculture is imbedded. This development is following the move in fisheries management toward EBM to replace traditional approaches based on attempting to maximize single-species yields.

Ecological carrying capacity is broadly defined as the level of mariculture that can be supported without leading to significant changes to ecological processes, species, populations, or communities in the growing environment. At the ecosystem level, ecologists have further defined this property as integrity or resilience, which is the capacity to maintain characteristic patterns, structure, and functional organization comparable to that in similar undisturbed ecosystems in the region. The development of ecological carrying capacity indicators and models is relatively new but has the potential to feed into EBM systems, which in turn would support the ideals and goals of the ecosystem-based approach to mariculture management. The ability to predict ecological carrying capacity is crucial to assessing the impact of development and expansion of large-scale bivalve mariculture operations and also helps in the identification of appropriate indicators and metrics that allow performance standards to be determined. To further the scientific basis for estimation of ecological carrying capacity, mariculture working groups under the auspices of the International Council for the Exploration of the Sea (2008) recommended that the following information gaps be filled:

- Development of guidelines toward defining an “unacceptable” ecological impact, based on theoretical and socioeconomic considerations, and identification of critical limits (i.e., performance standards or thresholds) at which the levels of shellfish mariculture stress indicate a

disruption of the system warranting management actions. (Germane to this is the concept of social carrying capacity, which would guide much of this work.)

- Research on the development, value, and application of predictive ecological models of shellfish [mariculture] systems.
- Time-series observations of ecological responses to shellfish [mariculture] development.
- Site-specific factors affecting ecological carrying capacity.
- Direction for scientists from stakeholders (e.g., habitat and farm managers and nongovernmental organizations) on potential [ecosystem components] that need to be evaluated in unbiased ecological carrying capacity assessments.
- Discussion on how models of [mariculture] systems complement the ecosystem approach to marine management. (International Council for the Exploration of the Sea, 2008)

The estimation of carrying capacity is confounded by the fact that bivalve mariculture can impact the system by both consuming (phytoplankton) and producing (recycled nutrients and biodeposits) with the concomitant impacts of both (Gibbs, 2007). Bivalve mariculture dominates the energy flow of a marine system when the phytoplankton consumed by the total population of cultured molluscs exceeds the combined reproduction rate and tidal replenishment rate of phytoplankton in that system (Dame and Prins, 1998). Thus, caution is needed in attributing cause of change and partitioning impacts between mollusc farm activity and other activities ongoing in the system in estimating ecological carrying capacity. Moreover, it is important to distinguish between the ecological carrying capacity and an estimate of carrying capacity that might be a result of stakeholder feedback (social carrying capacity), which may also include considerations of what might be an acceptable impact on ecological function of a system. To clearly define ecological carrying capacity, it is essential to identify indicators of relevance and to distinguish between indicator- or threshold-based management as opposed to management solely by predictive modeling.

The development of a sustainable long-term management plan is difficult, but recent advances in the measurement, modeling, and application of carrying-capacity estimates provide some guidance. Modeling ecological carrying capacity with feedback from stakeholders in the system holds promise, but due to its newness, it is also the least understood and practiced. Ultimately, it will be important to quantify the values presented by stakeholders in a science-based effort in order to determine the proper limits to bivalve mariculture in local waters.

CARRYING-CAPACITY MODELS

The models that have been generated to assess carrying capacity relating to bivalve mariculture are diverse and range from simple mass-balance models to coupled circulation–ecological–economic models (Table 5.1). Many of the available models estimate the capacity of a system to support a single species, rank the relative risk of culture activities in different settings, or optimize mollusc yields for a given area. Recent models consider potential impacts of phytoplankton removal by a filtering bivalve or community of bivalves, and some attempt to include effects on related species such as seaweeds, which are relevant to system energy flow and ecological stability in the marine food web. The modeling frameworks and supporting data have evolved during the past 10–15 years to the point of providing guidance for the development of mollusc farms, their management, and potential economic effects of bivalve mariculture (Table 5.1).

Carrying-capacity models are providing insights into the interactions between production and ecological carrying capacity (e.g., Jiang and Gibbs, 2005) and the consequences of these insights for bivalve mariculture systems (e.g., Ferreira et al., 2009). Production carrying capacity is usually higher because it does not include the feedbacks and interactions of the energy flow in the overall food web and the potential displacement of endemic populations by cultured species. Model-based predictions of the responses of a large-scale mussel culture system (Jiang and Gibbs, 2005) include a decrease in the mean trophic level of the ecosystem with an increase in total yield—more efficient energy throughput via the filtering bivalves—but with replacement of zooplankton in the food web by the cultured mussels as the dominant herbivores.

Gibbs (2004) developed models to determine the acceptable limits to bivalve mariculture production in the Marlborough Sounds region of New Zealand by examining the relationship between bivalve farms and fishery resources, noting that primary and secondary productivity that would provide food for commercially fished species could instead be diverted to bivalve production—a concept proposed more than 25 years ago by Lapointe et al. (1981) and Tenore et al. (1982) for mussel production in Spain. Gibbs (2004) specifically considered three types of interactions between bivalve culture and fisheries: (1) bivalve farms either attract or displace fish, (2) bivalves consume fish eggs and larvae, and (3) food webs are altered so that fish production is displaced by farmed bivalves. For the latter, Gibbs (2004) used food-web models to try to estimate how much bivalve mariculture could develop before it dominated the energy flow in the marine system. Jiang and Gibbs (2005) further consider the food-web approach using a mass-balance model to estimate a carrying capacity for cultured bivalves in Golden and Tasman Bays in New Zealand of 310 tons

per km² per year, which is considerably more than the estimated ecological carrying capacity of 65 tons per km² per year.

Other modeling studies showed that the presence of oysters primarily affected phytoplankton (Grangeré et al., 2008) and wild suspension feeders (Cugier et al., 2008), providing a direct feedback between the cultured species and the ecological carrying capacity of a system. The higher grazing pressure on phytoplankton induced by the addition of cultivated oysters, as well as the trophic competition existing between wild filter feeders and cultivated oysters, explained the strong decrease in phytoplankton biomass, production, and wild filter-feeder stocks (Cugier et al., 2008). The model-based estimates of production suggested that the bivalve stocking for this particular system went beyond the ecological carrying capacity. Similarly, biodeposition from cultured bivalve systems can affect the ecological carrying capacity through reduction in benthic species biomass and richness, alteration of nutrient fluxes, and regulation of local oxygen concentrations (e.g., Weise et al., 2009; Box 5.2). The ecological carrying capacity of a system is the product of near-field (e.g., biodeposition) and far-field effects (e.g., nutrient cycling, pelagic carrying capacity), and as a result, estimates of this quantity require modeling frameworks that include a range of space and time scales that are relevant to the processes affecting ecological carrying capacity. For example, recent modeling studies (Cranford and Hargrave, 1994; Cranford et al., 2007; Grant, 2008a) done at the spatial scale of phytoplankton depletion provide insights into the potential effects of particle depletion of particular sizes from mussel culture and highlight the significant ecological destabilization that could result from the altered competition and predator–prey interactions between resident species. Such models will provide industry and management with tools to comprehensively and efficiently assess the effects associated with bivalve-culture activities within an EBM framework.

The coupling of hydrodynamic models to ecological models with production estimates allows the interactions between mollusc culture, food-web processes, and physical attributes of systems to be examined. The availability of a three-dimensional hydrodynamic model for a system allows estimates of flow, exchange, and residence time over multiple space and time scales and provides a framework for testing scenarios about consequences of changes in circulation on bivalve mariculture systems. Numerous studies have shown the importance of accurate representation of the circulation to the estimation of production of mariculture systems (e.g., Guyondet et al., 2005). The scientific community's expertise and knowledge of circulation models has greatly improved, and community-based models now exist; however, this knowledge is resident in a community of scientists, usually physical oceanographers, that has not tradition-

TABLE 5.1 Representative Studies That Use Models to Estimate Carrying Capacity for Bivalve Mariculture^a

Study and Species	Carrying Capacity Type
Ferreira et al. (1997) Oysters	Ecological and production
Smaal et al. (1998) Bivalves	Ecological and production
Bacher et al. (1998) Oysters	Ecological and production
Niquil et al. (2001) Farmed and natural bivalve populations	Ecological
Duarte et al. (2003) Polyculture bivalves, scallops, and seaweed	Ecological
Gangnery et al. (2003) Oysters	Ecological and production
Nunes et al. (2003) Scallops, oyster, and kelp	Ecological and production
Jiang and Gibbs (2005) Bivalve culture, including total biota from phytoplankton to mammals	Ecological and production
Cranford et al. (2007) Mussels and watershed nitrogen inputs	Ecological
Ferreira et al. (2007) Bivalve species and polyculture	Ecological, production, and social
Grant et al. (2007) Mussels and lower trophic levels	Ecological and production
Byron et al. (2008)	Production and social

Model Framework	Simulation Application	Management Application
Coupled circulation, primary production, and oyster growth model	Estimation of production carrying capacity and optimum-seeding strategy	None
Conceptual	Theoretical evaluation of minimum carrying capacity requirements	None
Population dynamics model	Assessment of oyster standing stock production	None
Inverse analysis of carbon flow in lower trophic levels	Assessment of local food availability for oyster farming	None
Coupled two-dimensional circulation–biogeochemical model	Estimation of environmental carrying capacity for polyculture system	Potential
Population model for oysters and mussels	Assessment of standing stock and production changes and environmental effects	None
Individual-based species models and multi-cohort population models	Assessment of seeding and harvesting strategies of polyculture management strategies	Potential
EcoPath: linear food web	Estimation and comparison of ecological and production carrying capacity for bivalve culture	None
Nitrogen budget, lower trophic level, and mussel growth	Assessment of mussel production on nitrogen budgets and dynamics	None
Circulation, biogeochemical, bivalve growth, production, and eutrophication	Assessment of farm location and practice on production outputs and nutrient management	Potential
Coupled biological–circulation–chemical model	Assessment of effects of food depletion	None
EcoPath	Defined production and social carrying capacity	None

continued

TABLE 5.1 Continued

Study and Species	Carrying Capacity Type
Cugier et al. (2008)	Ecological
Ferreira et al. (2008) Blue mussels and Pacific oysters	Ecological, production, and social
Gubbins et al. (2008) Mussels, shellfish	Ecological
Sequeira et al. (2008) Wild and cultured bivalve species	Ecological and production
Ferreira et al. (2009) Mussels, oysters, and clams	Ecological, production, and social
Weise et al. (2009) Blue mussels	Ecological and production

^a For each modeling study, the species of interest, type of carrying capacity estimated, simulation application, and management application are indicated. (Studies are arranged in chronological order.)

ally been involved in mariculture issues. Furthermore, simply including hydrodynamic models with a proven track record in providing modeling frameworks for mariculture systems is not sufficient; the results from these models must be provided at space and time scales that are appropriate for the ecosystem context and for the mariculture system.

The availability of a hydrodynamic model allows estimates of oxygen and nutrient regeneration and flushing times of stratified systems, as applicable to most estuaries, which have a bearing on the capacity of the system to produce bivalves and the degree of interaction between cultured bivalves and other filter-feeding organisms in the system. The rate at which the waters of a system mix affects the nutrient supply, suspended organic matter flux, and oxygen regeneration (e.g., Aure et al.,

Model Framework	Simulation Application	Management Application
Two-dimensional coupled circulation–sediment model, lower trophic-level model, and bivalve-filtration model	Assessment of trophic balance between cultivated and wild filter-feeder species	Potential
Coupled circulation, lower trophic level, individual-based bivalve-growth, and population models	Integrated framework for determining sustainable carrying capacity in bivalve growing areas	Potential
Coupled circulation, lower trophic level, and bivalve-growth models	Set carrying capacity and investigate synergies with other species	Used to determine license-level activity
Coupled ecosystem–physiology–circulation and bivalve-growth models	Assessment of benthic diversity and impacts on clearance rates of suspended particles	Potential
Coupled circulation, lower trophic-level, bivalve-growth, population, and financial and profit models	Integrated framework for simulating potential harvest, key financial data, and water-quality impacts of bivalve farms	Potential
Coupled circulation and sediment models (DEPOMOD; Cromey et al., 2002)	Spatial deposition of bivalve deposits	None

2007; Ferreira et al., 2009). These factors have implications for ecological carrying capacity. Quantitatively assessing the importance of these ecosystem processes is probably best done through modeling studies that include a hydrodynamic-modeling component. These coupled modeling systems can also be used to test alternative mariculture system designs. For example, a coupled circulation–ecological model was used to evaluate the effect of artificial upwelling of nutrient-rich deeper water on phytoplankton growth and the potential increase in production carrying capacity for mussel cultivation (Aure et al., 2007; Grant et al., 2008b). The scenarios tested with the model showed that an artificial upweller could maximize mussel production in a limited region and potentially allow more efficient management of production.

Box 5.2

Nutrient Dynamics in the Thau Lagoon

The Thau Lagoon on the Mediterranean coast of France is an important area for mollusc culture and as such has been the focus for modeling studies of molluscs and nutrient dynamics. Notwithstanding the fact that the lagoon is an enclosed system and is atypical of mariculture production locations, its large-scale mollusc production and accessibility render it an interesting system to model and test scenarios relating to the interactions between mollusc culture and the environment. Bacher et al. (1995) postulate that the vertical exchange of material is important to mariculture and propose that oysters in culture can be considered a nitrogen sink that stabilizes the system. Mazouni et al. (1996) model benthic-pelagic nutrient fluxes in the Thau Lagoon where measured ammonium production was one to five times higher near culture systems than away from them. Oxygen flux was higher beneath the culture cages as well. Mazouni et al. (1996) also found that nutrient fluxes were higher near the culture systems and that the relative proportions of nutrients across the lagoon were influenced by temperature, and concluded that mollusc excretion was the primary source of ammonium utilized by phytoplankton as opposed to that fraction derived from sediments.

The residence time or, alternatively, flushing of a system influences the degree of nutrient exchange between the benthic and pelagic systems and thus influences subsequent local phytoplankton production (Bacher et al., 1995; Chapelle et al., 2000; Smaal et al., 2001). For example, the model developed by Chapelle et al. (2000) for the Thau Lagoon indicates that during meteorological events (e.g., rain) phytoplankton production is driven primarily by externally derived nutrients, whereas in dry summer periods, phytoplankton production is driven by nutrients derived from mollusc excretion and sediments.

The modeling frameworks that provide ecological and production carrying-capacity estimates include ecosystem components that are represented in models that range from simple box models to fully spatial-explicit (three-dimensional) models. The development of the former type is easier to implement and can be a first step in the specifications of carrying capacity before more complex modeling is undertaken. However, more detailed and realistic ecosystem models are the ultimate goal.

Inclusion of bivalve growth and bioenergetics models with coupled circulation–ecosystem models requires that the latter be configured to provide required inputs, such as food supply, at space and time scales that are appropriate for the bivalve population (e.g., Deksheniaks et al., 2000) or mariculture facility (see Table 5.1 for examples). Bioenergetically based models exist for some mollusc species (e.g., Hofmann et al., 1992; 2006; Flye-Sainte-Marie et al., 2007) and provide a basis for developing more mechanistically based models that allow testing of various scenarios

of controls on mollusc production. However, representation of basic processes, such as bivalve filtration (e.g., Powell et al., 1992), in bivalve models remains a research topic. Similarly, choosing the approach for modeling bivalve molluscs, the traditional scope for growth (Table 5.1) versus dynamic energy budget (e.g., Pouvreau et al., 2006; Roslanda et al., 2009) is a significant issue for research and will guide the future development of models for estimating ecological and production carrying capacity of molluscs.

While modeling efforts have advanced the estimation of bivalve carrying capacity, most efforts to date have been made to model ecological carrying capacities, with little attention given to social carrying capacities. McKindsey et al. (2006b) developed a framework for how social carrying-capacity studies can be used to calibrate ecological carrying capacities and frame a societal debate about what are “acceptable” impacts (Figure 5.1). Social carrying capacity can be determined through stakeholder involvement and feedback that is incorporated into ecosystem models (McKindsey et al., 2006b; Swart and van Anandel, 2008).

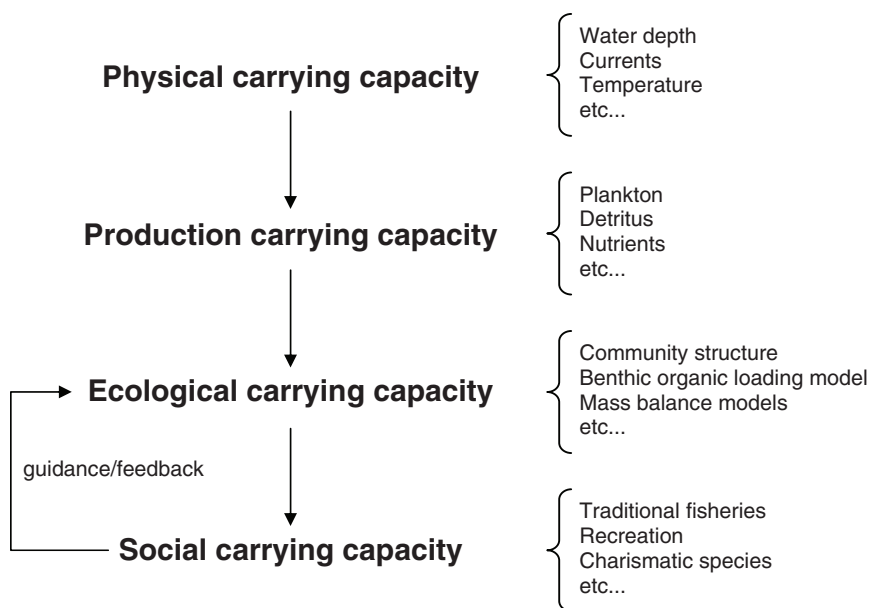


FIGURE 5.1 Types of carrying capacities identified in the literature for marine areas with methods used for their determination. In this model, social carrying capacity is used in an iterative manner to determine best methods for determining ecological carrying capacity (adapted from McKindsey et al., 2006b; with permission from Elsevier).

Byron et al. (2008) developed a stakeholder working group, consisting of both scientists and non-scientists, that is developing mass-balance models to determine ecological carrying capacities for bivalve mariculture in coastal lagoons so as to then define “unacceptable” impacts of oyster mariculture on the environment. The point of “unacceptable change” is first defined through the modeling process, in which the biomass of cultured bivalves is increased until there is an unacceptable change in energy flow between groups (e.g., Jiang and Gibbs, 2005), resulting in an “unbalanced” model ecosystem. The biomass of cultured molluscs at which the model becomes unbalanced defines the upper limit to what is acceptable—the ecological carrying capacity. Assuming that ecological carrying capacity will not be exceeded (i.e., social constraints dictate production restraint), stakeholders may decide that the ecological carrying capacity is too high and want to manage at a lower level—the social carrying capacity. In this sense, acceptability will be bounded by the model estimates at its upper limit (ecological carrying capacity) and by stakeholders at some lower limit (social carrying capacity), thus specifying the bounds of acceptability and supporting the Food and Agriculture Organization’s newly developed principles of an ecosystem-based approach to mariculture that includes environmental resilience and integrity, human well-being, and stakeholder equity and honors current policies and goals of other sectors (Soto et al., 2008). For example, the acceptable mollusc stocking density defined by ecological carrying capacity may exceed that defined by social carrying capacity. Regulations can prohibit mariculture in areas that impede navigation or diminish aesthetic values, which can determine the societal limits to the available area for bivalve mariculture and thus stocking density. Ecological carrying capacity models do not take such societal constraints into account. It is only through a feedback process (McKindsey et al., 2006b) between ecological and social carrying capacity that an ultimate compromise can be reached thereby mitigating user conflict.

MARINE SPATIAL PLANNING: LOCATING NEW OR EXPANDING PRESENT MARICULTURE OPERATIONS

Bivalve mariculture has been an important activity in the United States for more than 100 years; thus, many existing farms were sited well before the current social and ecological carrying-capacity concerns discussed in this report were considered. Today, the combination of greater concern over ecological effects, more intense use conflicts with growing coastal populations, and greater demand for mollusc leases driven by growing markets for seafood is forcing resource managers to evaluate existing mariculture operations and subject applications for new or expanded

leases to more pressure and scrutiny. While carrying capacity issues at the estuarine-landscape scale are clearly the first-level consideration (i.e., how much bivalve mariculture can the system tolerate), a marine spatial planning approach utilizing geographic information system (GIS) technology, which takes other ecological and social considerations into account, will be a useful tool to help extend permits for existing mariculture, locate new operations, and implement EBM practically (Arkema et al., 2006; Leslie and McLeod, 2007; Weinstein et al., 2007; Ruckelshaus et al., 2008).

Sustainable, economical mariculture generally requires that the bivalves be concentrated at high density over substantial areas and that the species have access to “clean” water (i.e., low in potential pathogens and with adequate oxygen, planktonic food, and water flow). For bivalves, these considerations suggest placement in areas well-removed from industrial pollution (e.g., heavy metal contamination), *E. coli* sources, intense stormwater runoff, or where harmful algal blooms are likely to occur, although these considerations have not always been taken into account when locating bivalve mariculture sites. Despite mariculturists’ efforts to protect them, many existing farms have gradually lost their ability to operate as anthropogenic disturbances have increased and compromised water quality (Glasoe and Christy, 2004). Failures of environmental management to sustain water quality could represent a violation of the Clean Water Act’s anti-degradation provision, according to which mariculture represents the highest use protected by this legislation. Such management failures arise largely from stormwater pollution and can be viewed as one form of externalizing costs of development (National Oceanic and Atmospheric Administration, 1992; Environmental Protection Agency, 1998; Booth et al., 2006; National Research Council, 2008). As aesthetic values associated with shorefront property have increasingly become more of an issue, the so-called not-in-my-backyard (NIMBY) factor has come into play: waterfront property owners do not want their views affected by commercial ventures, pushing mariculture operations toward more sparsely inhabited marine shores (see Chapter 6). Finally, placement away from potential predators of molluscs and from traditional migratory, breeding, and overwintering sites for protected species would reduce conflicts with wildlife management.

The conundrum is that these “pristine” sites that meet optimal environmental requirements for bivalve culture are more difficult to find and, if they exist, are more likely to be protected already for conservation purposes or adjacent to park lands. One example is the currently unresolved issue of whether a commercial oyster company should be allowed to continue in Drakes Estero, a Potential Wilderness within a National Seashore (see National Research Council, 2009). As an expanding human population increasingly lives adjacent to the ocean, the requirements for

excellent water quality and separation from public view will only become more difficult to meet, and the temptation for commercial placement adjacent to protected lands and environments will surely increase and be subject to social carrying capacity, shaped by how stakeholders in the United States view the purposes of parks and other places insulated from intense human presence.

From an ecological viewpoint, landscape-scale studies in terrestrial ecosystems, which have a longer history (Lindenmayer and Fischer, 2006), have shown that dispersal corridors can connect otherwise isolated populations and therefore enhance persistence, particularly for mobile vertebrates through time (Debinski and Holt, 2000). Where mariculture typically occurs (in estuaries, areas along more exposed sound shorelines, and proposed offshore ocean locations), the ecosystems are more “open” and spatially connected by larval dispersal so that terrestrial concerns about corridors and dispersal limitation become less important (Tanner, 2005; Cole et al., 2007). Although the effects of bivalve mariculture on this connectivity have not been evaluated at the estuarine-landscape scale, they are in theory less important for bivalves themselves and more important for larger, more mobile demersal nektonic species, like crabs and fish, which can benefit from structure at this scale. The effects of bivalve mariculture as a disturbance to other habitats like seagrass (e.g., fragmentation) and linkages between mariculture structures and natural structures like seagrass, salt marshes, and oyster reefs (e.g., corridors for movement) could be important for mobile nektonic and benthic organisms (e.g., Micheli and Peterson, 1999). Studies, which to date have focused on seagrass systems, suggest that fragmentation increases habitat edge and may actually enhance abundance and diversity of some decapod crustaceans and fish, while larger unfragmented meadows contain a higher abundance of smaller cryptic species (Salita et al., 2003; Selgrath et al., 2007; Macreadie et al., 2009). Progress has been made in mapping bivalve mariculture structures as habitat in some west-coast areas using GIS, but effects of habitat changes due to mariculture and functional value of these habitats has yet to be assessed fully (Ward et al., 2003; Carswell et al., 2006; Dumbauld et al., 2009).

Most bivalve species used in mariculture operations are reported to spend ample time as and to be distributed fairly widely as planktonic larvae: *Crassostrea gigas* (10–30 days), *Mytilus edulis* (5–7 weeks), and geoducks (18 days) (Strathmann, 1987). Variation in larval duration is caused by environmental conditions, especially temperature, and larvae of marine organisms have increasingly been shown to be retained in estuaries or move shorter distances than originally suspected as a consequence of behavioral adaptations that retain them near their source (Swearer et al., 2002; Baker and Mann, 2003; Cowen et al., 2006; Morgan et al., 2009). Thus

the location of reproductively viable molluscs has implications for controlling the spread of nonnative species under culture (e.g., in cases where diploid animals spawn in the wild) and also for enhancing populations of native species where mariculture could play a role in regional spatial planning for native molluscs and habitat restoration. Most culturing of the commercially significant bivalves requires spat or larvae obtained from certified sources. Recently, natural “retention zones” have been identified and seeded with small post-larval stages or even late-larval stages (Largier, 2004). The goal of these operations, along with those undertaken to create spawner sanctuaries (Doall et al., 2008), is to augment natural populations in areas optimal for their growth, survival, and reproduction. Suitably located bivalve culture operations could likewise serve as a larval source to enhance abundances of depleted wild stocks in seafloors open to public mollusc farming. In addition to enhancing native bivalve populations that are declining (Beck et al., 2009), bivalve restoration and presumably bivalve mariculture can serve to enhance habitat for other species and provide valuable ecosystem services, including production of other fish and invertebrates (Coen et al., 1999; 2007; Peterson et al., 2003; Grabowski and Peterson, 2007). Placement and zoning for bivalve mariculture facilities raises more difficult social issues than ecological ones, which interestingly have also shaped the current debate about marine protected areas and their role in enhancing exploited fish populations (Browman and Stergiou, 2004; Arkema et al., 2006; Game et al., 2008).

CONCLUSIONS

The bivalve mariculture community’s experience with carrying-capacity models is relatively recent, and it is only in the past few years that these models have been extended to include water circulation, ecological components, and multi-species dynamics. It is already apparent that these models can provide valuable tools for scenario testing and for setting production goals. However, recognition and estimation of uncertainty created by such factors as environmental variability, unknown or poorly constrained parameter values, and poorly known processes are a critical component of any model-based estimate of carrying capacity. Quantitative approaches for optimizing and constraining model parameter choices and evaluating model structures have been implemented with marine ecosystem models (e.g., Friedrichs et al., 2006; 2007; 2009; Stow et al., 2009), and parameter optimization approaches are now beginning to be applied in aquaculture models (Roslanda et al., 2009). Some attempts have been made to include evaluation of uncertainty in the parameters used in model-based estimates of production and ecological carrying capacity, which allows assessment of sources of error (e.g., Dowd, 2005; Vincenzi

et al., 2006). Optimization and uncertainty analyses are clearly areas that need additional effort to ensure advancement of operational aquaculture models. For this to occur, model development and data analysis need to develop in parallel and iteratively interacting activities for this to be most effective.

EBM has become an important concept in coastal zone management, which includes bivalve mariculture. Assessment of mariculture has occurred mostly at the local scale by measuring the “footprint” of mollusc farms. Scaling up these effects to whole systems has been limited by the difficulty in identifying a signal attributable solely to mariculture and by the capacity and limited resources to make meaningful measurements over larger areas. When many local farm units are considered, the scenario is even more complex because their impacts interact as a function of bathymetry, proximity, circulation, and coastal morphology. Practical indicators of benthic and pelagic effects of bivalve mariculture that can be applied at ecologically relevant scales are needed. Models that can estimate carrying capacity as a result of interactions between bivalve production, ecological, and social carrying capacities provide a promising method for addressing many of the issues that are associated with understanding multiple farm interactions and cumulative effects of other coastal zone activities (e.g., anthropogenic eutrophication, invasive species) at a scale relevant to coastal ecosystems.

The current generation of models is moving toward the development of frameworks that can provide estimates of production and ecological carrying capacity. These models include details of multiple factors that influence the structure and function of the marine ecosystems and the interactions of these systems with bivalve mariculture. With continued development and refinement, through the inclusion of fully three-dimensional circulation fields that capture the complexity of coastal and estuarine circulation and dose-dependent relationships, for example, these models may provide scientifically sound and relatively robust results that can guide the development and management of bivalve mariculture. Nevertheless, social considerations, such as use conflicts and aesthetics, may be the limiting factor for carrying capacity in many coastal settings. However, current models, while beginning to include aspects of social carrying capacity (Table 5.1), do not yet include the processes that influence social considerations directly.

Carrying capacity research continues to provide information on an ecosystem-wide level. Models are being developed that provide carrying-capacity information and estimates that relate to spatial and temporal scales that are relevant to the scales at which bivalve mariculture interacts with the marine food web. Based on recognition of some knowledge gaps,

McKindsey et al. (2006b) made the following recommendations to further the development of ecological carrying-capacity models:

- Studies need to continue to focus upon estimating the environmental interactions associated with all aspects of bivalve culture (e.g., seed collection, harvesting, husbandry).
 - A full range of culture activities should be considered in models.
 - Models should be spatially explicit.
 - Models need to consider temporally variable activities (e.g., seasonal harvesting).
 - Validation of models should be conducted across a range of habitat and culture conditions in order to assess their general applicability.
 - Uncertainty estimates for parameters, formulations, and results need to be an integral part of model studies.

Most of the potential measures of ecological carrying capacity now consider only a single or a constrained number of ecosystem components (Broekhuizen et al., 2002). As scientists learn more about the functioning of marine ecosystems, it is likely that their understanding of the factors affecting ecological carrying capacity will evolve; therefore, they need to develop a flexible approach to allow for these changes. While current modeling efforts try to incorporate the above points into estimates of ecological carrying capacity, the development of models for estimation of carrying capacity needs to progress in parallel with a coordinated and sustained empirical measurement effort that will provide the information needed to validate the projections from the models and subsequently modify the models in response.

FINDINGS AND RECOMMENDATIONS

Finding: Some attempts have been made to include an evaluation of uncertainty in the parameters used in model-based estimates of bivalve production and ecological carrying capacity.

Recommendation: Model development and empirical data collection and analysis must be parallel and interacting activities for uncertainty to be integrated effectively into the models.

Finding: Assessment of bivalve mariculture has occurred mostly at the local scale by measuring the “footprint” of the shellfish farm. Scaling up these effects to whole systems has been limited by the difficulty in identifying a signal attributable solely to mariculture and by the capacity and resources to make meaningful measurements over

larger areas. Similarly, most of the potential measures of ecological carrying capacity consider only a single or a few ecosystem components. Our understanding of factors that affect ecological carrying capacity will evolve as scientists learn more about the functioning of marine ecosystems.

Recommendation: Managers should utilize models based on empirical data that can estimate carrying capacity relative to bivalve production, ecosystem, and social constraints. The models provide an approach for addressing many of the issues that are associated with understanding multiple farm interactions and cumulative effects of other coastal zone activities at a scale relevant to coastal ecosystems.

Recommendation: Further development and refinement of models for estimating carrying capacity should be encouraged. This will require a coordinated and sustained measurement effort to provide the empirical data necessary for iterative modification of these models and to validate projections produced by the models. Models should be designed to address the needs of managers and mariculturists alike. In addition, model parameters and general model outputs should be presented in clear and concise terms that are understandable and acceptable to all users.

Finding: With continued development and refinement, the current generation of models may provide scientifically sound and relatively robust results that can guide the development and management of bivalve mariculture. However, current models do not include the processes that influence social needs and regulations.

Recommendation: The portfolio of research on carrying capacity should include work on social and political dimensions.

Finding: Carrying capacity is a function of the local environment, in terms of both ecological and social factors. Ecological carrying-capacity models do not take societal constraints into account. It is only through a feedback process between ecological and social carrying capacity that a compromise can be reached.

Recommendation: Assessment of carrying capacity for a bivalve mariculture facility should involve both natural and social scientists along with coastal managers.

6

Economic and Policy Factors Affecting Bivalve Mariculture

Numerous economic and regulatory factors have a direct bearing on the viability of bivalve mariculture. Mariculture producers must compete in product markets with wild-harvest molluscs and with imports, many of which come from high-volume and low-cost mariculture operations in countries with lower labor costs and, often, less stringent regulatory regimes than the United States. The regulatory regime for nearshore mariculture varies from state to state and sometimes from town to town (Duff et al., 2003). An extensive literature documents cases where uninformed, outdated, or inappropriate regulatory regimes impede mariculture development (National Research Council, 1978; Kennedy and Breisch, 1983; DeVoe and Mount, 1989; Bye, 1990; Rychlak and Peel, 1993; Ewart et al., 1995; Massachusetts Coastal Zone Management, 1995; National Oceanic and Atmospheric Administration, 1999). In some instances, inconsistencies in the law produce an uncertain legal environment for mariculture operations, and regulators may be in the conflicted position of both promoting the development of the industry and preventing conflicts with other uses of the land and water (National Research Council, 1992; DeVoe, 1999).

A number of studies have reviewed policies that both facilitate and constrain aquaculture and mariculture (Kane, 1970; Wildsmith, 1982; Eichenberg and Vestal, 1992; Rychlak and Peel, 1993; Barr, 1997; Hopkins et al., 1997; Rieser, 1997; Brennan, 1999; Rieser and Bunsick, 1999; McCoy, 2000). In this chapter, the committee reviews the major policy and economic factors that affect the size and location of bivalve mariculture industry development around the United States. While some laws and

regulations may constrain mariculture development, others can serve to advance its growth. Some states have developed effective practices for interagency coordination, technical assistance, sponsorship of research and development efforts, marketing assistance, and other forms of industry promotion (Jarvinen, 2000; Jarvinen and Magnusson, 2000).

REGULATION AND PERMITTING

As traditionally practiced in the United States, bivalve mariculture relies heavily on nearshore waters that are under state or town jurisdiction. These nearshore locations may be particularly conducive to bivalve growth because of high-planktonic food levels and suitable temperature, and they provide ready access—often without the need for a boat—for stock management and harvesting. They also expose the mariculture operations to extensive use conflicts because the nearshore waters of the United States are heavily used for recreational and aesthetic purposes. The legal regime governing U.S. coastal waters gives jurisdiction over these areas to individual states, with complex and sometimes inconsistent results.

Following Duff et al. (2003), the committee summarizes the main types of policies and regulations that govern bivalve mariculture, focusing on the following areas:

- leasing and tenure policies
- jurisdictional complexity
- land use, zoning, and tax policies
- interstate transport policies
- offshore mariculture policy

Leasing and Tenure Policies

Nearshore mariculture operations usually are sited on or in “public trust” resources (i.e., state intertidal and subtidal lands and state waters). Under the public trust doctrine, certain tidelands, coastal waters, and other public lands are held in trust by the government (in this case, the state) for the benefit of the state’s citizens for purposes that include fishing, navigation, and commerce (Duff et al., 2003). In some instances, public trust purposes also include ecological functions or public recreation (Eichenberg and Vestal, 1992). Public trusts under this doctrine operate much like private trusts, with defined property, trustee(s), and beneficiaries. Under the public trust doctrine and common law, the state as trustee is generally proscribed from divesting the property permanently. As a result, mariculture operations generally cannot purchase permanent rights to a marine

or estuarine site and must enter into lease or tenure arrangements. Since, in some instances, these are limited in term and subject to conditions and challenges, it can be difficult for mariculture operations to demonstrate long-term security of tenure (e.g., for the purpose of securing financing for farming operations and equipment).

The public trust doctrine applies to submerged lands and overlying waters under the jurisdiction of the states, but its application varies by state. For example, in Massachusetts, Maine, Pennsylvania, Rhode Island, and Virginia, the intertidal lands (between mean-high and mean-low water) may be held as private property (Underwood, 1997), but private owners must accommodate the public's right to "fish, fowl, and navigate" in or over them.¹ In Massachusetts, mariculture is not considered one of the public trust purposes that must be accommodated (Duff et al., 2003), but in Washington State, the right of oyster farmers to purchase and own tideland areas for the purpose of mollusc cultivation extends back to the 1800s (Woelke, 1969). Some states pass along responsibility for managing nearshore waters, including assignment of mariculture leases, to local town government.

To the extent that bivalve mariculture also requires federal permits, it may be subject to the "federal consistency" requirements of the Coastal Zone Management Act (16 USC 1451 et seq.), which may require a determination of the extent to which the mariculture operation is consistent with a state's coastal management plan. One federal permit that is commonly required for mariculture is the Section 10 (Rivers and Harbors Act) permit issued by the U.S. Army Corps of Engineers (USACE), which governs the installation of mariculture gear that may pose an obstruction to navigation in navigable waters. Application for a Section 10 permit in turn can trigger USACE's "public interest review process," which can involve the assessment of environmental impacts and the development of an environmental impact statement. In the course of evaluating Section 10 permit applications, USACE typically seeks comments from the National Marine Fisheries Service's Protected Resources Division, which determines the likelihood of any impacts to endangered or threatened species or marine mammals and from other federal (e.g., Environmental Protection Agency, U.S. Coast Guard, U.S. Fish and Wildlife Service) and relevant state agencies (Duff et al., 2003).

For existing commercial shellfish aquaculture operations, USACE has issued a "Nationwide Permit" (Federal Register, 2007) that "authorizes the installation of structures necessary for the continued operation" as well as "discharges of dredged or fill material necessary for shellfish seed-

¹ *Opinion of the Justices*, 424 N.E.2d 1092 (Mass. 1981); *Bell v. Town of Wells*, 557 A.2d 168 (Me. 1989).

ing, rearing, cultivating, transplanting, and harvesting activities.” The Nationwide Permit does not apply to new operations or expansions; to the cultivation of additional species; to the construction of structures, such as docks and piers; or to the deposition of shell material into the water as waste (Federal Register, 2007). This Nationwide Permit simplifies continued operation of existing shellfish mariculture projects in some regions. However, state and local authorities may place additional constraints that require a separate certification or waiver for authorization of continued operations.

Jurisdictional Complexity

In 1981, a comprehensive review of aquaculture regulations across the nation (the “Aspen Report” sponsored by the U.S. Fish and Wildlife Service; Aspen Research and Information Center, 1981) identified at least 120 federal laws that either directly (50 laws) or indirectly (70 laws) affected aquaculture, along with more than 1,200 state statutes regulating aquaculture in 32 states. The Aspen Report concluded that many aquaculture businesses must obtain at least 30 permits² to site and operate their businesses.

Regulatory jurisdiction over bivalve mariculture typically falls under the auspices of multiple local, state, and federal agencies. Many states recognize mariculture as a form of agriculture and give regulatory control to the state agriculture department, but these departments usually do not have jurisdiction over the public lands where mariculture takes place. Public land management typically falls under the authority of the state department responsible for environmental protection. Regulatory complexity is further increased when towns or counties are given jurisdiction over local waters. From the shellfish growers’ point of view, the effect of this regulatory complexity in many cases has been an expensive, time-consuming, and sometimes unsuccessful process for obtaining permits (Duff et al., 2003).

In response to concerns over real or perceived regulatory complexity, many states have designated a particular state agency as the “lead” and starting point for mariculture permit applications. Many coastal states also have created interagency coordinating committees or task forces to facilitate the mariculture permit process. Some states produce written guidance to help permit applicants understand the set of permits required for different mariculture operations and the process and sequence for obtaining them. For example, Connecticut has established an Interagency

² For comparison, a marina or a commercial bakery typically requires fewer than 10 permits.

Aquaculture Coordinating Committee comprising the departments of agriculture, environmental protection, consumer protection, and economic development to provide for the development and enhancement of mariculture in that state.³ Similarly, Pennsylvania established the Aquaculture Advisory Committee⁴ to encourage long-term investment by reducing the number of agencies involved (by transferring most authority to the state's Department of Agriculture) and including mariculture in promotional and economic developmental programs that are available to other industry sectors.⁵

Land Use, Zoning, and Tax Policies

Some states effectively subsidize mariculture operations by exempting them from sales or use taxes.⁶ States also may promote mariculture production via zoning designation or waterfront revitalization programs.⁷ In some cases, regulations have been promulgated for the express purposes of preventing competition between fishermen and mariculturists. New Jersey, Massachusetts, and North Carolina, for example, limit bivalve cultivation to bottom areas where bivalves do not grow naturally. These regulations have caused problems in New Jersey, where mariculture industry participants have pointed out that lease areas suitable for bivalve grow-out are unavailable (Duff et al., 2003).

Interstate Transport Policies

State rules concerning the importation of fish eggs, fingerlings, and bivalve seed from other states are non-uniform. Confusion, misinformation, and non-compliance have contributed to the introduction of non-native species and increased incidence of disease, harming some bivalve mariculture businesses and changing the nature of local or regional ecosystems (e.g., Simberloff, 2005). Although some states have restricted transport to a few trusted companies, other states do not follow a strict protocol or possess testing facilities or regulations for the transport of live fish, eggs, or seed. The existence of inconsistent policies for interstate shipment of these mariculture products has hampered the ability to develop a comprehensive interstate transport capability. When limited

³ Connecticut General Statute, Ch. 422 § 22-11e.

⁴ 3 Pa. C.S.A. § 4216 (Pennsylvania).

⁵ 3 Pa. C.S.A. § 4202 (Pennsylvania).

⁶ See § 20-10-3.1 Sales and use tax exemption (Rhode Island), 54:32B-8.16(a) (New Jersey), and 36 M.R.S.A. § 2013 (Maine).

⁷ See § 45-24-30 (6) (Rhode Island) and NY EXEC § 915 (5) Waterfront revitalization programs (New York).

supplies of bivalve seed are available, market prices tend to rise because of the lack of supply or competition (Duff et al., 2003).

A related constraint facing some mariculture operations concerns the export of their product to states where commercial fishery rules define the characteristics of the product. For example, a three-inch size restriction on the commercial harvest of oysters in Massachusetts prevents the sale or even the transport through the state of smaller oysters grown on farms in Connecticut or Rhode Island (Duff et al., 2003).

Offshore Mariculture Policy

Regulatory complexity, use conflicts, and (in some cases) water-quality issues⁸ in nearshore waters have led to greater interest in offshore or open-ocean mariculture. The technical and economic feasibility of open-ocean bivalve mariculture has been demonstrated to some degree (e.g., mussels in the northeastern United States; Langan and Horton, 2002; Kite-Powell et al., 2003).

The regulation of offshore mariculture in the United States remains unsettled. At present, there is no federal policy pertaining specifically to the permitting of mariculture in waters under federal jurisdiction, typically 3–200 nautical miles offshore, known as the exclusive economic zone. At a minimum, a Section 10 permit is required from USACE, and in some cases, approval from fisheries management councils may be required. In the absence of a settled and transparent regulatory framework, not only is expansion of the existing industry hampered, but potential future growth and research in this area is discouraged (Barr, 1997; Brennan, 1999; National Oceanic and Atmospheric Administration, 1999). Legal rules that establish and enforce private property rights and use privileges (e.g., though leasing) are critical to the development of the industry both onshore and offshore (Hoagland et al., 2003; 2007).

A bill defining federal policy and permit processes for mariculture in the exclusive economic zone, the National Offshore Aquaculture Act has been introduced several times, most recently in 2007 as H.R. 2010 and S. 1609 in the 111th Congress (National Oceanic and Atmospheric Administration, 2008a). The 2007 bill would address the current gaps in U.S. offshore mariculture regulation by:

- authorizing the Secretary of Commerce to issue offshore mariculture permits

⁸ For example, some nearshore shellfish harvesting areas are periodically closed for violating fecal coliform standards.

- requiring the Secretary of Commerce to establish environmental requirements for offshore mariculture
- requiring the Secretary of Commerce to work with other federal agencies to develop and implement a coordinated permitting process for offshore mariculture
 - exempting permitted offshore mariculture from fishing regulations that restrict size, season, and harvest methods
 - authorizing a research and development program for all types of mariculture

The National Offshore Aquaculture Act has not been passed by Congress to date, in part because of controversies over the adequacy of environmental regulations in the bill and because of the role of states in regulating offshore mariculture.

MARKETS, PRICES, AND TRADE

The extent and locations of bivalve mariculture activities around the United States are influenced by market and trade conditions. This section describes in broad terms some recent trends in the U.S. markets for oysters, clams, and mussels and points out implications for U.S. bivalve mariculture.

For finfish and crustaceans, aquaculture activities are easy to distinguish from wild-capture fisheries. For molluscs, the distinction is sometimes less clear. Natural oyster beds, for example, may be leased to private individuals who harvest and maintain them, relying on natural spat settlement but seeking to maximize yield by providing an ideal substrate. Wild clam beds may be seeded with juveniles raised in hatcheries (e.g., Peterson et al., 1995), either by clam farmers who have exclusive rights to harvest there or by towns or states seeking to enhance the clam stock for the general public (which may include small-scale commercial harvesters). (For the purposes of origin labeling [P.L. 107-171] of seafood sold in the United States, seafood is considered “farm-raised” if it originated in a hatchery.) In part because the line between wild-stock fisheries and mariculture of bivalve molluscs can be hard to define, the National Oceanic and Atmospheric Administration (NOAA) reports the commercial landings of oysters, clams, and mussels as a single quantity, regardless of whether the source is wild stock or mariculture (National Oceanic and Atmospheric Administration, 2009b). This makes it difficult to distinguish trends in mariculture and wild-harvest production using the NOAA data. NOAA reports separate mariculture production statistics as part of its annual “Fisheries of the United States” report (National Oceanic and

Atmospheric Administration, 2009c), but the accuracy of these numbers has been called into question by culturists (see below).

A second complication with the bivalve landings is that NOAA reports the landings and prices for oysters, clams, and mussels in units of meat weight (National Oceanic and Atmospheric Administration, 2009b), whereas other units of weight or volume are typically used for bivalves by growers and merchants (e.g., shell-on live weight, bushels, baskets, bags, individuals). There is no standard reporting process for bivalve landings held in common across all U.S. states. Also, the same species of bivalves may be sold into two different markets with different customary units of measurement that are deeply engrained in the tradition of the business. For example, oysters may be sold to the live half-shell market by the piece or by the bushel, or they may be sold in processed form (removed from the shell and cooked or smoked) by meat weight. NOAA converts reported landings from many markets into a single meat-weight equivalent. Some growers are skeptical about the accuracy of the conversion process and of the resulting data (Robert Rheault, personal communication).

Oysters

Global oyster production is reported by the Food and Agriculture Organization of the United Nations (2009) to have reached 4.9 million metric tons (live weight, the nominal weight at the time of harvest) in 2004. The culture of oysters dates back to Roman times (Clark, 1964). Hatchery production of seed was pioneered in the 1980s (Chew, 1984). Mariculture today accounts for about 94% of global oyster production (Food and Agriculture Organization of the United Nations, 2009). The Pacific oyster, *Crassostrea gigas*, accounts for 99% of cultured oyster production; it is the world's most commonly cultured bivalve species. More than 93% of oyster mariculture production takes place in Asia and the Pacific.

U.S. oyster production (Figure 6.1) is reported by NOAA to have accounted for about 10,000 metric tons (meat weight) on the east coast and in the Gulf of Mexico (*Crassostrea virginica*) and about 6,000 metric tons (meat weight) on the west coast (*Crassostrea gigas*) in 2006. About two-thirds of this is considered by NOAA to be mariculture production. Present U.S. total production levels are well below historic highs. Before the Chesapeake Bay wild oyster population further declined in the 1980s (National Research Council, 2004), *C. virginica* production exceeded 20,000 metric tons per year; historically, U.S. oyster production peaked in the late 1800s at more than 80,000 metric tons (meat weight) per year.

U.S. imports of oysters (Figure 6.1) declined from 1989 to 1996 but have been gradually rising since then to 11,000 metric tons per year

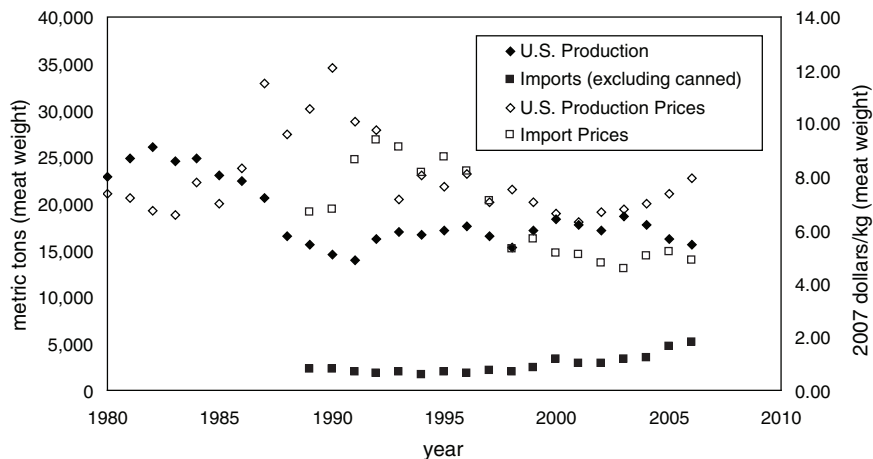


FIGURE 6.1 U.S. oyster production, including wild harvest and mariculture, (1980–2006) and imports (1989–2006) and prices in constant 2007 dollars. SOURCE: National Oceanic and Atmospheric Administration (2007; 2009b, d).

(meat weight). Most imports come from cultured oyster production in China and South Korea. The United States exports about 3,000 metric tons per year, about 19% of the total domestic oyster production. U.S. production accounts for about 4% of global oyster production, and the U.S. market (consumption) accounts for approximately 6% of global consumption (in volume terms). China accounts for about 82% of global oyster production (Food and Agriculture Organization of the United Nations, 2009).

According to NOAA data, average U.S. oyster prices have been declining in real terms since 1990 (Figure 6.1). This broad trend in average prices masks significant differences across product markets (half-shell versus canned) and production regions. For example, a half-shell oyster in New England may sell for three times the value of a half-shell oyster on the Gulf of Mexico (Robert Rheault, personal communication).

Clams

Global mariculture production of clams (including cockles and others) is reported by the Food and Agriculture Organization of the United Nations (2009) to have reached 4.1 million metric tons (live weight) in 2004. Clams are the fastest growing component of global mollusc production, with output rising at 9.1% per year. NOAA reported U.S. production

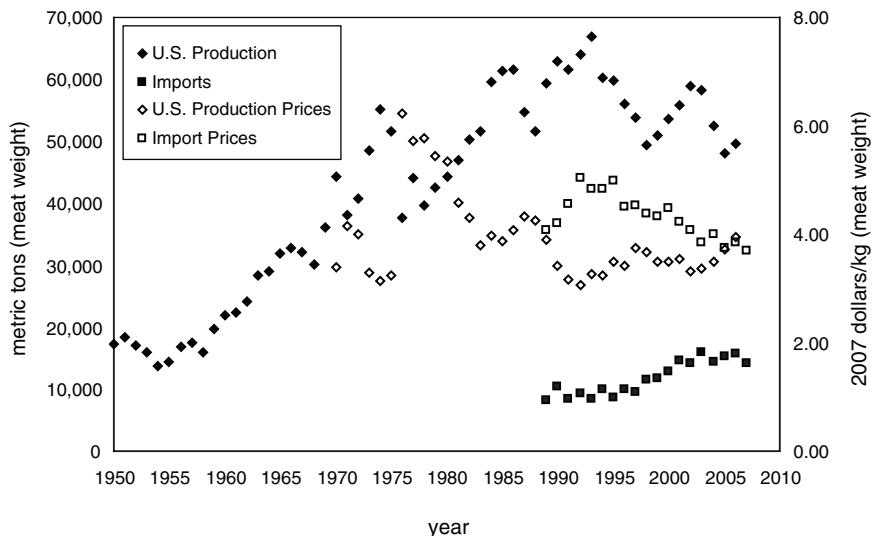


FIGURE 6.2 U.S. clam production, including wild harvest and mariculture, (1950–2006) and imports (1989–2007) and prices in constant 2007 dollars. Production data include quahogs, surf clams, Manila clams, soft-shell clams, and geoducks. SOURCE: National Oceanic and Atmospheric Administration (2007; 2009b, d).

of clams (Figure 6.2) at about 50,000 metric tons (meat weight) in 2006, with about 10% of the harvest coming from mariculture.

Imports provide another 15,000 metric tons per year (meat weight) and come primarily from China, Thailand, and Vietnam (processed) and from Canada (fresh and processed). U.S. mariculture and import volumes have been growing slowly; total U.S. consumption has been stable since the 1980s. Consumption in the U.S. market accounts for an estimated 6% of global clam production. Average U.S. prices of clams have been generally stable since the mid-1990s (Figure 6.2), but prices of imports have declined by more than 20% in real terms, likely reflecting increased supply due to strong growth in global clam mariculture.

Mussels

Global mariculture production of mussels is reported by the Food and Agriculture Organization of the United Nations (2009) to have reached 1.9 million metric tons (live weight) in 2004. Global mussel production is rising at 4.5% per year. U.S. production of mussels (Figure 6.3) is reported by NOAA to have peaked around 5,000 metric tons (meat weight) in 1988 and has been generally declining since then. There is very little maricul-

ture production of mussels in the United States. The Pacific Coast Shellfish Growers Association (2005) reports production of 1,600 metric tons (live weight) on the U.S. west coast, primarily in Washington and California, in 2005.

Imports of mussels rose from negligible amounts in the late 1980s to nearly 25,000 metric tons per year in 2007 and account for 95% of mussels consumed in the United States. This surge in U.S. imports coincided with strong growth of export-oriented mussel mariculture in Canada and New Zealand and more recently in Chile. Canada (fresh product, mainly *Mytilus edulis*) and New Zealand (processed, mainly *Perna canaliculus*) account for 41% and 49% of U.S. imports, respectively, by weight. Consumption in the U.S. market accounts for less than 3% of global mussel production. Per person consumption in the United States grew significantly over the past 15 years but still remains a small fraction of per person consumption in Western Europe. For example, per person consumption of mussels in the United States is on the order of 0.25 pounds per year, compared to more than 6 pounds per year in the Netherlands and more than 10 pounds per year in Spain (Food and Agriculture Organization of the United Nations, 2008b).

Figure 6.3 shows U.S. average price trends for fresh mussels, based on NOAA data, on a meat-weight basis. Average import prices dropped quickly as import volumes rose from 1990 to 1995 and have since stabi-

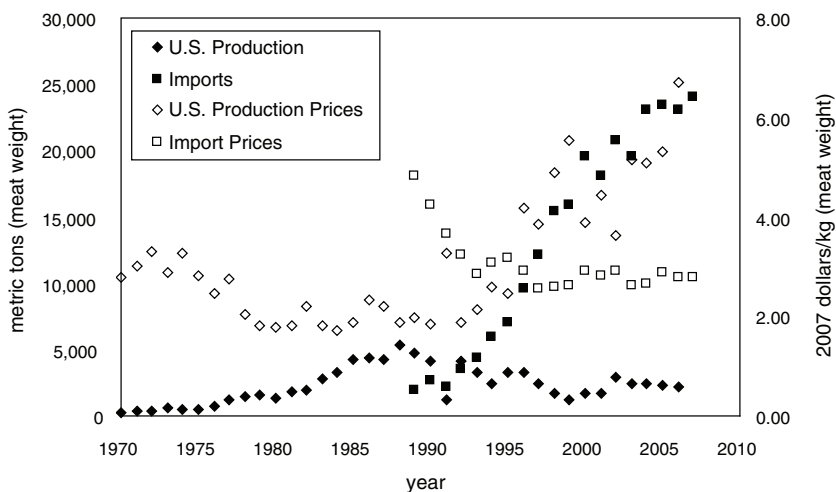


FIGURE 6.3 U.S. mussel production, including wild harvest and mariculture, (1970–2006) and imports (1989–2007) and prices in constant 2007 dollars. SOURCE: National Oceanic and Atmospheric Administration (2007; 2009b, d).

lized. Strong marketing campaigns accompanying imports contributed to growth in the U.S. market for mussels, both live and processed. U.S. producers have responded to low-price foreign competition by focusing on higher-priced, higher-grade live and fresh products destined for the local and regional niche market segments.

From the point of view of U.S. mariculture producers, the markets for the three major bivalve groups present both commonalities and stark differences. In all three markets, the United States is a small player in a large and growing global market for both fresh and processed product. Most U.S. production is consumed domestically and accounts for the majority of sales of oysters and clams in the United States. With small fractions of the domestic product destined for export, the United States is a net importer in all three markets, and U.S. mariculture producers generally face competition from low-cost imports of similar products. Domestic mariculture production is most significant in the oyster market, where it is roughly on par with wild-capture production and imports. Domestic mariculture is relatively weaker in the clam market, which is still dominated by wild-capture supply; it is weakest in the mussel market, which is dominated by imports.

Because it is difficult for U.S. growers to compete on price in the low-cost, processed bivalve segments of the global market, most U.S. bivalve mariculture producers today seek to serve local or regional niche markets for high-priced fresh or value-added products (Duff et al., 2003). In the past, U.S. northeast bivalve producers have complained about damages from “dumping” (fresh mussels from Canada) and from mislabeling of imported or non-local bivalves (cultured clams grown originally outside the northeast labeled improperly as local product) (Duff et al., 2003). In 2003, Congress enacted a “Country of Origin” provision (P.L. 107-171), requiring the labeling of seafood sold in the United States to indicate the country of origin and whether the product is wild or farm-raised. The labeling requirement went into effect for seafood in 2005; it has since been extended to other foods as well. This should make it easier for U.S. producers to distinguish domestic product from imports in the eyes of the consumer.

U.S. Seafood Supply and Trade Balance

Some advocates for aquaculture (including finfish, crustaceans, and molluscs) suggest that the United States should promote increased domestic production of seafood, in part because this would reduce the nation’s reliance on foreign imports (National Oceanic and Atmospheric Administration, 1999). Although there are risks associated with heavy reliance on imported seafood, there are significant economic benefits associated

with international seafood trade—it is a source of export earnings for many (sometimes less developed) nations, and U.S. consumers benefit from readily available and low-cost imported seafood products. The net benefits to the U.S. economy of reducing the nation’s seafood trade deficit by increasing domestic production are uncertain. A broad effort to boost aquaculture in the United States could in theory achieve this goal, but increasing bivalve mariculture alone is unlikely to make a significant difference in the nation’s overall seafood trade balance.

The United States imported 2.37 million metric tons of edible seafood products (including all types of finfish and shellfish) in 2008 and exported 1.16 million metric tons (National Oceanic and Atmospheric Administration, 2008b). The 2008 imports were valued at about \$14.2 billion and exports at about \$4 billion, creating an edible-seafood trade deficit of \$10.2 billion (National Oceanic and Atmospheric Administration, 2008b). (Non-edible seafood⁹ product imports in 2008 were valued at \$14.3 billion and exports at \$16.8 billion, so the United States is a net exporter, in value terms, of non-edible seafood products.)

NOAA (2009a) estimates that in round weight (live, whole fish) terms, U.S. domestic production from fisheries and aquaculture accounted for about 3.5 million metric tons in 2008; clams, oysters, and mussels accounted for approximately 1.5% of the total by weight and about 7.5% by value. Imports contributed the equivalent of 4.74 million metric tons, and exports accounted for 2.38 million metric tons, for net domestic consumption of 5.37 million metric tons of edible seafood. This supported an average U.S. seafood consumption of 16 pounds of edible seafood products per person (National Oceanic and Atmospheric Administration, 2009a).

The U.S. seafood trade deficit thus is due to large net imports of edible products. The majority of the edible fishery-product trade deficit consists of five species groups: shrimp, crabs, tunas, salmon, and lobsters. Since 1997, shrimp has been the largest single-species group contributor to the edible-seafood trade deficit. Groundfish, salmon, and lobster are the largest contributors by value to U.S. seafood exports. Reflecting the large global trade in seafood products, U.S. seafood imports come from a diverse set of exporting nations. Canada, China, and Thailand are the most significant sources of U.S. seafood imports (National Oceanic and Atmospheric Administration, 2005).

Two risks associated with imported seafood are health issues and the possibility of limited supply at some point in the future. While seafood consumption is generally considered to have significant health benefits, it can also contribute to health problems when seafood is contaminated

⁹ Non-edible seafood refers to fish products intended for purposes other than human consumption, such as fish meal.

via pollution in the water, in prey or feed, or through the application of antibiotics and when it is processed incorrectly (Kite-Powell et al., 2008). In the United States, seafood is implicated in a significant number of food-borne illnesses, and many observers have been critical of seafood inspection, particularly for imports (Ralston and Kite-Powell, in review). However, there is little evidence to suggest that imported seafood is responsible for a disproportionate degree of health risk.

Several studies have considered likely future trends in U.S. seafood consumption, production, and trade (Delgado et al., 2003; Nash, 2004; Hoagland et al., 2007). While it is possible that better management of certain U.S. fish stocks (e.g., cod) and hatchery enhancement of wild stocks could increase wild-capture landings in the future, there is little reason to expect aggregate landings to increase dramatically. If the U.S. population continues to grow, as it has recently (i.e., by about 1% per year), and assuming (conservatively) that per-person consumption of seafood remains roughly at present levels (16 pounds of edible meat per person per year¹⁰), U.S. seafood consumption will rise by 20% to about 6.2 million metric tons per year by 2025. If U.S. capture landings and existing aquaculture production remain at present levels, this leaves a projected shortfall in 2025 of 2.7 million metric tons per year (round weight) to be filled by some combination of additional U.S. aquaculture and net imports.

Nash (2004) and others suggest that U.S. aquaculture production could be increased significantly, with a concerted effort, from its present level of less than 500,000 metric tons per year. U.S. aquaculture production has grown by an average of 6% per year (in volume terms) since 1983, although this growth has been slower during the past decade, and both imports and exports of seafood products have grown at an average rate of about 2% per year for the past 15 years (Hoagland et al., 2007). Unless the balance of U.S. aquaculture production shifts toward species, such as shrimp, tuna, and salmon, or consumer tastes change dramatically, it is unlikely that domestic production can significantly reduce imports in the near future. Nash (2004) suggests that the United States could triple domestic production of bivalves to more than 300,000 metric tons per year (live weight) by 2025; in volume terms, this could displace all current bivalve imports. However, in bivalves as in other species, U.S. mariculture production is likely to focus on high-value niche markets for fresh product and may not compete directly with low-cost processed imports. Even if U.S. aquaculture production growth can be increased by easing constraints and encouraging investment, it is likely that low-cost imports

¹⁰ Global seafood consumption is around 35 pounds per person per year—twice the U.S. consumption rate.

will remain attractive and continue to supply a significant fraction of U.S. seafood in the coming decades.

LOCAL TRADITIONS AND NOT-IN-MY-BACKYARD (NIMBY) ISSUES

Local traditions and use conflicts in the nearshore waters represent both a constraint and, in some instances, an opportunity for bivalve mariculture. In communities or settings where mariculture has not been part of the established or traditional waterfront, recreational-use patterns (boating, fishing, swimming) and aesthetic considerations (ocean and bay views from waterfront homes) may lead to public objections to permitting and siting mariculture operations (Vestal, 1999). In places where there is a history of bivalve culture or an established shellfish fishing industry, the public may be more receptive to devoting additional nearshore areas to new mariculture proposals. The inclination to support mariculture may be weakened if there is a large influx of residents who do not share the community's cultural fishing traditions. Even in some traditional fishing communities, strong objections to mariculture can arise based on loss of public-trust bottom that historically served to support extractive fishing operations. Shellfish growers can increase the social carrying capacity and reduce political opposition to mariculture leases by engaging constructively with the local community, for example, by supporting local charitable causes and designing their operations to minimize visual and physical conflicts with established uses.

Bivalve mariculture proposals that require some portion of nearshore waters or tidelands to be "off limits" to foot or boat traffic may run afoul of public rights of use and access. For example, bivalve mariculture operations that utilize gear (e.g., cages, bags, racks, longlines) on the bottom or in the water column may interfere with other uses of the coastal zone, such as recreational and commercial fishing, shipping, and boating. In several northeast states, mariculture is given lower priority than navigation, fishing, and most other uses of the coastal zone. The subordination of mariculture and other "non-traditional" uses of coastal areas is evident in a number of state constitutions.¹¹ This has constrained some operations (Duff et al., 2003).

Some states accord a preference for certain uses of submerged lands to owners of upland property adjacent to navigable waters (riparian rights). The most important preference is a right of access by dredging, filling, or wharfing. Mariculture may be constrained by riparian rights to the extent that these activities displace mariculture operations or put shellfish

¹¹ Rhode Island Constitution Art. 1, § 17 Fishery rights – Shore privileges.

farmers who are non-riparian owners at a competitive disadvantage. The application of riparian rights varies by state (Duff et al., 2003).

In coastal settings where excess nutrient inputs are causing ecological problems or where historic natural bivalve stocks have been depleted, prospects for permitting of bivalve mariculture can sometimes be improved by educating the local community about the ecological benefits (e.g., water filtration, nutrient removal, habitat enhancement for finfish and crabs) of bivalve mariculture. Numerous towns around the United States have successfully developed marine water-resource management plans that balance recreational and aesthetic considerations with bivalve mariculture; see for example the recently developed plan for Duxbury Bay in Massachusetts (Duxbury Bay Management Commission, 2009).

FINDINGS AND RECOMMENDATIONS

Finding: The United States is a net importer of bivalve products, and this represents an opportunity for the expansion of bivalve mariculture production within the United States.

Finding: While some laws and regulations may constrain bivalve mariculture development, others can serve to advance its growth. Local traditions and use conflicts can have this dual effect as well.

Recommendation: States should streamline the permitting process for bivalve mariculture in state waters and identify areas within state waters where such activities are encouraged. Shellfish growers should engage the local community and design their operations to minimize conflicts.

Finding: Inconsistencies in the law produce an uncertain legal environment for mariculture operations. Confusion, misinformation, and non-compliance of interstate transportation policies have contributed to the introduction of nonnative species and the increase in incidence of disease. The existence of inconsistent policies for interstate shipment of these mariculture products has hampered the ability to develop a comprehensive interstate transport program.

Recommendation: States should collaborate on the development and implementation of consistent bivalve mariculture and transportation policies.

7

Ecosystem Services of Bivalves: Implications for Restoration

OVERVIEW OF ECOSYSTEM SERVICES PROVIDED BY BIVALVE MOLLUSCS

Over the past quarter century, collaborations among mollusc biologists, biological oceanographers, fluid dynamicists, ecosystems ecologists, and natural resource economists have developed an appreciation of the many roles that suspension-feeding bivalves play in organizing estuarine and, to a lesser degree, coastal marine ecosystems. Following publication of the seminal book *Nature's Services* (Daily, 1996), ecologists and natural resource economists have collaborated extensively to identify and partially quantify important services provided by organisms and natural habitats. This research has important applications to natural resource management. Traditional approaches to managing environmental resources often failed to recognize the costs of taking those services for granted and allowed development to degrade natural ecosystems and processes in ways that reduce the often substantial value of ecosystem services (Costanza et al., 1997). Appreciation of ecosystem services also helps prioritize and direct ecological restoration to enhance those resources that provide high levels of ecosystem services, for example, by targeting species that have declined from levels that prevailed before intense human modifications of the environment. This line of research has transformed perceptions about the value of oysters in particular, indicating that oysters and the reefs that they form can provide valuable ecosystem services (Lenihan and Peterson, 1998; Coen et al., 2007) that probably greatly exceed the value of oysters as an exploited commodity (Grabowski and Peterson, 2007). Many of the impacts

of suspension-feeding bivalves on the estuarine and marine ecosystem are potentially beneficial. This chapter acknowledges the potential ecosystem services that can be provided by suspension-feeding bivalves—as long as negative influences are effectively avoided or mitigated.

Although oysters have been the dominant target of these evaluations of bivalve ecosystem services, the beneficial biogeochemical functions provided by oysters are also provided by other suspension-feeding bivalves (Herman and Scholten, 1990; Dame, 1996; Dame and Olenin, 2005). All suspension-feeding bivalves filter particles, including phytoplankton, particulate organic matter, inorganic particles, and planktonic larvae of some marine invertebrates, from the water column and discharge biodeposits, a process that removes phytoplankton and biotic and abiotic particulates from suspension, clarifies the water column, may reduce settlement of some native marine invertebrates, and transfers organic- and nutrient-rich particulates to the bottom (Dame, 1996; Newell, 2004; Dumbauld et al., 2009). Oysters are physiologically capable of maintaining their active filtering function at higher concentrations of particulates, in large part because of their ability to reject particles before actual ingestion and eliminate them as pseudofecal biodeposits, whereas clams, cockles, and scallops lower their clearance rates as particle concentrations increase (Vahl, 1980; Prins et al., 1991; Hawkins et al., 1998a, b). The wide range of environmental conditions over which oysters can reduce turbidity and deposit organic material onto the bottom potentially renders their filtering services most valuable among suspension-feeding bivalves, especially when they exist as reefs of densely concentrated individuals. Pacific oysters (*Crassostrea gigas*) build structural reefs that project up into the water column in areas otherwise characterized by relatively flat sedimentary bottom, providing important habitat for other organisms (Coen et al., 2007; Grabowski and Peterson, 2007). This habitat provision service is less pronounced in infaunal and non-reef forming bivalves (e.g., native Olympia oysters [*Ostrea lurida*]). Blue mussels (*Mytilus edulis*) occupying soft-sediment habitats do not project up into the water column to any substantial degree, and the structures that they provide do not benefit from the vertical relief so important to oyster reefs (Lenihan and Peterson, 1998; Lenihan, 1999; Schulte et al., 2009). Nevertheless, they provide complex interstitial and outward-projecting structural habitat for many marine invertebrates and modify the community composition (Buschbaum et al., 2009). *Mytilus californianus* and other mussels occupying rocky habitats do provide structural habitat used by many small crustaceans and other invertebrates and fish (Paine and Suchanek, 1983). The shared biogeochemical functions of water clarification and biodeposition make all suspension-feeding bivalves a valued provider of ecological services to shallow-water ecosystems (detailed for oysters in Grabowski and Peterson [2007]).

BIVALVE ECOSYSTEM SERVICES

Turbidity Reduction by Filtration

Oysters and other suspension-feeding bivalves help buffer shallow waters of estuaries and coastal oceans against developing and sustaining excessive phytoplankton blooms in response to anthropogenic loading of nitrogen (Officer et al., 1982). These bivalves also remove inorganic sediments from suspension, thereby counteracting sedimentation from soil erosion (Landry, 2002). Chlorophyll concentration and turbidity are fundamental indicators of water quality. The filtration exerted by suspension-feeding bivalves can remove inorganic particles from the water column and the phytoplankton from suspension and can counteract a negative symptom of eutrophication (Haamer, 1996). This effect of suspension-feeding bivalves is most dramatically illustrated (see Box 1.1) by studies of the invasive clam *Potamocorbula* in San Francisco Bay (Alpine and Cloern, 1992; Thompson, 2005) and the zebra mussel after its invasion of and proliferation in the Great Lakes (MacIsaac, 1996; Strayer, 2009). Coupled biology–fluid dynamics studies have demonstrated how mussels also reduce phytoplankton concentration (Frechette et al., 1989) and how model clams in sediments (Monismith et al., 1990; Newell and Koch, 2004) affect particulate concentrations in the water column, consistent with field measurements on various real clams (Peterson and Black, 1991). The resulting enhancement of water clarity allows deeper light penetration, which has been shown to increase growth of submerged aquatic vegetation (SAV) (Everett et al., 1995; Carroll et al., 2008; Wall et al., 2008). SAV habitat has declined dramatically in many lagoons and estuaries around the world (Lotze et al., 2006; Orth et al., 2006; Waycott et al., 2009). Because of the importance of SAVs as a nursery habitat for many commercially important fish, crustaceans, and molluscs, the ecosystem services attributable to turbidity reduction by suspension-feeding bivalves include enhancement of an estuarine nursery habitat that itself serves valuable functions in the estuary. Growing use of remote sensing with ocean color from satellite images has important potential for assessing the magnitude and spatial and landscape scales of bivalve filtration on turbidity and phytoplankton concentrations (International Ocean Colour Coordinating Group, 2009).

Biodeposition of Organics Containing Plant Nutrients

The process of bivalve depositing nutrients and organic carbon and nitrogen to the bottom helps to fertilize benthic micro- and macroalgae and SAVs. Modeling and empirical studies have demonstrated that this fertilization process contributes to higher SAV production, a second

mechanism by which bivalves serve the estuarine ecosystem by promoting growth and development of SAV habitat (Reusch et al., 1994; Everett et al., 1995; Peterson and Heck, 1999; 2001a, b; Carroll et al., 2008). Organic deposition presumably also promotes the growth of deposit-feeding and herbivorous benthic invertebrates, which serve as prey for crabs and demersal fish, so the value of soft-sediment habitats to demersal predators on higher trophic levels may be enhanced by organic deposition from suspension-feeding bivalves. Oysters probably generate greater per capita organic deposition than other bivalve types because of their high filtration rate and capacity to discharge pseudofeces and thereby continue filtration under conditions of high turbidity. In areas of limited flow and long water residence times, biodeposition by dense concentrations of bivalves can be detrimental, causing oxygen depletion in the sediments.

Induction of Denitrification Associated with Organic Deposition

Several researchers have demonstrated that the biodeposits created by mussels and oysters induce denitrification, a process that helps counteract eutrophication by returning nitrogen into the atmosphere as inert nitrogen gas (Hatcher et al., 1994; Newell et al., 2002, 2005; Nizzoli et al., 2007). This function depends upon the capacity of the biodeposits to create anoxic microzones in the surface sediments where denitrifying bacteria are promoted. It seems likely that this ecosystem service is also associated with biodeposition by bivalves in general.

Sequestration of Carbon

Suspension-feeding bivalves produce external shells constructed of calcium carbonate. These shells thereby sequester carbon for long periods of time, dependent on the depositional environment in which the shells come to rest post mortem. Shells remaining in contact with brackish waters of estuaries or seawater in the coastal ocean will be subject to relatively rapid bioerosion by sponges and chemical dissolution as a function of acidity of the waters (e.g., Peterson, 1976). Shells incorporated deep into the sedimentary strata beneath the seafloor and shells buried in soils on land will remain intact indefinitely, allowing the molluscs to provide a long-lasting service of preventing the carbon from re-entering the atmosphere. Since molluscs are brought to land after harvest and their empty shells often discarded or buried terrestrially, mariculture probably increases the net long-term carbon sequestration in shells, as many of them are permanently removed from the growing waters. Removal of shell from the estuary or coastal ocean, however, inhibits the

degree to which the calcium carbonate can act as a buffer to acidification and as a promoter of recruitment and survival of those recruits by adding structural complexity to the sediments.

Provision of Structural Habitat That Promotes Epibiotic Diversity and Fish and Crustacean Production

Bivalve molluscs differ greatly in the habitat they provide, depending on whether they are completely infaunal in life position or whether they occupy sedimentary or hard bottoms. Among all molluscs, oysters are the most important providers of biogenic habitat because some can construct hard-bottom reef habitat that can rise well above the bottom in areas otherwise characterized by sediment. Eastern oysters (*Crassostrea virginica*) construct the most substantial reefs, although elevations of natural subtidal reefs have been substantially reduced by repeated habitat damage by dredges and other harvest gear (DeAlteris et al., 2004; Lenihan and Peterson, 1998). The presence of this hard substrate enhances biodiversity of macroalgae and benthic invertebrates that require stable hard substratum for attachment (Wells, 1961; Bahr and Lanier, 1981; Bruno and Bertness, 2001). The benthic invertebrate production together with the provision of structural habitat enhances use of the area by fish and mobile crustaceans by increasing prey availability and providing protection from higher-order predators amid the reef structure (Coen et al., 1999; Lenihan et al., 2001; Peterson et al., 2003; Coen and Grizzle, 2007). Empty shells of semi-infaunal bivalve, like pen shells (*Pinna* and *Atrina* spp.) and gaper clams (*Tresus* spp.), which remain in place after death of the molluscs, offer this habitat service to a lesser degree (Palacios et al., 2000; Gutierrez et al., 2003). Some mussels, such as the blue mussel, can form extensive beds on sedimentary habitats increasing habitat heterogeneity and harboring significantly different species assemblages from the surrounding sediments (Buschbaum et al., 2009). On hard substrata, shells of bivalve molluscs (e.g., mussels) do not represent the only local hard-bottom habitat. Nevertheless, the multiple layering of mussels in beds creates unique habitat occupied by at least 300 species of invertebrates (Paine and Suchanek, 1983; Beadman et al., 2004). Habitat provision is trivial to absent for completely infaunal clams (e.g., quahogs, soft-shell clams, cockles, surf clams). Some infaunal bivalves do serve as anchors for holdfasts of macroalgae, like *Katelysia rhinophera* hosting *Hormosira banksii* in Princess Royal Harbor, Western Australia (Black and Peterson, 1987), and such macroalgal growth is habitat for many smaller crustaceans and fish.

Not only do suspension-feeding bivalves influence the ecosystem through providing hard surfaces and interstitial spaces that offer habitat

for epibiota and fish and mobile crustaceans, but dense assemblages of these species also affect near-bottom flow regimes by emergent structure baffling water flows (Lenihan, 1999) and by creating strong current flows from exhalant siphons (O'Riordan et al., 1993). Changing flow patterns have significant direct and indirect effects on the geology, chemistry, and biology of the bottom habitats.

Habitat and Shoreline Stabilization

Some bivalve molluscs play important roles in stabilizing the bottom or protecting the shoreline from erosion by waves and currents. Oyster reefs rising up from the sedimentary bottom and positioned in linear arrays along marsh shorelines serve as natural living breakwaters that trip wave energy before it can strike and erode the marsh shoreline (Myer et al., 1997; Piazza et al., 2005). The giant clam (*Tridacna gigas*) helps cement and stabilize the calcium carbonate sediments and thereby promote recruitment of corals and recovery of coral reefs (Edgardo Gomez, personal communication). Mussels on rocky shores are not likely to play any role in stabilizing the rock substrate, and infaunal bivalves and scallops play only a modest role in stabilizing sediments.

USE OF MOLLUSCS TO PROMOTE ESTUARINE RESTORATION

Wild stocks of bivalve molluscs are susceptible to overexploitation by fishermen and have generally been depleted from estuaries and coastal oceans worldwide. Bivalve molluscs in soft sediments occupy an essentially two-dimensional bottom habitat; are largely sessile; can often be visually located by some surface clues, such as siphon openings, if not directly in the line of sight of fishermen; and, along with epifaunal bivalves like mussels, are readily accessed by fishermen because of their occupation of shallow or intertidal depths. All these characteristics combined with failures of fisheries management help to explain widespread depletion of bivalve molluscs.

The bivalve molluscs of estuarine sedimentary habitats are generally the most seriously depleted, whereas mussels are so abundant on rocky shores that they can sustain current fishing mortality in many locations (although see Lasiak [1991] for concerns and examples). Eastern oysters have declined in the Chesapeake Bay, Pamlico Sound, and other western Atlantic estuaries and coastal lagoons to perhaps only 1–2% of historic abundance prior to 1900 (Newell, 1988; Rothschild et al, 1994; Kirby, 2004). Worldwide, oysters have been grossly depleted from estuaries by overfishing, sedimentation, pollution, habitat damage, and disease (Lotze et al., 2006; Beck et al., 2009). Quahogs (*Mercenaria mercenaria*) are greatly

depleted by overfishing in eastern states (Peterson, 2002; Kraeuter et al., 2005; Myers et al., 2007). Soft-shell clam (*Mya arenaria*) populations are much depressed in many states by overfishing, predation by the invasive green crab, and perhaps also disease, and bay scallop fisheries have nearly disappeared for lack of scallops (Peterson et al., 2001; Myers et al., 2007). With the exception of less-accessible areas like Alaska and subtidal areas (e.g., geoducks in Washington), native hard-shell clam and oyster fisheries on the Pacific coast of the United States have declined and/or sometimes been replaced by introduced species like the manila clam (*Venerupis philippinarum*) and Pacific oyster (Lindsay and Simons, 1997; Robinson, 1997; Shaw, 1997).

Because of growing recognition of the ecosystem services provided by suspension-feeding bivalves, environmental advocates have increasingly pursued bivalve restoration as a component of restoring historical baseline conditions and functioning of estuaries (Rice, 2000). This remediation has been especially strong for oysters, in part because of their exceptional capacity for biogeochemical services associated with filtration under high turbidities but also because of the importance of habitat services provided by oyster reefs. Restoration of oyster filtration and deposition can restore water clarity, buffer against excess phytoplankton blooms induced by anthropogenic nutrient loading, filter out inorganic sediments, and lower turbidity (Everett et al., 1995; Carroll et al., 2008). Restoring native oysters can not only bring back an important species toward historical baseline levels but may also restore the filtration functions that improve water quality and enhance resilience of the estuarine ecosystem to eutrophication (Jackson et al., 2001a; Lotze et al., 2006). Oyster restoration also helps re-establish the biogenic habitat functions played by oyster reefs. Restoration of Eastern oyster reefs has been slow, in part because the less costly, shallowly constructed reefs tend to sink and become covered with silt, therefore reducing their habitat value (Stokstad, 2009). Indirectly, oyster restoration can also aid recovery of a critical nursery habitat, SAV, by improving light penetration to the bottom and by fertilizing the grasses via biodeposits (Carroll et al., 2008; Wall et al., 2008). This may lead to further enhancement of fish and crustacean production of species supported by SAV habitat.

Although most environmental advocacy of bivalve restoration has focused on oysters, other suspension-feeding bivalves play similar biogeochemical roles in the ecosystem. For example, restoring quahogs into existing SAV beds has been proposed by environmental organizations because of this biogeochemical function, and many species of bivalves could eventually be incorporated into ecological remediation and restoration plans.

A ROLE FOR MOLLUSCAN MARICULTURE IN ESTUARINE AND COASTAL OCEAN RESTORATION

If enhancing the abundance of suspension-feeding bivalves in estuarine and coastal ocean ecosystems helps restore beneficial functions and conditions that characterized the ecosystems prior to extensive human intervention, then to the degree that it replicates those functions, mariculture of these same or functionally analogous suspension-feeding bivalves to some degree holds the same promise (Haamer, 1996; Rice, 2000; Smaal et al., 2001; Landry, 2002; Newell, 2004). Consequently, bivalve mariculture deserves consideration as an estuarine, and perhaps also a coastal, ocean ecosystem restoration tool. Oysters may represent the most desirable type of bivalve for restoration of estuarine ecosystems because of their wide tolerance of turbidity, but other bivalve species can provide the same beneficial biogeochemical functions. Bivalve mariculture could serve to mitigate certain water-quality challenges, like excess chlorophyll or turbidity. In principle, culturists could receive appropriate compensation for mitigation based upon the level of environmental improvement achieved, and they could also sell their product, providing economic support to grow the industry and to enhance locally grown seafood production.

Mariculture of bivalve molluscs differs from restoration of native bivalves in the wild in several ways. Most culture methods for bivalves involve introduction of artificial materials to hold or protect the molluscs during grow-out. Although the structure provided by mariculture gear does not match the structure created by the corresponding wild molluscs, the structures associated with mariculture gear can themselves provide structural habitat for benthic epibiota, mobile crustaceans, and fish (DeAlteris et al., 2004; Powers et al., 2007). Because so much Eastern oyster reef habitat was lost to shell mining and oyster dredging, some mariculture structures that occupy a wide range of the water column may provide more functional hard-substrate habitat than degraded natural reefs. Natural populations of other oysters do not construct nearly as substantial vertical reefs, in which case mariculture gear may provide more high-relief, structural habitat. However, the introduction of artificial hard substrates often leads to colonization by invasive tunicates and other non-native clonal invertebrates, clearly not members of the historical baseline ecosystems. Thus, regular removal and responsible disposal of nonnative epifauna from racks, bags, nets, lines, cages, and other mariculture gear should be included in managing any bivalve mariculture used for restoration. In addition, some of this gear has the potential to entangle water birds, marine mammals, and turtles so site-specific testing of alternative gears and appropriate adaptive management to avoid gear impacts on vertebrates is in order. Management concerns include potential degradation of bottom habitat by overloading bivalve molluscs in shallow

areas without sufficient physical flushing to disperse organic loading and resultant sediment anoxia and by other processes, such as application of bottom-disturbing harvest gear. Most bivalve mariculture requires active management and maintenance of the gear, which involves direct human visitation, on foot or by boat. This activity can disturb sensitive or protected species, implying a need to manage human activity so as to avoid disturbance of valued species. In addition, mariculture of molluscs can introduce nonnative hitchhikers and disease microbes so protocols for transport, isolation, quarantine, breeding, and introduction of first-generation molluscs need to be followed to minimize risks of unintended introductions (International Council for the Exploration of the Sea, 2005). Furthermore, hatchery health and inspection protocols need to be followed to insure that eyed larvae for importation are free of any diseases not already present in the recipient location.

Because harvest for human consumption of suspension-feeding bivalves requires growing waters that are low in pathogens and pass the standard fecal coliform bacterial assays, it is often tempting to locate mollusc farms near parks, sanctuaries, reserves, and other locations where pollution from stormwater and industrial contamination is minimal. Such locations often coincide with the most valuable wildlife habitats so conflicts between bivalve mariculture and wildlife protection can arise (Würsig and Gailey, 2002). Resolution of these conflicts is usually feasible, but a proper set of siting and operations protocols that avoids unacceptable negative consequences of human disturbance and gear entanglements is required in and around parks, sanctuaries, and reserves. Furthermore, the social considerations associated with protection of natural areas, especially Wilderness Areas within national parks, could lead to exclusion of mariculture operations as a policy decision because of incompatibility with the concept and goals of a wilderness.

FINDINGS AND RECOMMENDATIONS

Finding: There is a need for improved quantifying of ecosystem service values so that markets for these ecosystem services could be further explored. Through a market-based approach, the present practice of externalizing the lost value could be changed to a system that assesses the true costs to those who contribute to the deterioration of natural estuarine and coastal marine ecosystems services.

Recommendation: Research at the interface of biology and natural resource economics should be aggressively supported to explore the various proposed ecosystem services of bivalve molluscs and to develop rigorous economic methods of putting values on those services. This could include methods that specify market values for those

services that yield to this approach and methods involving “willingness to pay” and other public preference approaches where markets do not exist. This research should then be utilized by policy makers to achieve social equity in putting costs of service losses on those responsible and using fees paid for lost services to restore those ecosystem services and thereby preserve them for the general public trust.

Finding: Many estuaries suffer from eutrophication and potentially could benefit from increasing the biomass of suspension-feeding bivalves to provide resilience to eutrophication and reduce the symptoms of excessive nutrient and sediment loading. In addition to limiting effects of eutrophication and sedimentation, restoring the beneficial biogeochemical functioning of suspension-feeding bivalves, especially oysters, could provide additional ecosystem services associated with filtration of phytoplankton and inorganic particles from the water column and deposition of organic biodeposits. These effects will be greatest in shallow and well-mixed water bodies, such as those typically found in estuaries, coastal bays, and lagoons.

Recommendation: Policies should be developed to encourage restoration of the biogeochemical filtration functions associated with suspension-feeding bivalves in estuaries. Such policies should consider both recovery of wild stocks and mariculture of (preferably native) suspension-feeding bivalves to restore the filtration functions and associated ecosystem services. For restoration purposes, particular attention should be given to (1) establishing genetic husbandry guidelines to prevent loss of genetic diversity; (2) avoiding negative effects of disturbance of vertebrates and other valued species; (3) controlling spread of nonnative fouling organisms, especially certain tunicates; (4) regulating bivalve stocking to require use of eyed larvae from certified hatcheries with an effective and comprehensive disease inspection or to first-generation seed spawned from adult bivalves under quarantine conditions in order to minimize species introductions and disease spread; (5) insuring that bivalve shellfish loading does not exceed levels that have unacceptable negative impacts on the benthos through excessive organic loading or on other components of the ecosystem through clearance of planktonic foods and organic particles from the water column; (6) preventing unacceptable damage to bottom habitat by harvest gear; and (7) assessing the social tolerance for mariculture on a site-specific basis.

References

- Abbe, G.R. 1988. Population structure of the American oyster, *Crassostrea virginica*, on an oyster bar in central Chesapeake Bay: Changes associated with shell planting and increased recruitment. *Journal of Shellfish Research* 7:33-40.
- Adams, C., A. Hodges, and T. Stevens. 2009. *Estimating the Economic Impact for the Commercial Hard Clam Culture Industry on the Economy of Florida*. Food and Resource Economics Department, Florida Sea Grant College Program, University of Florida, Gainesville, Florida.
- Alaska Sea Grant. 2009. *Aquaculture*. [Online]. Available: <http://seagrant.uaf.edu/map/aquaculture/index.html> [2009, September 14].
- Alexandre, A., R. Santos, and E. Serrao. 2005. Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. *Marine Ecology Progress Series* 298:115-122.
- Allen, Jr., S.K. and S.L. Downing. 1986. Performance of triploid Pacific oysters, *Crassostrea gigas* (Thunberg). 1. Survival, growth, glycogen-content, and sexual-maturation in yearlings. *Journal of Experimental Marine Biology and Ecology* 102:197-208.
- Allen, Jr., S.K. and T.J. Hilbish. 2000. *Genetic Considerations for Hatchery-Based Restoration of Oyster Reefs: A Summary from the September 21-22, 2000 Workshop Held at Virginia Institute of Marine Science*. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia.
- Allen, Jr., S.K. and E.M. Burreson. 2002. *Standing Policy for Non-Native Oyster Research in Virginia*. Virginia Institute of Marine Science Press, Williamsburg, Virginia.
- Allen, Y.C., C.A. Wilson, H.H. Roberts, and J. Supan. 2005. High resolution mapping and classification of oyster habitats in nearshore Louisiana using sidescan sonar. *Estuaries* 28(3):435-446.
- Allendorf, F.W., R.F. Leary, P. Spruell, and J.K. Wenberg. 2001. The problem with hybrids: Setting conservation guidelines. *Trends in Ecology and Evolution* 16(11):613-622.
- Allison, N., G.E. Millward, and M.B. Jones. 1998. Particle processing by *Mytilus edulis*: Effects on bioavailability of metals. *Journal of Experimental Marine Biology and Ecology* 222(1-2):149-162.

- Alpine, A.E. and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37(5):946-955.
- Anderson, J.L. 2002. Aquaculture and the future: Why fisheries economists should care. *Marine Resource Economics* 17:133-151.
- Anderson, M.J. and A.J. Underwood. 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology* 184(2):217-236.
- Anderson, R.M. and R.M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 291(1054):451-524.
- Andrews, J.D. 1976. Epizootiology of oyster pathogens *Minchinia nelsoni* and *costalis*. In *Proceedings of the First International Colloquium on Invertebrate Pathology and IXth Annual Meeting of the Society for Invertebrate Pathology*, Angus, T.A., P. Faulkner, and A. Rosenfiend (eds.). Queen's University Printing Department, Queen's University, Kingston, Ontario, Canada.
- Andrews, J.D. 1980. A review of introductions of exotic oysters and biological planning for new importations. *Marine Fisheries Review* 42:1-11
- Andrews, J.D. and M. Frierman. 1974. Epizootiology of *Minchinia nelsoni* in susceptible wild oysters in Virginia, 1959 to 1971. *Journal of Invertebrate Pathology* 24(2):127-140.
- Arakawa, K.Y. 1990. Natural spat collecting in the Pacific oyster *Crassostrea gigas* (Thunberg). *Marine and Fresh Water Behaviour and Physiology* 17(2):95-128.
- Arkema, K.K., S.C. Abrahamson, and B.M. Dewberry. 2006. Marine ecosystem-based management: From characterization to implementation. *Frontiers in the Ecology and the Environment* 4(10):525-532.
- Asche, F., A.G. Guttormsen, T. Sebolonsen, and E.H. Sissener. 2005. Competition between farmed and wild salmon: The Japanese salmon market. *Agricultural Economics* 33:333-340.
- Asmus, H., R.M. Asmus, and K. Reise. 1990. Exchange processes in an intertidal mussel bed: A Sylt-flume study in the Wadden Sea. *Berichte der Biologischen Anstalt Helgoland* 6:1-79.
- Asmus, R.M. and H. Asmus. 1991. Mussel beds: Limiting or promoting phytoplankton? *Journal of Experimental Marine Biology and Ecology* 148:215-232.
- Aspen Research and Information Center. 1981. *Aquaculture in the United States: Regulatory Constraints*. Aspen Systems Corporation, Rockville, Maryland.
- Aure, J., Ø. Strand, S. Rune-Erga, and T. Strohmeier. 2007. Primary production enhancement by artificial upwelling in a western Norwegian fjord. *Marine Ecology Progress Series* 352:39-52.
- Ayres, 1991. Introduced Pacific oysters in Australia. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, Greer, M.C. and J.C. Leffler (eds.). Maryland Sea Grant College, University of Maryland, College Park, Maryland.
- Bacher, C., H. Bioteau, and A. Chapelle. 1995. Modelling the impact of a cultivated oyster population on the nitrogen dynamics: The Thau lagoon case (France). *Ophelia* 42:29-54.
- Bacher, C., P. Duarte, J.G. Ferreira, M. Héral, and O. Raillard. 1998. Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. *Aquatic Ecology* 31:379-394.
- Bahr, L.M. and W.P. Lanier. 1981. *The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile*. U.S. Fish and Wildlife Service, Washington, DC.
- Baker, P. and R. Mann. 2003. Late stage bivalve larvae in a well-mixed estuary are not inert particles. *Estuaries* 26(4A):837-845.

- Barber, B.J., S.E. Ford, and R.N. Wargo. 1991. Genetic variation in the timing of gonadal maturation and spawning of the Eastern oyster, *Crassostrea virginica* (Gmelin). *The Biological Bulletin* 181(2):216-221.
- Barr, B.W. 1997. Mariculture in offshore critical habitat areas: A case study of Stellwagen Bank National Marine Sanctuary. *Ocean and Coastal Law Journal* 2(2):273-287.
- Baudinet, D., E. Alliot, B. Berland, G. Grenz, M. Plane-Cuny, P. Plante, and C. Salen-Picard. 1990. Incidence of mussel culture on biogeochemical fluxes at the sediment-water interface. *Hydrobiologia* 207(1):187-196.
- Beadman, H.A., M.J. Kaiser, M. Galanidi, R. Shucksmith, and R.I. Willows. 2004. Changes in species richness with stocking density of marine bivalves. *Journal of Applied Ecology* 41(3):464-475.
- Beattie, J.H. 1992. Geoduck enhancement in Washington State. *Bulletin of the Aquaculture Associate of Canada* 92(4):18-24.
- Beck, M.B., R.D. Brumbaugh, L. Airoidi, A. Carranza, L.D. Coen, C. Crawford, O. Defeo, G.J. Edgar, B. Hancock, M. Kay, M.W. Luckenbach, C.L. Toropova, and G. Zhang. 2009. *Shellfish Reefs at Risk: A Global Analysis of Problems and Solutions*. The Nature Conservancy, Arlington, Virginia.
- Becker, B.H., D.T. Press, and S.G. Allen. 2009. Modeling the effects of El Niño, density-dependence, and disturbance on harbor seal (*Phoca vitulina*) counts in Drakes Estero, California: 1997-2007. *Marine Mammal Science* 25(1):1-18.
- Bell, J.D., P.C. Rothlisberg, J.L. Munro, N.R. Loneragan, W.J. Nash, R.D. Ward, and N.L. Andrew. 2005. *Advances in Marine Biology: Restocking and Stock Enhancement of Marine Invertebrate Fisheries, Volume 49*, Southward, A.J., C.M. Young, and L.A. Fuiman (eds.). Elsevier Academies Press, San Diego, California.
- Bell, J.D., K.M. Leber, H.L. Blankenship, N.R. Loneragan, and R. Masuda. 2008. A new era for restocking, stock enhancement and sea ranching of coastal fisheries resources. *Reviews in Fisheries Science* 16(1-3):1-9.
- Belle, S., R.A. Bullis, R. Elston, R. Goldberg, R.W. Hardy, J.A. Hargreaves, G.S. Lockwood, R.A. Mayo, C.L. Nelson, B. Reid, A.G.J. Tacon, and K.K. Quagraine. 2008. *Revisions to the Supplemental to Interim Final Report (Bivalve Molluscs) of the Aquaculture Working Group, In Response to Public Comments*. National Organic Program, U.S. Department of Agriculture, Washington, DC.
- Berge, J.A., B. Bjerkeng, O. Pettersen, M.T. Schaanning, and S. Øxnevad. 2006. Effects of increased sea water concentrations of CO₂ on growth of the bivalve *Mytilus edulis* L. *Chemosphere* 62(4):681-687.
- Besanko, D. 1987. Performance versus design standards in the regulation of pollution. *Journal of Public Economics* 34(1):19-44.
- Bierne, N., S. Launey, Y. Naciri-Graven, and F. Bonhomme. 1998. Early effect of inbreeding as revealed by microsatellite analyses on *Ostrea edulis* larvae. *Genetics* 148:1893-1906.
- Bishop, M.J. and C.H. Peterson. 2006. When r-selection may not predict introduced-species proliferation: Predation of a nonnative oyster. *Ecological Applications* 16(2):718-730.
- Black, R. and C.H. Peterson. 1987. Biological vs. physical explanations for the non-random pattern of host occupation by a macroalga attaching to infaunal bivalve molluscs. *Oecologia* 73(2):213-221.
- Blum, J.C., A.L. Chang, M. Liljeström, M.E. Schenk, M.K. Steinberg, and G.M. Ruiz. 2007. The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. *Journal of Experimental Marine Biology and Ecology* 342(1):5-14.
- Blumstein, D.L., L.L. Anthony, R. Harcourt, and G. Ross. 2003. Testing a key assumption of wildlife buffer zones: Is flight initiation distance a species-specific trait? *Biological Conservation* 110(1):97-100.

- Boese, B.L. 2002. Effects of recreational clam harvesting on eelgrass (*Zostera marina*) and associated infaunal invertebrates: In situ manipulative experiments. *Aquatic Biology* 73(1):63-74.
- Boese, B.L., B.D. Robbins, and G. Thursby. 2005. Desiccation is a limiting factor for eelgrass (*Zostera marina* L.) distribution in the intertidal zone of a northeastern Pacific (USA) estuary. *Botanica Marina* 48(4):274-283.
- Boese, B.L., J.E. Kaldy, P.J. Clinton, P.M. Eldridge, and C.L. Folger. 2009. Recolonization of intertidal *Zostera marina* L. (eelgrass) following experimental shoot removal. *Journal of Experimental Marine Biology and Ecology* 374(1):69-77.
- Booth, D.B., B. Visitacion, and A.C. Steinemann. 2006. *Damages and Costs of Stormwater Runoff in the Puget Sound Region*. The Water Center, Department of Civil and Environmental Engineering, University of Washington, Seattle, Washington.
- Born, A.F., A.J. Immink, and D.M. Bartley. 2004. Marine and coastal stocking: Global status and information needs. In *Marine Ranching*, Bartley, D.M. and K.M. Leber (eds.). Food and Agriculture Organization of the United Nations, Rome, Italy.
- Bostrom, C., E.L. Jackson, and C.A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science* 68(304):383-403.
- Boudry, P., B. Collet, F. Cornette, V. Hervouet, and F. Bonhomme. 2002. High variance in reproductive success of the Pacific oyster (*Crassostrea gigas*, Thunberg) revealed by microsatellite-based parentage analysis of multifactorial crosses. *Aquaculture* 204(3-4):283-296.
- Bower, S. 2006. Disease implications associated with the use of exotic species in aquaculture. *Bulletin of the Aquaculture Association of Canada* 106(1-2):31-42.
- Boyd, C.E., C. Lim, J. Queiroz, K. Salie, L. de Wet, and A. McNevin. 2008. *Best Management Practices for Responsible Aquaculture*. [Online]. Available: http://pdacrsp.oregonstate.edu/pubs/featured_titles/boyd.pdf [2009, September 14].
- Brennan, W.J. 1999. *Aquaculture in the Gulf of Maine: A Compendium of Federal, Provincial and State Regulatory Controls, Policies and Issues*. Aquaculture Committee, Gulf of Maine Council for the Marine Environment, Boston, Massachusetts.
- Brewer, P.G. 1997. Ocean chemistry of the fossil fuel CO₂ signal: The haline signature of "business as usual." *Geophysical Research Letters* 24:1367-1369.
- Breyer, S.G. 1982. *Regulation and Its Reform*. Harvard University Press, Cambridge, Massachusetts.
- Bricelj, V.M. and R.E. Malouf. 1984. Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. *Marine Biology* 84(2):155-165.
- Bricelj, V.M., R.E. Malouf, and C. de Quinfeldt. 1984. Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. *Marine Biology* 84(2):164-173.
- Broekhuizen, N., J. Zeldis, S.A. Stephens, J.W. Oldman, A.H. Ross, J. Ren, and M.R. James. 2002. *Factors Related to the Sustainability of Shellfish Aquaculture Operations in the Firth of Thames: A Preliminary Analysis*. Environment Waikato and Auckland Regional Council, Hamilton, New Zealand.
- Bronson, C. 2007. *Aquaculture Best Management Practices Rule*. Division of Aquaculture, Florida Department of Agriculture and Consumer Affairs, Tallahassee, Florida.
- Brooks, J.L. and S.I. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150(3692):28-35.
- Browman, H.I. and K.I. Stergiou. 2004. Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology Progress Series* 274:269-270.
- Bruneau, J.F. 2004. A note on permits, standards and technology innovation. *Journal of Environmental Economics and Management* 48:1192-1199.

- Bruno, J.F. and M.D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology*, Bertness, M.D., S.D. Gaines, and M.E. Hay (eds.). Sinauer Associates, Sunderland, Massachusetts.
- Buhle, E.R. and J.L. Ruesink. 2009. Impacts of invasive oyster drills on Olympia oyster (*Ostrea conchaphila* Carpenter 1864) recovery in Willapa Bay, Washington, United States. *Journal of Shellfish Research* 28(1):87-96.
- Burge, C.A., F.J. Griffin, and C.S. Friedman. 2006. Summer mortality and herpes virus infections of the Pacific oyster, *Crassostrea gigas*, in Tomales Bay, California. *Diseases of Aquatic Organisms* 72:31-43.
- Burge, C.A., L.R.J. Righetti, E.P. Mulder, B.A. Braid, F.J. Griffin, G.N. Cherr, P.G. Olin, D. Cheney, A. Suhrbier, B. MacDonald, and C.S. Friedman. 2007. Examination of factors affecting survival of the Pacific oyster, *Crassostrea gigas*, along the west coast of North America: Multiple stressors, family lines and seasonality. *Journal of Shellfish Research* 26(1):163-172.
- Buroker, N.E. 1983. Population genetics of the American oyster *Crassostrea virginica* along the Atlantic coast and the Gulf of Mexico. *Marine Biology* 75(1):99-112.
- Burreson, E.M., N.A. Stokes, and C.S. Friedman. 2000. Increased virulence in an introduced pathogen: *Haplosporidium nelsoni* (MSX) in the Eastern oyster, *Crassostrea virginica*. *Journal of Aquatic Animal Health* 12:1-8.
- Buschbaum, C., S. Dittmann, J.S. Hong, I.S. Hwang, M. Strasser, M. Thiel, N. Valdivia, S.P. Yoon, and K. Reise. 2009. Mytilid mussels: Global habitat engineers in coastal sediments. *Helgoland Marine Research* 63(1):47-58.
- Buschmann, A.H., D.A. Lopez, and M. Medina. 1996. A review of environmental effects and alternative production strategies of marine aquaculture in Chile. *Aquacultural Engineering* 15(6):397-421.
- Bushek, D., D. Richardson, M.Y. Bobo, and L.D. Coen. 2004. Quarantine of oyster shell cultch reduces the abundance of *Perkinsus marinus*. *Journal of Shellfish Research* 23:369-373.
- Bye, V.J. 1990. Legal, political, and social constraints in aquaculture. In *Aquaculture Europe '89—Business Joins Science*, DePauw, N. and R. Billiard (eds.). European Aquaculture Society, Bredene, Belgium.
- Byrnes, J.E., P.L. Reynolds, and J.J. Stachowicz. 2007. Invasions and extinctions reshape coastal marine food webs. *PLoS One* 2(3):e295.
- Byron, C., D. Alves, D. Bengtson, R. Rheault, and B. Costa-Pierce. 2008. *Working towards Consensus: Application of Shellfish Carrying Capacity in Management of Rhode Island Aquaculture*. Rhode Island Aquaculture Working Group, Rhode Island Coastal Resources Management Council, Wakefield, Rhode Island.
- Cabaco, S., A. Alexandre, and R. Santos. 2005. Population-level effects of clam harvesting on the seagrass *Zostera noltii*. *Marine Ecology Progress Series* 298:123-129.
- Caldeira, K. and M.E. Wickett. 2003. Oceanography: Anthropogenic carbon and ocean pH. *Nature* 425:365-365.
- Caldow, R.W.G., H.A. Beadman, S. McGroarty, R.A. Stillman, J.D. Goss-Custard, S.E.A. le V. dit Durell, A.D. West, M.J. Kaiser, K. Mould, and A. Wilson. 2004. A behavior-based modeling approach to reducing shorebird-shellfish conflicts. *Ecological Applications* 14(5):1411-1427.
- Callier, M.D., C.W. McKindsey, and G. Desrosiers. 2008. Evaluation of indicators used to detect mussel farm influence on the benthos: Two case studies in the Magdalen Islands, Eastern Canada. *Aquaculture* 279(1-4):77-88.
- Carignan, V. and M.A. Villard. 2002. Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment* 78(1):45-61.
- Carlton, J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanography and Marine Biology Annual Review* 23:313-371.

- Carlton, J.T. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. *Bulletin of Marine Science* 41(2):452-465.
- Carlton, J.T. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. *Conservation Biology* 3(3):265-273.
- Carlton, J.T. 1992a. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. In *Dispersal of Living Organisms into Aquatic Ecosystems*, Rosenfield, A. and R. Mann (eds.). Maryland Sea Grant Program, University of Maryland, College Park, Maryland.
- Carlton, J.T. 1992b. Introduced marine and estuarine mollusks of North America: An end-of-the-20th-century perspective. *Journal of Shellfish Research* 11(2):489-505.
- Carlton, J.T., J.K. Thompson, L.E. Schemel, and F.H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Marine Ecology Progress Series* 66:81-84.
- Carpenter, S.R. and J.F. Kitchell. 1992. Trophic cascade and biomanipulation: Interface of research and management. *Limnology and Oceanography* 37(1):208-213.
- Carroll, J., C.J. Gobler, and B.J. Peterson. 2008. Resource limitation of eelgrass in New York estuaries: Light limitation and nutrient stress alleviation by hard clams. *Marine Ecology Progress Series* 369:39-50.
- Carswell, B., S. Cheesman, and J. Anderson. 2006. The use of spatial analysis for environmental assessment of shellfish aquaculture in Baynes Sound, Vancouver Island, British Columbia, Canada. *Aquaculture* 253(1-4):408-414.
- Carver C.E., A. Chisholm, and A.L. Maillet. 2003. Strategies to mitigate the effect of *Ciona intestinalis* (L.) biofouling on shellfish production. *Journal of Shellfish Research* 22:621-631.
- Castagna, M. and J.N. Kraeuter. 1977. *Mercenaria* culture using stone aggregate for predator protection. *Proceedings of the National Shellfisheries Association* 67:1-6.
- Castel, J., P.J. Labourg, V. Escaravage, I. Auby, and M.E. Garcia. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meiobenthos and macrobenthos in tidal flats. *Estuarine, Coastal and Shelf Science* 28:71-85.
- Chapelle, A.M., J.M. Deslous-Paoli, P. Souchu, N. Mazouni, A. Vaquer, and B. Millet. 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon: Impact of oysters farming and inputs from the watershed. *Ecological Modelling* 127(2-3):161-181.
- Chapman, W.M. and A.H. Banner. 1949. Contributions to the life history of the Japanese oyster drill, *Tritonalia japonica*, with notes on other enemies of the Olympia oyster, *Ostrea lurida*. *Washington Department of Fisheries Biological Report* 49(A):168-200.
- Chauvaud, L., J.K. Thompson, J.E. Cloern, and G. Thouzeau. 2003. Clams as CO₂ generators: The *Potamocorbula amurensis* example in San Francisco Bay. *Limnology and Oceanography* 48:2086-2092.
- Chew, K.K. 1984. Recent advances in the cultivation of mollusks in the Pacific United States and Canada. *Aquaculture* 39(1-4):69-81.
- Chew, K.K. 1990. Global bivalve shellfish introductions. *World Aquaculture* 21:9-22.
- Chopin, T. 2008. Integrated multi-trophic aquaculture (IMTA) will also have its place when aquaculture moves to the open ocean. *Fish Farmer* 31(2):40-41.
- Chopin, T., C. Yarish, R. Wilkes, E. Belyea, S. Lu, and A. Mathieson. 1999. Developing Porphyra salmon integrated aquaculture for bioremediation and diversification of the aquaculture industry. *Journal of Applied Phycology* 11(5):463-472.
- Chopin, T., A.H. Buschmann, C. Halling, M. Troell, N. Kautsky, A. Neori, G. Kraemer, J. Zertuche-Gonzalez, C. Yarish, and C. Neefus. 2001. Integrating seaweeds into aquaculture systems: A key towards sustainability. *Journal of Phycology* 37(6):975-986.

- Christensen, N.L., A.M. Bartuska, J.H. Brown, S.R. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee. 2006. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6:665-691.
- Christensen, P.B., R.N. Glud, T. Dalsgaard, and P. Gillespie. 2003. Impacts of longline mussel farming on oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture* 218(1-4):567-588.
- Chung, I.K., Y.H. Kang, and Y.F. Yang. 2008. Seasonal assembly of seaweed species in the Sustainable Seaweed Integrated Aquaculture System (SSIAS) in Korea. In *Proceedings of the World Aquaculture Society*, Busan, Korea.
- Cigarria, J., J. Fernandez, and L.P. Magadan. 1998. Feasibility of biological control of algal fouling in intertidal oyster culture using periwinkles. *Journal of Shellfish Research* 17(4):1167-1169.
- Claereboudt, M.R., D. Bureau, J. Cote, and J.H. Himmelman. 1994. Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. *Aquaculture* 121:327-342.
- Clark, E. 1964. *The Oysters of Lochariaquer*. Pantheon Books, New York.
- Clay, J.W. 2008. The role of better management practices in environmental management. In *Environmental Best Management Practices for Aquaculture*, Tucker, C.S. and J.A. Hargreaves (eds.). Wiley-Blackwell, Hoboken, New Jersey.
- Clutton-Brock, J. 1981. *Domesticated Animals from Early Times*. University of Texas Press, Austin, Texas.
- Clynick, B.G., C.W. McKindsey, and P. Archambault. 2008. Distribution and productivity of fish and macroinvertebrates in mussel aquaculture sites in the Magdalen Islands (Quebec, Canada). *Aquaculture* 283(1-4):203-210.
- Coen, L., M.W. Luckenbach, and D.L. Breitberg. 1999. The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. In *Fish Habitat: Essential Fish Habitat and Rehabilitation*, Benaka, L.R. (ed.). American Fisheries Society, Bethesda, Maryland.
- Coen, L. and R.E. Grizzle. 2007. The importance of habitat created by molluscan shellfish to managed species along the Atlantic coast of the United States. In *Habitat Management Series*, Atlantic States Marine Fisheries Commission, Washington, DC.
- Coen, L., R.D. Brumbaugh, D. Bushek, R. Grizzle, M.W. Luckenbach, M.H. Posey, S.P. Powers, and S.G. Tolley. 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* 341:303-307.
- Cohen, R.R.H., P.V. Desler, E.J.P. Phillips, and R.L. Cory. 1984. The effects of the Asiatic clam *Corbicula fluminea* on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29(1):170-180.
- Cole, V.J., M.G. Chapman, and A.J. Underwood. 2007. Landscapes and life-histories influence colonisation of polychaetes to intertidal biogenic habitats. *Journal of Experimental Marine Biology and Ecology* 348(1-2):191-199.
- Coleman, N. 1996. *Potential for the Establishment of Wild Populations and Biological Risk Assessment of the Introduction of Pacific Oysters in Victoria*. Marine and Freshwater Resources Institute, Melbourne, Victoria, Australia.
- Collie, J.S., S.J. Hall, M.J. Kaiser, and I.R. Poiner. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal Animal Ecology* 69(5):785-798.
- Common Wadden Sea Secretariat. 2008. *The Trilateral Cooperation on the Protection of the Wadden Sea*. [Online]. Available: <http://www.waddensea-secretariat.org/> [2009, September 14].
- Costa-Pierce, B.A. 2002. Ecology as the paradigm for the future of aquaculture. In *Ecological Aquaculture: The Evolution of the Blue Revolution*, Costa-Pierce, B.A. (ed.). Blackwell Science, Oxford, England, United Kingdom.

- Costa-Pierce, B.A. 2008. An ecosystem approach to marine aquaculture: A global review. In *Building an Ecosystem Approach to Aquaculture*, Soto, D. and J. Aguilar-Manjarrez (eds.). Food and Agriculture Organization of the United Nations, Rome, Italy.
- Costanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, S. Naehm, K. Limburg, J. Paruelo, R.V. O'Neill, R. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253-260.
- Coutts, A.D.M. and B.M. Forrest. 2007. Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum*. *Journal of Experimental Marine Biology and Ecology* 342(1):154-162.
- Cowen, R.K., C.B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* 311(5760):522-527.
- Cranfield, H.J., K.P. Michael, and I.J. Doonan. 1999. Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9(5):461-483.
- Cranfield, H.J., G. Carbines, K.P. Michael, A. Dunn, D.R. Stotter, and D.J. Smith. 2001. Promising signs of regeneration of blue cod and oyster habitat changed by dredging in Foveaux Strait, southern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35(5):897-908.
- Cranford, P.J. and B.T. Hargrave. 1994. In situ time-series measurement of ingestion and absorption rates of suspension-feeding bivalves: *Placopecten magellanicus*. *Limnology and Oceanography* 39(3):730-738.
- Cranford, P.J., P.M. Strain, M. Dowd, B.T. Hargrave, J. Grant, and M.C. Archambault. 2007. Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal embayment. *Marine Ecology Progress Series* 347:61-78.
- Creswell, R.L. and A.A. McNevin. 2008. Better management practices for bivalve molluscan aquaculture. In *Environmental Best Management Practices for Aquaculture*, Tucker, C.S. and J.A. Hargreaves (eds.). Blackwell Publishing, Oxford, England, United Kingdom.
- Cromeey, C.J., T.D. Nickell, and K.D. Black. 2002. DEPOMOD—Modelling the deposition and biological effects of waste solids from marine cage farms. *Aquaculture* 214(1-4):211-239.
- Crow, J.F. 1998. 90 years ago: The beginning of hybrid maize. *Genetics* 148(3):923-928.
- Cugier, P., C. Struski, M. Blanchard, J. Mazurié, J. Pouvreau, and F. Olivier. 2008. *Studying the Carrying Capacity of Mont Saint Michel Bay (France): Respective Role of the Main Filter-Feeders Communities*. [Online]. Available: <http://www.ices.dk/iceswork/asc/2008/themesessions/Theme%20synopses/H-list-ed.pdf> [2009, September 14].
- Cunningham, C.W. and T.M. Collins. 1994. Developing model systems for molecular biogeography: Vicariance and interchange in marine invertebrates. In *Molecular Ecology and Evolution: Approaches and Applications*, Schierwater, B., B. Streit, G.P. Wagner, and R. DeSalle (eds.). Birkhauser Verlag, Basel, Switzerland.
- Dahlbäck, B. and L.A.H. Gunnarsson. 1981. Sedimentation and sulfate reduction under mussel culture. *Marine Biology* 63(3):269-275.
- Daily, G.C. (ed.). 1996. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Chapel Hill, North Carolina.
- D'Amours, O., P. Archambault, C.W. McKindsey, and L.E. Johnson. 2008. Local enhancement of epibenthic macrofauna by aquaculture activities. *Marine Ecology Progress Series* 371:73-84.
- D'Andrea, A.F. and T.H. DeWitt. 2009. Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-dependent effects on organic matter remineralization and nutrient cycling. *Limnology and Oceanography* 54(6):1911-1932.
- Dame, R.F. 1986. Book review. "The Oyster: The Life and Lore of the Celebrated Bivalve," by Hedeen, R.A. *Estuaries* 9(4):382-383.

- Dame, R.F. 1996. *Ecology of Marine Bivalves: An Ecosystem Approach*. CRC Press, Boca Raton, Florida.
- Dame, R.F. 2005. Oyster reefs as complex systems. In *The Comparative Roles of Suspension-Feeders in Ecosystems*, Dame, R.F. and S. Olenin (eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Dame, R.F. and S. Libes. 1993. Oyster reefs and nutrient retention in tidal creeks. *Journal of Experimental Marine Biology and Ecology* 171(2):251-258.
- Dame, R.F. and T.C. Prins. 1998. Bivalve carrying capacity in coastal ecosystems. *Aquatic Ecology* 31(4):409-421.
- Dame, R.F. and S. Olenin (eds.). 2005. *The Comparative Roles of Suspension-Feeders in Ecosystems: Proceedings of the NATO Advanced Research Workshop on the Comparative Roles of Suspension-Feeders in Ecosystems, Nida, Lithuania, 4-9 October 2003*. Springer, Dordrecht, The Netherlands.
- Dankers, N. and D.R. Zuidema. 1995. The role of mussel (*Mytilus edulis*) and mussel culture in the Dutch Wadden Sea. *Estuaries* 18(1A):71-80.
- Daszak, P., A.A. Cunningham, and A.D. Hyatt. 2001. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta Tropica* 78(2):103-116.
- David, P. 1998. Heterozygosity-fitness correlations: New perspectives on old problems. *Heredity* 80:531-537.
- Dayton, P.K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41(4):351-389.
- Dayton, P.K., S.F. Thrush, M.T. Agardy, and R.J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5(3):205-232.
- de Grave, S., S.J. Moore, and G. Burnell. 1998. Changes in benthic macrofauna associated with intertidal oyster, *Crassostrea gigas* (Thunberg) culture. *Journal of Shellfish Research* 17:1137-1142.
- de Jong, M.J. 2009. Overview of relevant knowledge about ecosystem engineers in the Wadden Sea: Contribution to the nature restoration program Wadden Sea. In *Science Memo of Stichting WAD*. Groningen, The Netherlands.
- DeAlteris, J.T. 1988. The geomorphic development of Wreck Shoal, a subtidal oyster reef of the James River, Virginia. *Estuaries* 11(4):240-249.
- DeAlteris, J.T., B.D. Kilpatrick, and R.B. Rheault. 2004. A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. *Journal of Shellfish Research* 23:867-874.
- DeAngelis, D.L., W.M. Post, and C.C. Travis. 1986. *Positive Feedback in Natural Systems*. Springer-Verlag, Berlin, Germany.
- Debinski, D.M. and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14(2):342-355.
- DeCasabianca, M.L., T. Laugier, and D. Collart. 1997. Impact of shellfish farming eutrophication on benthic macrophyte communities in the Thau lagoon, France. *Aquaculture International* 5(4):301-314.
- Dégremont, L., B. Ernande, E. Bedier, and P. Boudry. 2007. Summer mortality of hatchery-produced Pacific oyster spat (*Crassostrea gigas*). I. Estimation of genetic parameters for survival and growth. *Aquaculture* 262(1):41-53.
- Dekshenieks, M.M., E.E. Hofmann, J.M. Klinck, and E.N. Powell. 2000. Quantifying the effects of environmental variability on an oyster population using a coupled oyster-circulation model. *Estuaries* 23(5):593-610.
- Delgado, C.L., N. Wada, M.W. Rosegrant, S. Meijer, and M. Ahmed. 2003. *Fish to 2020: Supply and Demand in Changing Global Markets*. International Food Policy Research Institute, Washington, DC.

- Dempster, T. and M. Taquet. 2004. Fish aggregation device (FAD) research: Gaps in current knowledge and future directions for ecological studies. *Reviews in Fish Biology and Fisheries* 14(1):21-42.
- Dennison, W.C. and R.S. Alberte. 1985. Role of daily light period in the depth distribution of *Zostera marina*. *Marine Ecology Progress Series* 25:51-61.
- Dennison, W.C., R.J. Orth, K.A. Moore, J.C. Stevenson, V. Carter, S. Kollar, P.W. Bergstrom, and R.A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience* 43(2):86-94.
- Derraik, J.G.B. 2002. The pollution of the marine environment by plastic debris: A review. *Marine Pollution Bulletin* 44(9):842-852.
- DeVoe, M.R. 1999. Marine aquaculture in the United States: Current and future policy and management challenges. In *Trends and Future Challenges for U.S. National Ocean and Coastal Policy: Proceedings of a Workshop*, Cicin-Sain, B., R.W. Knecht, and N. Foster (eds.). National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- DeVoe, M.R. and A.S. Mount. 1989. An analysis of ten state aquaculture leasing systems: Issues and strategies. *Journal of Shellfish Research* 8(1):233-239.
- Dewitt, T.H., A.F. D'Andrea, C.A. Brown, B.D. Griffen, and P.M. Eldridge. 2004. Impact of burrowing shrimp populations on nitrogen cycling and water quality in western North American temperate estuaries. In *Proceedings of the Symposium on Ecology of Large Bioturbators in Tidal Flats and Shallow Sublittoral Sediments—From Individual Behavior to Their Role as Ecosystem Engineers*. Nagasaki University, Nagasaki, Japan.
- Diana, J.S. 2009. Aquaculture production and biodiversity conservation. *BioScience* 59(1):27-38.
- Dinamani, P. 1991. Introduced Pacific oysters in New Zealand. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France and Washington State*, Greer, M.C. and J.C. Leffler (eds.). Maryland Sea Grant College, University of Maryland, College Park, Maryland.
- Dionne, M., J.S. Lauzon-Guay, D.J. Hamilton, and M.A. Barbeau. 2006. Protective socking material for cultivated mussels: A potential non-disruptive deterrent to reduce losses to diving duck. *Aquaculture International* 14(6):595-613.
- Doall, M.H., D.K. Padilla, C.P. Lobue, C. Clapp, A.R. Webb, and J. Hornstein. 2008. Evaluating northern quahog (= hard clam, *Mercenaria mercenaria* L.) restoration: Are transplanted clams spawning and reconditioning? *Journal of Shellfish Research* 27(5):1069-1080.
- Doney, S.C., V.J. Fabry, R.A. Feely, and J.A. Kleypas. 2009. Ocean acidification: The other CO₂ problem. *Annual Review of Marine Science* 1:169-192.
- Dowd, M. 2005. A bio-physical coastal ecosystem model for assessing environmental effects of marine bivalve aquaculture. *Ecological Modelling* 183(2-3):323-346.
- Downing, P.B. and J. White. 1986. Innovation in pollution control. *Journal of Environmental Economics and Management* 13:18-29.
- Drapeau, A., L.A. Comeau, T. Landry, H. Stryhn, and J. Davidson. 2006. Association between longline design and mussel productivity in Prince Edward Island, Canada. *Aquaculture* 261(3):879-889.
- Duarte, C.M., N. Marba, and M. Holmer. 2007. Rapid domestication of marine species. *Science* 316(5823):382-383.
- Duarte, C.M., M. Holmer, Y. Olsen, D. Soto, N. Marba, J. Guiu, K. Black, and I. Karakassis. 2009. Will the oceans help feed humanity? *Bioscience* 59:967-976.
- Duarte, P., R. Meneses, A.J.S. Hawkins, M. Zhu, J. Fang, and J. Grant. 2003. Mathematical modelling to assess the carrying capacity for multi-species culture within coastal waters. *Ecological Modelling* 168(1-2):109-143.
- Duff, J.A., T.S. Getchis, and P. Hoagland. 2003. *A Review of Legal and Policy Constraints to Aquaculture in the U.S. Northeast*. Northeast Regional Aquaculture Center, South Dartmouth, Massachusetts.

- Dumbauld, B.R., K.M. Brooks, and M.H. Posey. 2001. Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of Pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington. *Marine Pollution Bulletin* 42(10):826-844.
- Dumbauld, B.R. and S. Wyllie-Echeverria. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquatic Botany* 77(1):27-42.
- Dumbauld, B.R., S. Booth, D. Cheney, A. Suhrbier, and H. Beltran. 2006. An integrated pest management program for burrowing shrimp control in oyster aquaculture. *Aquaculture* 261(3):976-992.
- Dumbauld, B.R., D.L. Holden, and O.P. Langness. 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest estuaries? *Environmental Biology Fishes* 83(3):283-296.
- Dumbauld, B.R., J.L. Ruesink, and S.S. Rumrill. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in west coast (USA) estuaries. *Aquaculture* 290(3-4):96-223.
- Duxbury Bay Management Commission. 2009. *Duxbury Aquaculture Management Plan*. Duxbury Bay Management Commission, Duxbury, Massachusetts.
- Edwards, P.K. and B. Leung. 2009. Re-evaluating eradication of nuisance species: Invasion of the tunicate, *Ciona intestinalis*. *Frontiers in Ecology and the Environment* 7(6):326-332.
- Eichenberg, T. and B. Vestal. 1992. Improving the legal framework for marine aquaculture: The role of water quality laws and the public trust doctrine. *Territorial Sea Journal* 2:339-404.
- Eldon, B. and J. Wakeley. 2006. Coalescent processes when the distribution of offspring number among individuals is highly skewed. *Genetics* 172:2621-2633.
- Elliott-Fisk, D.L., S. Allen, A. Harbin, J. Wechsler, D. Press, D. Schirokauer, and B. Becker. 2005. *Point Reyes National Seashore Drakes Estero Assessment of Oyster Farming Final Completion Report*. [Online]. Available: http://www.crmc.ri.gov/aquaculture/riaquaworkinggroup/drakes_estero_rpt.pdf [2010, February, 4].
- Elston, R.A. 2004. *Shellfish High Health Program Guideline: A Voluntary Program for Producers of Live Shellfish*. Saltonstall-Kennedy Program, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- Elston, R.A., C.A. Farley, and M.L. Kent. 1986. Occurrence and significance of Bonamiasis in European flat oysters *Ostrea edulis* in North America. *Diseases of Aquatic Organisms* 2(1):49-54.
- Elton, C. 1927. *Animal Ecology*. Sidgwick and Jackson Ltd., London, England, United Kingdom.
- Enright, C., D. Krailo, L. Staples, M. Smith, C. Vaughan, D. Ward, P. Gaul, and E. Borgese. 1983. Biological control of fouling algae in oyster aquaculture. *Journal of Shellfish Research* 3:41-44.
- Enright, C.T., R.W. Elnor, A. Griswold, and E.M. Borgese. 1993. Evaluation of crabs as control agents for biofouling in suspended culture of European oysters. *World Aquaculture* 24:49-51.
- Environmental Protection Agency. 1998. *EPA Project Beach*. Office of Water, Washington, DC.
- Erbland, P.J. and G. Ozbay. 2008. Comparison of the macrofaunal communities inhabiting a *Crassostrea virginica* oyster reef and oyster aquaculture gear in Indian River Bay, Delaware. *Journal of Shellfish Research* 27(4):757-768.
- Estes, J.A. and J.F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185(4156):1058-1060.
- Evans, F., S. Matson, J. Brake, and C. Langdon. 2004. The effects of inbreeding on performance traits of adult Pacific oysters (*Crassostrea gigas*). *Aquaculture* 230(1):89-98.
- Everett, R.A., G.M. Ruiz, and J.T. Carlton. 1995. Effect of oyster mariculture on submerged aquatic vegetation: An experimental test in a Pacific Northwest estuary. *Marine Ecology Progress Series* 125:205-217.

- Ewart, J.W. and S.E. Ford. 1993. *History and Impact of MSX and Dermo Disease on Oyster Stocks in the Northeast Region*. Northeastern Regional Aquaculture Center, University of Massachusetts, Dartmouth, North Dartmouth, Massachusetts.
- Ewart, J.W., J. Hankins, and D. Bullock. 1995. *State Policies for Aquaculture Effluents and Solid Wastes in the Northeast Region*. Northeastern Regional Aquaculture Center, University of Massachusetts, Dartmouth, North Dartmouth, Massachusetts.
- Fabry, V.J., B.A. Seibel, R.A. Feely, and J.C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65:414-432.
- Federal Register. 2007. Nationwide permit: (48) Existing commercial shellfish aquaculture activities. *Federal Register* 72(47):11144-11147.
- Feely, R.A., C.L. Sabine, K. Lee, W. Berelson, J. Kleypas, V.J. Fabry, and F.J. Millero. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305(5682):362-366.
- Feldman, K.L., D.A. Armstrong, B.R. Dumbauld, T.H. DeWitt, and D.C. Doty. 2000. Oysters, crabs, and burrowing shrimp: Review of an environmental conflict over aquatic resources and pesticides use in Washington State's (USA) coastal estuaries. *Estuaries* 23(2):141-176.
- Ferreira, J.G., P. Duarte, and B. Ball. 1997. Trophic capacity of Carlingford Lough for oyster culture—Analysis by ecological modelling. *Aquatic Ecology* 31(4):361-378.
- Ferreira, J.G., A.J.S. Hawkins, and S.B. Bricker. 2007. Management of productivity, environmental effects and profitability of shellfish aquaculture: The Farm Aquaculture Resource Management (FARM) model. *Aquaculture* 264(1-4):160-174.
- Ferreira, J.G., A.J.S. Hawkins, P. Monteiro, H. Moore, M. Service, P.L. Paoce, L. Ramos, and A. Sequeira. 2008. Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas. *Aquaculture* 275:138-151.
- Ferreira, J.G., A. Sequeira, A.J.S. Hawkins, A. Newton, T.D. Nickell, R. Pastres, J. Forte, A. Bodoy, and S.B. Bricker. 2009. Analysis of coastal and offshore aquaculture: Application of the FARM model to multiple systems and shellfish species. *Aquaculture* 289(1-2):32-41.
- Ferraro, S.P. and F.A. Cole. 2007. **Benthic macrofauna-habitat associations in Willapa Bay, Washington, USA**. *Estuarine, Coastal and Shelf Science* 71(3-4):491-507.
- Flye-Sainte-Marie, J., F. Jean, C. Paillard, S. Ford, E. Powell, E. Hofmann, and J. Klinck. 2007. Ecophysiological dynamic model of individual growth of *Ruditapes philippinarum*. *Aquaculture* 266(1-4):130-134.
- Folke, C. and N. Kautsky. 1989. The role of ecosystems for a sustainable development of aquaculture. *AMBIO* 18(4):234-243.
- Fonseca, M.S., G.W. Thayer, A.J. Chester, and C. Foltz. 1984. Impact of scallop harvesting on eelgrass (*Zostera marina*) meadows: Implications for management. *North American Journal of Fisheries Management* 4:286-293.
- Food and Agriculture Organization of the United Nations. 1989. *Culture of Kelp (Laminaria japonica) in China*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Food and Agriculture Organization of the United Nations. 2006. *State of World Aquaculture 2006*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Food and Agriculture Organization of the United Nations. 2008a. Building an ecosystem approach to aquaculture. In *FAO Fisheries and Aquaculture Proceedings No. 14*, Soto, D., J. Aguilar-Manjarrez, and N. Hishamunda (eds.). Food and Agriculture Organization of the United Nations, Rome, Italy.
- Food and Agriculture Organization of the United Nations. 2008b. *FishStat Fishery Statistics Database*. [Online]. Available: <http://www.fao.org/fishery/statistics/software/fishstat/en> [2009, August 14].
- Food and Agriculture Organization of the United Nations. 2009. *The State of World Fisheries and Aquaculture 2008*. Food and Agriculture Organization of the United Nations, Rome, Italy.

- Ford, S.E. 1992. Avoiding the transmission of disease in commercial culture of molluscs, with special reference to *Perkinsus marinus* (dermo) and *Haplosporidium nelsoni* (MSX). *Journal of Shellfish Research* 11(2):539-546.
- Ford, S.E. and H.H. Haskin. 1982. History and epizootiology of *Haplosporidium nelsoni* (MSX), an oyster pathogen in Delaware Bay, 1957-1980. *Journal of Invertebrate Pathology* 40(1):118-141.
- Forrest, B.M., G.A. Hopkins, T.J. Dodgshun, and J.P.A. Gardner. 2007. Efficacy of acetic acid treatments in the management of marine biofouling. *Aquaculture* 262:319-332.
- Foster-Smith, R.L. 1975. The effect of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* (L.), *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). *Journal of Experimental Marine Biology and Ecology* 17:1-22.
- Franks, J.S. 2000. Pelagic fishes at offshore petroleum platforms in the northern Gulf of Mexico: Diversity, interrelationships, and perspective. *Aquatic Living Resources* 13(4):502-515.
- Frechette, M., C.A. Butman, and W.R. Geyer. 1989. The importance of the benthic boundary-layer flow processes in supplying phytoplankton to the benthic suspension-feeder, *Mytilus edulis*. *Limnology and Oceanography* 34(1):19-36.
- Freire, J. and E. Gonzalez-Gurriaran. 1995. Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ria De Arousa (Galicia, NW Spain). *Marine Ecology Progress Series* 119:139-154.
- Friedman, C.S. 1996. Haplosporidian infections of the Pacific oyster, *Crassostrea gigas* (Thunberg) in California, U.S.A. *Journal of Shellfish Research* 15(3):597-600.
- Friedman, C.S. and F.O. Perkins. 1994. Range extension of *Bonamia ostreae* to Maine, U.S.A. *Journal of Invertebrate Pathology* 64:179-181.
- Friedman, C.S. and C.A. Finley. 2003. Anthropogenic introductions of the etiological agent of withering syndrome into northern California abalone populations via conservation efforts. *Canadian Journal of Fisheries and Aquatic Sciences* 60(11):1424-1431.
- Friedman, C.S., D. Manzer, and R.P. Hedrick. 1991. A haplosporidian from Pacific oysters (*Crassostrea gigas*). *Journal of Invertebrate Pathology* 58:367-372.
- Friedman, C.S., W. Roberts, G. Kismohandaka, and R.P. Hedrick. 1993. Transmissibility of a coccidian parasite of abalone, *Haliotis* spp. *Journal of Shellfish Research* 12(2):201-205.
- Friedman, C.S., M. Thomson, C. Chun, P.L. Haaker, and R.P. Hedrick. 1997. Withering syndrome of the black abalone, *Haliotis cracherodii* (Leach): Water temperature, food availability, and parasites as possible causes. *Journal of Shellfish Research* 16(2):403-411.
- Friedman, C.S., K.B. Andree, K. Beauchamp, J.D. Moore, T.T. Robbins, J.D. Shields, and R.P. Hedrick. 2000. "*Candidatus Xenohaliotis californiensis*", a newly described pathogen of abalone, *Haliotis* spp., along the west coast of North America. *International Journal of Systematic and Evolutionary Microbiology* 50(2):847-855.
- Friedman, C.S., B.B. Scott, R. Estes Strenge, and T.B. McCormick. 2007. Oxytetracycline as a tool to manage and prevent losses of the endangered white abalone, *Haliotis sorenseni*, due to withering syndrome. *Journal of Shellfish Research* 26(3):877-885.
- Friedrichs, M.A.M., R. Hood, and J. Wiggert. 2006. Ecosystem model complexity versus physical forcing: Quantification of their relative impact with assimilated Arabian Sea data. *Deep-Sea Research Part II* 53(5-7):576-600.
- Friedrichs, M.A.M., J.A. Dusenberry, L.A. Anderson, R. Armstrong, F. Chai, J.R. Christian, S.C. Doney, J. Dunne, M. Fujii, R. Hood, D. McGillicuddy, J.K. Moore, M. Schartau, Y.H. Spitz, and J.D. Wiggert. 2007. Assessment of skill and portability in regional marine biogeochemical models: The role of multiple planktonic groups. *Journal of Geophysical Research Oceans* 112:C08001.

- Friedrichs, M.A.M., M.E. Carr, R.T. Barber, M. Scardi, D. Antoine, R.A. Armstrong, I. Asanuma, M.J. Behrenfeld, E.T. Buitenhuis, F. Chai, J.R. Christian, A.M. Ciotti, S.C. Doney, M. Dowell, J. Dunne, B. Gentili, W. Gregg, N. Hoepffner, J. Ishizaka, T. Kameda, I. Lima, J. Marra, F. Mélin, J.K. Moore, A. Morel, R.T. O'Malley, J. O'Reilly, V.S. Saba, M. Schmeltz, T.J. Smyth, J. Tjiputra, K. Waters, T.K. Westberry, and A. Winguth. 2009. Assessing the uncertainties of model estimates of primary productivity in the tropical Pacific Ocean. *Journal of Marine Systems* 76(1-2):113-133.
- Fujio, Y. 1982. A correlation of heterozygosity with growth rate in the Pacific oyster, *Crassostrea gigas*. *Tohoku Journal of Agricultural Research* 33(2):66-75.
- Gaffney, P.M. 1994. Heterosis and heterozygote deficiencies in marine bivalves: More light? In *Genetics and Evolution of Aquatic Organisms*, Beaumont, A.R. (ed.). Chapman and Hall, London, England, United Kingdom.
- Gaffney, P.M. 2006. The role of genetics in shellfish restoration. *Aquatic Living Resources* 19:277-282.
- Gaffney, P.M. 2008. A BAC-based physical map for the Pacific oyster genome. *Journal of Shellfish Research* 27:1009.
- Gaffney, P.M., C.M. Bernat, and S.K. Allen. 1993. Gametic incompatibility in wild and cultured populations of the eastern oyster, *Crassostrea virginica* (Gmelin). *Aquaculture* 115:273-284.
- Game, E.T., E. McDonald-Madden, M.L. Puotinen, and H.P. Possingham. 2008. Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology* 22(6):1619-1629.
- Gangnery, A., J.M. Chabirand, F. Lagarde, P. Le Gail, J. Oheix, C. Bacher, and D. Buestel. 2003. Growth model of the Pacific oyster, *Crassostrea gigas*, cultured in Thau lagoon (Méditerranée, France). *Aquaculture* 215(1-4):267-290.
- Gardner, G.R., J.C. Harshbarger, J. Lake, T.K. Sawyer, K.L. Price, M.D. Stephenson, P.L. Haaker, and H.A. Togstad. 1995. Association of prokaryotes with symptomatic appearance of withering syndrome in black abalone *Haliotis cracherodii*. *Journal of Invertebrate Pathology* 66:111-120.
- Gibbs, M.T. 2004. Interactions between bivalve shellfish farms and fishery resources. *Aquaculture* 240(1-4):267-296.
- Gibbs, M.T. 2007. Sustainability indicators for suspended bivalve aquaculture activities. *Ecological Indicators* 7(1):94-107.
- Gill, J.A., K. Norris, and W.J. Sutherland. 2001. Why behavioral responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97(2):265-268.
- Gilles, K.W. and J.S. Pearse. 1986. Disease in sea urchins *Strongylocentrotus purpuratus*: Experimental infection and bacterial virulence. *Diseases of Aquatic Organisms* 1:105-114.
- Glasby, T.M., S.D. Connell, M.G. Holloway, and C.L. Hewitt. 2007. Nonindigenous biota on artificial structures: Could habitat creation facilitate biological invasions? *Marine Biology* 151(3):887-895.
- Glasoe, S. and A. Christy. 2004. *Coastal Urbanization and Microbial Contamination of Shellfish Growing Areas: Literature Review and Analysis*. Puget Sound Action Team, Olympia, Washington.
- Glude, J.B. 1957. Copper, a possible barrier to oyster drills. *Proceedings of the National Shellfisheries Association* 47:73-82.
- Godet, L., N. Toupoint, J. Fournier, P. Le Mao, C. Retiere, and F. Olivier. 2009. Clam farmers and oystercatchers: Effects of the degradation of *Lanice conchilega* beds by shellfish farming on the spatial distribution of shorebirds. *Marine Pollution Bulletin* 58(4):589-595.
- Godley, B.J., M.J. Gaywood, R.J. Law, C.J. McCarthy, C. McKenzie, I.A.P. Patterson, R.S. Penrose, R.J. Reid, and H.M. Ross. 1998. Patterns of marine turtle mortality in British waters (1992-1996) with reference to tissue contaminant levels. *Journal of the Marine Biological Association of the United Kingdom* 78:973-984.

- Gouletquer, P. and M. Heral. 1991. Introduced Pacific oysters in New Zealand. In *The Ecology of Crassostrea gigas in Australia, New Zealand, France, and Washington State*, Greer, M.C. and J.C. Leffler (eds.). Maryland Sea Grant Program, University of Maryland, College Park, Maryland.
- Grabowski, J.H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85(4):995-1004.
- Grabowski, J.H. and C.H. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. In *Ecosystem Engineers: Plants to Protists*, Cuddington, K., J.E. Byers, W. Wilson, and A. Hastings (eds.). Academic Press, New York.
- Gracey, A.Y., M.L. Chaney, J.P. Boomhower, W.R. Tyburczy, K. Connor, and G.N. Somero. 2008. Rhythms of gene expression in a fluctuating intertidal environment. *Current Biology* 18(19):1501-1507.
- Graham, M. 1935. Modern theory of exploiting a fishery, and application to North Sea trawling. *ICES Journal of Marine Science* 10(3):264-274.
- Grangeré, K., A. Gangnery, C. Bacher, and A. Ménesguen. 2008. *Modelling Nitrogen Cycle in a Small Intertidal Estuary: Respective Influence of Environmental Factors and Cultivated Oysters*. [Online]. Available: <http://www.ices.dk/iceswork/asc/2008/themesessions/Theme%20synopses/H-list-ed.pdf> [2009, September 21].
- Grant, J., A. Hatcher, D.B. Scott, P. Pocklington, C.T. Schafer, and G.V. Winters. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. *Estuaries* 18(1):124-144.
- Grant, J., K.J. Curran, T.L. Guyondet, G. Tita, C. Bacher, V. Koutitonsky, and M. Dowd. 2007. A box model of carrying capacity for suspended mussel aquaculture in Lagune de la Grande-Entrée, Iles-de-la-Madeleine, Québec. *Ecological Modelling* 200(1-2):193-206.
- Grant, J., C. Bacher, P.J. Cranford, T. Guyondet, and M. Carreau. 2008a. A spatially explicit ecosystem model of seston depletion in dense mussel culture. *Journal of Marine Systems* 73(1-2):155-168.
- Grant, J., R. Filgueira, C. Bacher, and O. Strand. 2008b. *Operational Models of Carrying Capacity Applied to a Norwegian Fjord*. [Online]. Available: <http://www.ices.dk/iceswork/asc/2008/themesessions/Theme%20synopses/H-list-ed.pdf> [2009, September 21].
- Green, M.A., M.E. Jones, C.L. Boudreau, R.L. Moore, and B.A. Westman. 2004. Dissolution mortality of juvenile bivalves in coastal marine deposits. *Limnology Oceanography* 49(3):727-734.
- Grewe, P.M., J.G. Patil, D.J. McGoldrick, P.C. Rothlisberg, S. Whyard, L.A. Hinds, C.M. Hardy, S. Vignarajan, and R.E. Thresher. 2007. Preventing genetic pollution and the establishment of feral populations: A molecular solution. In *Ecological and Genetic Implications of Aquaculture Activities*, Bert, T.M. (ed.). Springer, Dordrecht, The Netherlands.
- Grizzle, R.E. 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.
- Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology and Evolution* 17(1):22-27.
- Grumbine, R.E. 1994. What is ecosystem management? *Conservation Biology* 8(1):27-38.
- Gubbins, M.J., C. Greathead, T. Amundrud, P. Gillibrand, P. Tett, M. Inall, A.J.S. Hawkins, and I.M. Davies. 2008. *Towards Determination of the Carrying Capacity of Scottish Sea Lochs for Shellfish Aquaculture*. [Online]. Available: <http://www.ices.dk/iceswork/asc/2008/themesessions/Theme%20synopses/H-list-ed.pdf> [2009, September 21].
- Günther, R.T. 1897. The oyster culture of the ancient Romans. *Journal of the Marine Biological Association of the United Kingdom* 4:360-365.
- Guo, X.M., G.A. DeBrosse, and S.K. Allen. 1996. All-triploid Pacific oysters (*Crassostrea gigas* Thunberg) produced by mating tetraploids and diploids. *Aquaculture* 142(3-4):149-161.

- Gutierrez, J.L., C.G. Jones, D.L. Strayer, and O.O. Iribarne. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos* 101(1):79-90.
- Guyondet, T., V.G. Koutitonsky, and S. Roy. 2005. Effects of water renewal estimates on the oyster aquaculture potential of an inshore area. *Journal of Marine Systems* 58(1-2):35-51.
- Haaker, P.L., D.V. Richards, C.S. Friedman, G. Davis, D.O. Parker, and H. Togstad. 1992. Abalone withering syndrome and mass mortality of black abalone, *Haliotis cracherodii* in California. In *Abalone of the World: Biology, Fisheries, and Culture*, Shephard, S.A., M. Tegner, and S. Guzman del Proo (eds.). Blackwell Scientific, Oxford, England, United Kingdom.
- Haamer, J. 1996. Improving water quality in a eutrophied fjord system with mussel farming. *AMBIO* 25(5):356-362.
- Hamilton, D.J. 2000. Direct and indirect effects of predations by common eiders and abiotic disturbance in an intertidal community. *Ecological Monographs* 70(1):21-43.
- Harding, J.M. and R. Mann. 2000. Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*), and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef. *Bulletin of Marine Science* 66(1):29-45.
- Harding, J.M. and R. Mann. 2001. Oyster reefs as fish habitats: Opportunistic use of restored reefs by transient fishes. *Journal of Shellfish Research* 20:951-959.
- Harris, D.R. and G.C. Hilman. 1989. *Foraging and Farming: The Evolution of Plant Exploitation*. Unwin Hyman, London, England, United Kingdom.
- Harvell, C.D., K. Kim, J.M. Burkholder, R.R. Colwell, R.R. Epstein, D.J. Grimes, E.E. Hofmann, E.K. Lipp., A.D.M.E. Osterhaus, R.M. Overstreet, J.W. Porter, G.W. Smith, and G.R. Vasta. 1999. Emerging marine diseases-climate links and anthropogenic factors. *Science* 285(5433):1505-1510.
- Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296(5576):2158-2162.
- Haskin, H.H. and S.E. Ford. 1987. Breeding for disease resistance in molluscs. In *Report of the Symposium on Selection, Hybridization, and Genetic Engineering in Aquaculture of Fish and Shellfish for Consumption and Stocking*, Chevassus, B. and A.G. Coche (eds.). Bordeaux, France.
- Hasson, K.W., Y. Fany, T. Reisinger, J. Venuti, and P.W. Varner. 2006. White-spot syndrome virus (WSSV) introduction into the Gulf of Mexico and Texas freshwater systems through imported, frozen bait-shrimp. *Diseases of Aquatic Organisms* 71(2):91-100.
- Hatcher, A., J. Grant, and B. Schofield. 1994. Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Marine Ecology Progress Series* 115:219-235.
- Hauser, L., G.J. Adcock, P.J. Smith, J.H. Bernal-Ramirez, and G.R. Carvalho. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences of the United States of America* 99(18):11724-11747.
- Hauxwell, J., J. Cebrian, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82(4):1007-1022.
- Haven, D.S. and J.P. Whitcomb. 1983. The origin and extent of oyster reefs in the James River, Virginia. *Journal of Shellfish Research* 3:141-151.
- Hawkins, A.J.S., B.L. Bayne, S. Bougrier, M. Heral, J.I.P. Iglesias, E. Navarro, R.F.M. Smith, and M.B. Urrutia. 1998a. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. *Journal of Experimental Marine Biology and Ecology* 219(1-2):87-103.

- Hawkins, A.J.S., R.F.M. Smith, S.H. Tan, and Z.B. Yasin. 1998b. Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucullata* and *Pinctada margarifera*. *Marine Ecology Progress Series* 166:173-185.
- Hecht, T. and P. Britz 1992. The current status, future prospects and environmental implications of mariculture in South Africa. *South African Journal of Science* 88:335-342.
- Heck, Jr., K.L., G. Hays, and R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123-136.
- Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? In *Genetics and Evolution of Aquatic Organisms*, Beaumont, A.R. (ed.). Chapman and Hall, London, England, United Kingdom.
- Hedgecock, D. and J.P. Davis. 2007. Heterosis for yield and crossbreeding of the Pacific oyster *Crassostrea gigas*. *Aquaculture* 272(S1):S17-S29.
- Hedgecock, D., D.J. McGoldrick, B.L. Bayne. 1995. Hybrid vigor in Pacific oysters: An experimental approach using crosses among inbred lines. *Aquaculture* 137(1-4):285-298.
- Hedgecock, D., P.M. Gaffney, P. Goulletquer, X. Guo, K. Reece, and G.W. Warr. 2005. The case for sequencing the Pacific oyster genome. *Journal of Shellfish Research* 24:429-441.
- Hedgecock, D., J.Z. Lin, S. DeCola, C.D. Haudenschild, E. Meyer, D.T. Manahan, and B. Bowen. 2007a. Transcriptomic analysis of growth heterosis in larval Pacific oysters (*Crassostrea gigas*). *Proceedings of the National Academy of Sciences of the United States of America* 104(7):2313-2318.
- Hedgecock, D., S. Edmands, and P. Barber. 2007b. Genetic approaches to measuring connectivity. *Oceanography* 20(3):70-79.
- Hedgecock, D., S. Launey, A.I. Pudovkin, Y. Naciri, S. Lapègue, and F. Bonhomme. 2007c. Small effective number of parents (N_b) inferred for a naturally spawned cohort of juvenile European flat oysters *Ostrea edulis*. *Marine Biology* 150(6):1173-1182.
- Hedrick, P. 2005. Large variance in reproductive success and the N_e/N ratio. *Evolution* 59(7):1596-1599.
- Helfand, G.E. 1991. Standards versus standards: The effects of different pollution restrictions. *American Economic Review* 81(3):622-634.
- Herman, P.M.J. and H. Scholten. 1990. Can suspension-feeders stabilize estuarine ecosystems? In *Trophic Relationships in the Marine Environment: Proceedings of the 24th European Marine Biology Symposium*, Barnes, M. and R.N. Gibson (eds.). Aberdeen University Press, Aberdeen, Scotland, United Kingdom.
- Hershberger, W.K., J.A. Perdue, and J.H. Beattie. 1984. Genetic selections and systematic breeding in Pacific oyster culture. *Aquaculture* 39(1-4):237-245.
- Hidu, H., C. Conary, and S.R. Chapman. 1981. Suspended culture of oysters: Biological fouling control. *Aquaculture* 22:189-192.
- Hindar, K., I.A. Fleming, P. McGinnity, and A. Diserud. 2006. Genetic and ecological effects of salmon farming on wild salmon: Modelling from experimental results. *ICES Journal of Marine Science* 63(7):1234-1247.
- Hoagland, P., K.M. Riaf, D. Jin, and H.L. Kite-Powell. 2003. A comparison of access systems for natural resources: Drawing lessons for ocean aquaculture in the U.S. exclusive economic zone. In *Open-Ocean Aquaculture: From Research to Commercial Reality*, Bridger, C.J. and B.A. Costa-Pierce (eds.). World Aquaculture Society, Baton Rouge, Louisiana.
- Hoagland, P., H. Kite-Powell, D. Jin, M. Schumacher, L. Katz, and D. Klinger. 2007. *Economic Sustainability of Marine Aquaculture: A Report to the Marine Aquaculture Task Force*. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.
- Hofmann, E.E., E.N. Powell, J.M. Klinck, and E.A. Wilson. 1992. Modeling oyster populations. III. Critical feeding periods, growth and reproduction. *Journal of Shellfish Research* 11:399-416.

- Hofmann, E.E., J.M. Klinck, J.N. Kraeuter, E.N. Powell, R.E. Grizzle, S.C. Buckner, and V.M. Bricelj. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: Development of the age- and length-frequency structure of the population. *Journal of Shellfish Research* 25(2):417-444.
- Holling, C.S. (ed.). 1978. *Adaptive Environmental Assessment and Management*. Wiley-Blackwell, Chichester, England, United Kingdom.
- Holsman, K.K., P.S. McDonald, and D.A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a northeast Pacific estuary. *Marine Ecology Progress Series* 308:183-195.
- Hooper, C., P. Hardy-Smith, and J. Handlinger. 2007. Ganglioneuritis causing high mortalities in farmed Australian abalone (*Haliotis laevigata* and *Haliotis rubra*). *Australian Veterinary Journal* 85(5):188-103.
- Hoover, C.A. and P.M. Gaffney. 2005. Geographic variation in nuclear genes of the eastern oyster, *Crassostrea virginica* Gmelin. *Journal of Shellfish Research* 24:103-112.
- Hopkins, D.D., R. Goldberg, and A. Marston. 1997. An environmental critique of government regulations and policies for open ocean aquaculture. *Ocean and Coastal Law Journal* 2:235-260.
- Horinouchi, M. 2007. Review of the effects of within-patch scale structural complexity on seagrass fishes. *Journal of Experimental Marine Biology and Ecology* 350(1-2):111-129.
- Hosack, G.R., B.R. Dumbauld, J.L. Ruesink, and D.A. Armstrong. 2006. Habitat associations of estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. *Estuaries and Coasts* 29(6B):1150-1160.
- Howarth, R.W. 1988. Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology and Systematics* 19:89-110.
- Howlett, M. and J. Rayner. 2004. (Not so) "Smart regulation"? Canadian shellfish aquaculture policy and the evolution of instrument choice for industrial development. *Marine Policy* 28(2):171-184.
- Huguenin, J.E. 1977. The reluctance of the oyster drill (*Urosalpinx cinerea*) to cross metallic copper. *Proceedings of the National Shellfisheries Association* 67:80-84.
- Huguenin, J.E. and S.S. Huguenin. 1982. Biofouling resistant shellfish trays. *Journal of Shellfish Research* 2:41-46.
- Iglesias, J.I.P., M.B. Urrutia, E. Navarro, P. Alvarez-Jornaa, X. Larretxea, S. Bougrierb, and M. Heral. 1996. Variability of feeding processes in the cockle *Cerastoderma edule* (L.) in response to changes in seston concentration and composition. *Journal of Experimental Marine Biology and Ecology* 197(1):121-143.
- Inglis, G.J., B.J. Hayden, and A.H. Ross. 2000. *An Overview of Factors Affecting the Carrying Capacity of Coastal Embayments for Mussel Culture*. National Institute of Water and Atmospheric Research, Auckland, New Zealand.
- International Council for the Exploration of the Sea. 2005. *ICES Code of Practice on the Introductions and Transfers of Marine Organisms 2005*. Copenhagen, Denmark.
- International Council for the Exploration of the Sea. 2008. *Report of the Working Group on Marine Shellfish Culture (WGMASC)*. Aberdeen, Scotland, United Kingdom.
- International Ocean Colour Coordinating Group. 2009. Remote sensing in fisheries and aquaculture. In *Reports of the International Ocean-Colour Coordinating Group*, Forget, M.H., V. Stuart, and T. Platt (eds.). International Ocean-Colour Coordinating Group, Dartmouth, Nova Scotia, Canada.
- Irish Sea Fisheries Board. 2003. *ECOPACT: Environmental Code of Practice for Irish Aquaculture Companies and Traders*. Irish Sea Fisheries Board, Dublin, Ireland.
- Jablonski, S. 2008. The interaction of the oil and gas offshore industry with fisheries in Brazil: The "Stena Tay" experience. *Brazilian Journal of Oceanography* 56(4):289-296.

- Jackson, E.L., A.A. Rowden, M.J. Attrill, S.J. Bossey, and M.B. Jones. 2001b. The importance of seagrass beds as a habitat for fishery species. *Oceanography and Marine Biology* 39:269-303.
- Jackson, J.B.D., 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. 2001a. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638.
- Jaramillo, E., C. Bertran, and A. Bravo. 1992. Mussel biodeposition in an estuary in southern Chile. *Marine Ecology Progress Series* 82:85-94.
- Jarvinen, D. 2000. Federal and state support for aquaculture development in the United States. *Aquaculture Economics and Management* 4(3-4):209-225.
- Jarvinen, D. and G. Magnusson. 2000. Public resources for private mariculture: Northeastern United States, Atlantic Canada and Scotland after NAFTA and GATT. *Marine Policy* 24(1):21-32.
- Jennings, S. and M. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34:209-224.
- Jiang, W. and M.T. Gibbs. 2005. Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. *Aquaculture* 244(1-4):171-185.
- Johnson, D. 2008. Environmental indicators: Their utility in meeting the OSPAR Convention's regulatory needs. *ICES Journal of Marine Science* 65(8):1387-1391.
- Johnson, L.E., J.M. Bossenbroek, and C.E. Craft. 2006. Patterns and pathways in the post-establishment spread of non-indigenous aquatic species: The slowing invasion of North American inland lakes by zebra mussels. *Biological Invasions* 8(3):475-489.
- Joint Subcommittee on Aquaculture Shrimp Virus Working Group. 1997. *An Evaluation of Potential Shrimp Virus Impacts on Cultured Shrimp and Wild Shrimp Populations in the Gulf of Mexico and Southeastern U.S. Atlantic Coastal Waters*. [Online]. Available: <http://www.nmfs.noaa.gov/trade/jsash16.pdf>. [2009, September 21].
- Jory, D.E., M.R. Carriker, and E.S. Iversen. 1984. Preventing predation in molluscan mariculture. *Journal of the World Mariculture Society* 15(1-4):421-432.
- Kaiser, M.J. 2001. Ecological effects of shellfish cultivation. In *Environmental Impacts of Aquaculture*, Black, K.D. (ed.). CRC Press, Boca Raton, Florida.
- Kaiser, M.J., I. Laing, S.D. Utting, and G.M. Burnell. 1998. Environmental impacts of bivalve mariculture. *Journal of Shellfish Research* 17(11):59-66.
- Kaiser, M.J., K.R. Clarke, H. Hinz, M.C.V. Austen, P.J. Somerfield, and I. Karakassis. 2006. Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series* 311:1-14.
- Kane, T.E. 1970. Aquaculture and the law. In *Sea Grant Technical Bulletin 2*. University of Miami Sea Grant College Program, Miami, Florida.
- Karl, S.A. and J.C. Avise. 1992. Balancing selection at allozyme loci in oysters: Implications from nuclear RFLPs. *Science* 256(5053):100-102.
- Karlson, R. 1978. Predation and space utilization patterns in a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology* 31(3):225-239.
- Kelly, J.P., J.G. Evens, R.W. Stallcup, and D. Wimpfheimer. 1996. Effects of oyster culture on habitat use by wintering shorebirds in Tomales Bay, California. *California Fish and Game* 82(4):160-174.
- Kemp, W.M., R. Batiuk, R. Bartleson, P. Bergstrom, V. Carter, C.L. Gallegos, W. Hunley, L. Karrh, E.W. Koch, J.M. Landwehr, K.A. Moore, L. Murray, M. Naylor, N.B. Rybicki, J.C. Stevenson, and D.J. Wilcox. 2004. Habitat requirements for submerged aquatic vegetation in Chesapeake Bay: Water quality, light regime, and physical-chemical factors. *Estuaries* 27(3):363-377.

- Kemper, C., D. Pemberton, M. Cawthorn, S. Heinrich, J. Mann, B. Würsig, P.D. Shaughnessy, and R. Gales. 2003. Aquaculture and marine mammals: Coexistence or conflict? In *Marine Mammals: Fisheries, Tourism and Management Issues*, Gales, N., M. Hindell, and R. Kirkwood (eds.). CSIRO Publishing, Collingwood, New South Wales, Australia.
- Kennedy, V.S. and L.L. Breisch. 1983. Sixteen decades of political management of the oyster fishery in Maryland's Chesapeake Bay. *Journal of Environmental Management* 164:153-171.
- Kidwell, S.M. and D. Jablonski. 1983. Taphonomic feedback: Ecological consequences of shell accumulation. In *Biotic Interactions in Recent and Fossil Benthic Communities*, Tevesz, M.J.S. and P.L. McCall (eds.). Plenum Press, New York.
- Kirby, M.X. 2004. Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences of the United States of America* 101(35):13096-13099.
- Kirk, M., D. Esler, and W.S. Boyd. 2007. Morphology and density of mussels on natural and aquaculture structure habitats: Implications for sea duck predators. *Marine Ecology Progress Series* 346:179-187.
- Kite-Powell, H.L., P. Hoagland, D. Jin, and K. Murray. 2003. Economics of open ocean growout of shellfish in New England: Sea scallops and blue mussels. In *Open-Ocean Aquaculture: From Research to Reality*, Bridger, C. and B. Costa-Pierce (eds.). World Aquaculture Society, Charleston, South Carolina.
- Kite-Powell, H.L., L.E. Fleming, L.C. Backer, E. Faustman, P. Hoagland, A. Tsuchiya, L. Younglove, B.A. Wilcox, and R.J. Gast. 2008. **Linking the oceans to public health: Current efforts and future directions.** *Environmental Health* 7(S2):S6.
- Kraan, C., T. Piersma, A. Dekinga, A. Koolhaas, and J. van der Meer. 2007. Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: Short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science* 64(9):1735-1742.
- Kraan, C., J.A. van Gils, B. Spaans, A. Dekinga, A.I. Bijleveld, M. van Roomen, R. Kleefstra, and T. Piersma. 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology* 78(6):1259-1268.
- Kraeuter, J.N. and M. Castagna. 1985. The effects of seed size, shell bags, crab traps, and netting on the survival of the northern hard clam *Mercenaria mercenaria* (Linne). *Journal of Shellfish Research* 5:69-72.
- Kraeuter, J.N., M.J. Kennish, J. Dobarro, S.R. Fegley, and G.E. Flimlin, Jr. 2003. Rehabilitation of the northern quahog (hard clam) (*Mercenaria mercenaria*) habitat by shelling—11 years in Barnegat Bay, New Jersey. *Journal of Shellfish Research* 22:61-67.
- Kraeuter, J.N., S. Buckner, and E.N. Powell. 2005. A note on a spawner–recruit relationship for a heavily exploited bivalve: The case of northern quahogs (hard clams), *Mercenaria mercenaria*, in Great South Bay, New York. *Journal of Shellfish Research* 24:1043-1052.
- Kraeuter, J.N., J.M. Klinck, E.N. Powell, E.E. Hofmann, S. Buckner, R.E. Grizzle, and V.M. Bricelj. 2008. Effects of the fishery on the northern quahog (= hard clam, *Mercenaria mercenaria* L.) population in Great South Bay, New York: A modeling study. *Journal of Shellfish Research* 27:653-666.
- Kurihara, H. 2008. Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275-284.
- Kurlansky, M. 2007. *The Big Oyster: A Molluscular History of New York*. Vintage Books, London, England, United Kingdom.
- Laffargue, P., M.L. Begout, and F. Lagardere. 2006. Testing the potential effects of shellfish farming on swimming activity and spatial distribution of sole (*Solea solea*) in a mesocosm. *ICES Journal of Marine Science* 63(6):1014-1028.

- Lafferty, K.D. 1997. Environmental parasitology: What can parasites tell us about human impacts on the environment? *Parasitology Today* 13(7):251-255.
- Lafferty, K.D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Application* 14(5):1566-1573.
- Lafferty, K.D. and A.M. Kuris. 1993. Mass mortality of abalone *Haliotis cracherodii* on the California Channel Islands: Tests of epidemiologic hypotheses. *Marine Ecology Progress Series* 96:239-248.
- Lafferty, K.D., J.W. Porter, and S.E. Ford. 2004. Are diseases increasing in the ocean? *Annual Review of Ecology Evolution and Systematics* 35:31-54.
- Landry, T. 2002. The potential role of bivalve shellfish in mitigating negative impacts of land use on estuaries. In *Effects of Land Use Practices on Fish, Shellfish, and Their Habitats on Prince Edward Island, Canadian Technical Report of Fisheries and Aquatic Sciences*, Cairns, D.K. (ed.). Department of Fisheries and Oceans, Charlottetown, Prince Edward Island, Canada.
- Langan, R. and C. Horton. 2002. Submerged longline culture of blue mussels in exposed oceanic environments: Design, operation and production strategies. *Bulletin of the Aquaculture Association of Canada* 102(3):96.
- Langdon, C., F. Evans, D. Jacobson, and M. Blouin. 2003. Improved family yields of Pacific oysters *Crassostrea gigas* Thunberg derived from selected parents. *Aquaculture* 220(1-4):227-244.
- Lannan, J.E. 1980. Broodstock management of *Crassostrea gigas*: III. Selective breeding for improved larval survival. *Aquaculture* 21(4):347-351.
- Lapointe, B.E., F.X. Niell, and J.M. Fuentes. 1981. Community structure, succession, and production of seaweeds associated with mussel-rafts in the Ria de Arosa, N.W. Spain. *Marine Ecology Progress Series* 5:243-253.
- Largier, J. 2004. The importance of retention zones in the dispersal of larvae. *American Fisheries Society Symposium* 42:105-122.
- Larsen, P.F. 1985. The benthic macrofauna associated with the oyster reefs of the James River Estuary, Virginia, U.S.A. *International Review of Hydrobiology* 70(6):797-814.
- Lasiak, T. 1991. The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal peoples of Transkei, southern Africa. *Biological Conservation* 56:245-264.
- Launey, S. and D. Hedgecock. 2001. High genetic load in the Pacific oyster. *Genetics* 159:255-265.
- Leavitt, D.F. (ed.). 2004. *Best Management Practices for the Shellfish Culture Industry in South-eastern Massachusetts*. [Online]. Available: http://www.mass.gov/agr/aquaculture/docs/Shellfish_BMPs_v09-04a.pdf [2009, September 21].
- LeBlanc, A.R., T. Landry, and G. Miron. 2003. Fouling organisms of the blue mussel *Mytilus edulis*: Their effect on nutrient uptake and release. *Journal of Shellfish Research* 22:633-638.
- LeBlanc, N., J. Davidson, R. Tremblay, M. McNiven, and T. Landry. 2007. The effect of anti-fouling treatments for the clubbed tunicate on the blue mussel, *Mytilus edulis*. *Aquaculture* 264(1-4):205-213.
- Lee, H.J. and E.G. Boulding. 2007. Mitochondrial DNA variation in space and time in the northeastern Pacific gastropod, *Littorina keenae*. *Molecular Ecology* 16(15):3084-3103.
- Lee, H.J. and E.G. Boulding. 2009. Spatial and temporal population genetic structure of four northeastern Pacific littorinid gastropods: The effect of mode of larval development on variation at one mitochondrial and two nuclear DNA markers. *Molecular Ecology* 18(10):2165-2184.

- Lee, K., L.T. Tong, F.J. Millero, C.L. Sabine, A.G. Dickson, C. Goyet, G.H. Park, R. Wanninkhof, R.A. Feely, and R.M. Key. 2006. Global relationships of total alkalinity with salinity and temperature in surface waters of the world's oceans. *Geophysical Research Letters* 33:L19605.
- Leguerrier, D., N. Niquil, A. Petiau, and A. Boday. 2004. Modeling the impact of oyster culture on a mudflat food web in Marennes-Oléron Bay (France). *Marine Ecology Progress Series* 273:147-162.
- Lenihan, H.S. 1999. Physical-biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecological Monographs* 69(3):251-275.
- Lenihan, H.S. and C.H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* 8(1):128-140.
- Lenihan, H.S. and F. Micheli. 1999. Biological effects of shellfish harvesting on oyster reefs: Resolving a fishery conflict by ecological experimentation. *Fishery Bulletin* 98(1):86-95.
- Lenihan, H.S. and C.H. Peterson. 2004. Conserving oyster reef habitat by switching from dredging and tonging to diver-harvesting. *Fishery Bulletin* 102:298-305.
- Lenihan, H.S., C.H. Peterson, J.H. Grabowski, J.E. Byers, G.W. Thayer, and D.R. Colby. 2001. Cascading of habitat degradation: Oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications* 11(3):764-782.
- Leslie, H.M. and K.L. McLeod. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in the Ecology and the Environment* 5(10):540-548.
- Leslie, H.M. and A.P. Kinzig. 2009. Resilience science. In *Ecosystem-Based Management for the Oceans*, McLeod, K.L. and H.M. Leslie (eds.). Island Press, Washington, DC.
- Lesser, M.P., S.E. Shumway, T. Cucci, and J. Smith. 1992. Impact of fouling organisms on mussel rope culture: Interspecific competition for food among suspension-feeding invertebrates. *Journal of Experimental Marine Biology and Ecology* 165(1):91-102.
- Lessios, H.A. 1988. Populations dynamics of *diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panama. *Marine Biology* 99(4):515-526.
- Lewison, R.L., L.B. Crowder, A.J. Read, and S.A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19(11):598-604.
- Li, G. and D. Hedgecock. 1998. Genetic heterogeneity detected by PCR-SSCP, among samples of larval Pacific oysters (*Crassostrea gigas* Thunberg), supports the hypothesis of large variance in reproductive success. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1025-1033.
- Lin, H.J., T.C. Wanga, H.M. Su, and J.J. Hung. 2005. Relative importance of phytoplankton and periphyton on oyster-culture pens in a eutrophic tropical lagoon. *Aquaculture* 243(1-4):279-290.
- Lindenmayer, D.B. and J. Fischer. 2006. *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, DC.
- Lindsay, C.E. and D. Simons. 1997. The fisheries for Olympia oysters, *Ostreola conchaphila*; Pacific oysters, *Crassostrea gigas*; and Pacific razor clams, *Siliqua patula*, in the State of Washington. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Mackenzie, C.L.J., V.G.J. Burrell, A. Rosenfield, and W.L. Hobart (eds.). U.S. Department of Commerce, Seattle, Washington.
- Lloyd, B.D. 2003. *Potential Effects of Mussel Farming on New Zealand's Marine Mammals and Seabirds: A Discussion Paper*. Department of Conservation, Wellington, New Zealand.
- Locke, A., K.G. Doe, W.L. Fairchild, P.M. Jackman, and E.J. Reese. 2009. Preliminary evaluation of effects of invasive tunicate management with acetic acid and calcium hydroxide on non-target marine organisms in Prince Edward Island, Canada. *Aquatic Invasions* 4(1):221-236.
- Loosanoff, V.L. and C.A. Nomejko. 1951. Existence of physiologically different races of oysters, *Crassostrea virginica*. *Biological Bulletin* 101(2):151-156.

- Loosanoff, V.L., C.L. MacKenzie, Jr., and L.W. Shearer. 1960. Use of chemicals to control shellfish predators. *Science* 131(3412):1522-1523.
- Lopez, D.A., V.A. Riquelme, and M.L. Gonzalez. 2000. The effects of epibionts and predators on the growth and mortality rates of *Argopecten purpuratus* cultures in southern Chile. *Aquaculture International* 8(5):431-442.
- Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson, and J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312(5781):1806-1809.
- Luckenbach, M. and A. Birch. 2009. Nutrient sequestration in macroalgae associated with clam culture: Potential nutrient trading credit for aquaculture. *Journal of Shellfish Research* 28(3):661-741.
- Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* 45(3):622-629.
- Lyons, M.M., R. Smolowitz, M. Gomez-Chiarri, and J.E. Ward. 2007. Epizootiology of quahog parasite unknown (QPX) disease in northern quahogs (= hard clams) *Mercenaria mercenaria*. *Journal of Shellfish Research* 26(2):371-381.
- MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist* 36(3):287-299.
- MacKenzie, Jr., C.L. 1970. Oyster culture in Long Island Sound 1966-69. *Commercial Fisheries Review* 32(1):27-40.
- Macreadie, P.I., J.S. Hindell, G.P. Jenkins, R.M. Connolly, and M.J. Keough. 2009. Fish responses to experimental fragmentation of seagrass habitat. *Conservation Biology* 23(3):644-652.
- Maine Aquaculture Association. 2006. *Recommended Code of Practice for Aquaculture in Maine*, Howell, L. and S. Belle (eds.). Maine Aquaculture Association, Hallowell, Maine.
- Mallet, A.L., C.E. Carver, and M. Hardy. 2009. The effect of floating bag management strategies on biofouling, oyster growth and biodeposition levels. *Aquaculture* 287(3-4):315-323.
- Malueg, D.A. 1989. Emission credit trading and the incentive to adopt new pollution abatement technology. *Journal of Environmental Economics and Management* 16(1):52-57.
- Mann, R. 2000. Restoring the oyster reef communities in the Chesapeake Bay: A commentary. *Journal of Shellfish Research* 19:335-339.
- Mann, R. and E.N. Powell. 2007. Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *Journal of Shellfish Research* 26:905-917.
- Marba, N. and C.M. Duarte. 1995. Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *Journal of Ecology* 83(3):381-389.
- Marine Stewardship Council. 2002. *MSC Principles and Criteria for Sustainable Fishing*. Marine Stewardship Council, London, England, United Kingdom.
- Markowitz, T.M., A.D. Harlin, B. Würsig, and C.J. McFadden. 2004. Dusky dolphin foraging habitat: Overlap with aquaculture in New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14(2):133-149.
- Maryland Aquaculture Coordinating Council. 2007. *Best Management Practices: A Manual for Maryland Aquaculture*. [Online]. Available: http://www.marylandseafood.org/pdf/best_management_practices_manual.pdf [2009, September 22].
- Massachusetts Coastal Zone Management. 1995. *Massachusetts Aquaculture White Paper and Strategic Plan*. Executive Office of Environmental Affairs, Boston, Massachusetts.
- Mattsson, J. and O. Linden. 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. *Sarsia* 68(22):97-102.
- Mazouni, N. 2004. Influence of suspended oyster cultures on nitrogen regeneration in a coastal lagoon, Thau, France. *Marine Ecology Progress Series* 276:103-113.
- Mazouni, N., J.C. Gaertner, J.M. Deslous-Paoli, S. Landrein, and M. Doedenberg. 1996. Nutrient and oxygen exchanges at the water-sediment interface in a shellfish farming lagoon (Thau, France). *Journal of Experimental Marine Biology and Ecology* 205(1-2):91-113.

- Mazouni, N., J.C. Gaertner, and J.M. Deslous-Paoli. 1998. Influence of oyster culture on water column characteristics in a coastal lagoon (Thau, France). *Hydrobiologia* 373/374:149-156.
- McCoy, H.D. 2000. *American and International Aquaculture Law*. Supranational Publishing Company, Peterstown, West Virginia.
- McDonald, J.H., B.C. Verrelli, and L.B. Geyer. 1996. Lack of geographic variation in anonymous nuclear polymorphisms in the American oyster, *Crassostrea virginica*. *Molecular Biology and Evolution* 13(8):1114-1118.
- McGinnity, P., P. Prodohl, K. Ferguson, R. Hynes, N. O'Maoileidigh, N. Baker, D. Cotter, B. O'Hea, D. Cooke, G. Rogan, J. Taggart, and T. Cross. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London Series B, Biological Sciences* 270(1532):2443-2450.
- McKindsey, C.W., M.R. Anderson, P. Barnes, S. Courtenay, T. Landry, and M. Skinner. 2006a. *Effects of Shellfish Aquaculture on Fish Habitat*. Canadian Science Advisory Secretariat, Fisheries and Oceans Canada, Mont-Joli, Quebec, Canada.
- McKindsey, C.W., H. Thetmeyer, T. Landry, and W. Silvert. 2006b. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. *Aquaculture* 261(2):451-462.
- McKindsey, C.W., T. Landry, F.X. O'Beirn, and I.N. Davies. 2007. Bivalve aquaculture and exotic species: A review of ecological considerations and management issues. *Journal of Shellfish Research* 26(2):281-294.
- Menge, B.A. 1995. Indirect effects in marine intertidal interaction webs: Patterns and importance. *Ecological Monographs* 65(1):21-74.
- Menge, B.A. 1997. Detection of indirect effects: Were experiments in rocky intertidal interactions long enough? *American Naturalist* 149(5):801-823.
- Metzger, E., C. Simonucci, E. Viollier, G. Sarazin, F. Prevot, and D. Jezequel. 2007. Benthic response to shellfish farming in Thau lagoon: Pore water signature. *Estuarine Coastal and Shelf Science* 72(3):406-419.
- Michael, P. and K.K. Chew. 1976. Growth of Pacific oyster *Crassostrea gigas* and related fouling problems under tray culture at Seabeck Bay, Washington. *Proceedings of the National Shellfisheries Association* 66:36-41.
- Micheli, F. and C.H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* 13(4):869-881.
- Monismith, S.G., J.R. Koseff, J.K. Thompson, C.A. O'Riordan, and H.M. Nepf. 1990. A study of model bivalve siphonal currents. *Limnology and Oceanography* 35(3):680-696.
- Montero, J.P. 2002. Permits, standards, and technological innovation. *Journal of Environmental Economics and Management* 44(1):23-44.
- Moore, J.D., T.T. Robbins, and C.S. Friedman. 2000. Withering syndrome in farmed red abalone, *Haliotis rufescens*: Thermal induction and association with a gastrointestinal Rickettsiales-like procaryote. *Journal of Aquatic Animal Health* 12:26-34.
- Moore, J.D., T.T. Robbins, R.P. Hedrick, and C.S. Friedman. 2001. Transmission of the Rickettsiales-like procaryote "*Candidatus Xenohaliotis californiensis*" and its role in withering syndrome of California abalone *Haliotis* spp. *Journal of Shellfish Research* 20(2):867-874.
- Moore, K.A., H.A. Neckles, and R.J. Orth. 1996. *Zostera marina* (eelgrass) growth and survival along a gradient of nutrients and turbidity in the lower Chesapeake Bay. *Marine Ecology Progress Series* 142:247-259.
- Moore, K.A. and D. Wieting (eds.). 1999. *Marine Aquaculture, Marine Mammals, and Marine Turtles Interactions Workshop Held in Silver Spring, Maryland, 12-13 January, 1999*. National Oceanic and Atmospheric Administration, Silver Spring, Maryland.

- Morgan, S.G., J.L. Fischer, S.H. Miller, S.T. McAfee, and J. Largier. 2009. Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90(12):3489-3502.
- Munroe, D. and R.S. McKinley. 2007. Commercial Manila clam (*Tapes philippinarum*) culture in British Columbia, Canada: The effects of predator netting on intertidal sediment characteristics. *Estuarine, Coastal and Shelf Science* 72(1-2):319-328.
- Myer, D.L., E.C. Townsend, and G.W. Thayer. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology* 5(1):93-99.
- Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers, and C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315(5820):846-850.
- Nash, C.E. 2004. Achieving policy objectives to increase the value of the seafood industry in the United States: The technical feasibility and associated constraints. *Food Policy* 29(6):621-641.
- Nash, C.E., R.N. Iwamoto, and C.V.W. Mahnken. 2000. Aquaculture risk management and marine mammal interactions in the Pacific Northwest. *Aquaculture* 183(3-4):307-323.
- National Oceanic and Atmospheric Administration. 1992. *The 1990 National Shellfish Register of Classified Estuarine Waters: Data Supplement*. Strategic Assessment Branch, Office of Oceanography and Marine Assessment, National Ocean Service, Rockville, Maryland.
- National Oceanic and Atmospheric Administration. 1998. *NOAA's Aquaculture Policy*. National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- National Oceanic and Atmospheric Administration. 1999. *Special Summer of 1999 Aquaculture Workshop Report*. National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- National Oceanic and Atmospheric Administration. 2005. *Seafood Supply and U.S. Trade*. [Online]. Available: http://www.globefish.org/files/UStrade_218.pdf [2009, September 20].
- National Oceanic and Atmospheric Administration. 2007. *Annual Commercial Landing Statistics*. [Online]. Available: http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html [2009, August 21].
- National Oceanic and Atmospheric Administration. 2008a. *The National Offshore Aquaculture Act of 2007*. [Online]. Available: <http://aquaculture.noaa.gov/us/2007.html> [2009, August 21].
- National Oceanic and Atmospheric Administration. 2008b. *Imports and Exports of Fishery Products: Annual Summary, 2008*. [Online]. Available: <http://www.st.nmfs.noaa.gov/st1/trade/documents/TRADE2008.pdf> [2009, September 2].
- National Oceanic and Atmospheric Administration. 2009a. *Fisheries of the United States 2008*. Fisheries Statistics Division, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- National Oceanic and Atmospheric Administration. 2009b. *Cumulative Trade Data by Product*. [Online]. Available: http://www.st.nmfs.noaa.gov/st1/trade/cumulative_data/TradeDataProduct.html [2009, August 21].
- National Oceanic and Atmospheric Administration. 2009c. *Data Caveats*. [Online]. Available: <http://www.st.nmfs.noaa.gov/st1/commercial/landings/caveat.html> [2009, August 21].
- National Oceanic and Atmospheric Administration. 2009d. *NOAA Fisheries: Office of Science and Technology*. [Online]. Available: <http://www.st.nmfs.noaa.gov/st1/publications.html> [2009, August 21].
- National Research Council. 1978. *Aquaculture in the United States: Constraints and Opportunities*. National Academy Press, Washington, DC.
- National Research Council. 1992. *Marine Aquaculture: Opportunities for Growth*. National Academy Press, Washington, DC.

- National Research Council. 2000. *Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution*. National Academy Press, Washington, DC.
- National Research Council. 2002. *Effects of Trawling and Dredging on Seafloor Habitat*. National Academy Press, Washington, DC.
- National Research Council. 2004. *Nonnative Oysters in the Chesapeake Bay*. The National Academies Press, Washington, DC.
- National Research Council. 2006. *Dynamic Changes in Marine Ecosystems: Fishing, Food Webs, and Future Options*. The National Academies Press, Washington, DC.
- National Research Council. 2008. *Urban Stormwater Management in the United States*. The National Academies Press, Washington, DC.
- National Research Council. 2009. *Shellfish Mariculture in Drakes Estero, Point Reyes National Seashore, California*. The National Academies Press, Washington, DC.
- Navedo, J.G. and J.A. Masero. 2008. Effects of traditional clam harvesting on the foraging ecology of migrating curlews (*Numenius arquata*). *Journal of Experimental Marine Biology and Ecology* 355(1):59-65.
- Naylor, R.L., S.R. Williams, and D.R. Strong. 2001. Aquaculture—A gateway for exotic species. *Science* 294:1655-1656.
- Neckles, H.A., F.T. Short, S. Barker, and B.S. Kopp. 2005. Disturbance of eelgrass *Zostera marina* by commercial mussel *Mytilus edulis* harvesting in Maine: Dragging impacts and habitat recovery. *Marine Ecology Progress Series* 285:57-73.
- Nell, J.A. 2002. Farming triploid oysters. *Aquaculture* 210(1-4):69-88.
- Newell, C.R., D.E. Campbell, and S.M. Gallagher. 1998. Development of the mussel aquaculture lease site model MUSMOD©: A field program to calibrate model formulations. *Journal of Experimental Marine Biology and Ecology* 219(1-2):143-169.
- Newell, R.I.E. 1988. Ecological changes in the Chesapeake Bay: Are they the result of over-harvesting of the American oyster, *Crassostrea virginica*? In *Understanding the Estuary: Advances in Chesapeake Bay Research*, Lynch, M.P. and E.C. Krone (eds.). Chesapeake Bay Research Consortium, Baltimore, Maryland.
- Newell, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. *Journal of Shellfish Research* 23:51-62.
- Newell, R.I.E., J.C. Cornwell, and M.S. Owens. 2002. Influence of simulated bivalve bio-deposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology and Oceanography* 47(5):1367-1379.
- Newell, R.I.E. and E.W. Koch. 2004. Modeling seagrass density and distribution in response to changes to turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27(5):793-806.
- Newell, R.I.E., T.R. Fisher, R.R. Holyoke, and J.C. Cornwell. 2005. Influence of eastern oysters on N and P regeneration in Chesapeake Bay, USA. In *The Comparative Roles of Suspension-Feeders in Ecosystems: Proceedings of the NATO Advanced Research Workshop on the Comparative Roles of Suspension-Feeders in Ecosystems, Nida, Lithuania, 4-9 October 2003*, Dame, R. and S. Olenin (eds.). Springer, Dordrecht, The Netherlands.
- Newell, R.I.E., W.M. Kemp, J.D. Hagy, C.F. Cerco, J.M. Testa, and W.R. 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.
- Newkirk, G.F. 1980. Review of the genetics and the potential for selective breeding of commercially important bivalves. *Aquaculture* 19:209-228.
- Nichols, F.H., J.K. Thompson, and L.E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Marine Ecology Progress Series* 66:95-101.
- Niquil, N., S. Pouvreau, A. Sakka, L. Legendre, L. Addressi, R. Le Borgne, L. Charpy, and B. Delesalle. 2001. Trophic web and carrying capacity in a pearl oyster farming lagoon (Takapoto, French Polynesia). *Aquatic Living Resources* 14(3):165-175.

- Nixon, S.W., C.A. Oviatt, J. Garber, and V. Lee. 1976. Diel metabolism and nutrient dynamics in a salt marsh embayment. *Ecology* 57(4):740-750.
- Nizzoli, D., M. Bartoli, and P. Viaroli. 2007. Oxygen and ammonium dynamics during a farming cycle of the bivalve *Tapes philippinarum*. *Hydrobiologia* 587:25-36.
- Nunes, J.P., J.G. Ferreira, F. Gazeau, J. Lencart-Silva, X.L. Zhang, M.Y. Zhu, and J.G. Fang. 2003. A model for sustainable management of shellfish polyculture in coastal bays. *Aquaculture* 219:257-277.
- Oesterling, M. and M. Luckenbach. 2008. *Best Management Practices for the Virginia Shellfish Culture Industry*. [Online]. Available: http://web.vims.edu/adv/aqua/MRR%202008_10.pdf?svr=www [2009, September 21].
- Office Internationale des Epizooties. 2006. Infection with *Xenohaliotis californiensis*. In *Aquatic Animal Health Code (9th Edition)*. World Organization for Animal Health, Paris, France.
- Officer, C.B., T.J. Smayda, and R. Mann. 1982. Benthic filter feeding: A natural eutrophication control. *Marine Ecology Progress Series* 9:203-210.
- Olesen, B., N. Marba, C.M. Duarte, R.S. Savelle, and M.D. Fortes. 2004. Recolonization dynamics in a mixed seagrass meadow: The role of clonal versus sexual processes. *Estuaries* 27(5):770-780.
- Olsen, S.B. and D. Nickerson. 2003. *The Governance of Coastal Ecosystems at the Regional Scale: An Analysis of the Strategies and Outcomes of Long-Term Programs*. Coastal Resources Center, University of Rhode Island, Narragansett, Rhode Island.
- O'Riordan, C.A., S.G. Monismith, and J.R. Koseff. 1993. A study of concentration boundary-layer formation over a bed of model bivalves. *Limnology and Oceanography* 38(8):1712-1729.
- Orth, R.J., J.R. Fishman, D.J. Wilcox, and K.A. Moore. 2002. Identification and management of fishing gear impacts in a recovering seagrass system in the coastal bays of the Delmarva Peninsula, USA. *Journal of Coastal Research* 37:111-129.
- Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck, Jr., 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(12):987-996.
- Pace, D.A., A.G. Marsh, P.K. Leong, A.J. Green, D. Hedgecock, and D.T. Manahan. 2006. Physiological bases of genetically determined variation in growth of marine invertebrate larvae: A study of growth heterosis in the bivalve *Crassostrea gigas*. *Journal of Experimental Marine Biology and Ecology* 335(2):188-209.
- Pacific Coast Shellfish Growers Association. 2001. *Environmental Policy*. Pacific Coast Shellfish Growers Association, Olympia, Washington.
- Pacific Coast Shellfish Growers Association. 2005. *Shellfish Production on the West Coast*. [Online]. Available: <http://www.pcsga.org/pub/uploads/production.pdf> [2009, August 21].
- Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100(910):65-75.
- Paine, R.T. 1980. Food webs, linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49(3):667-685.
- Paine, R.T. and T.H. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants: A tunicate-mussel comparison. *Evolution* 37(4):821-831.
- Palacios, R., D. Armstrong, and J. Orensanz. 2000. Fate and legacy of an invasion: Extinct and extant populations of the soft-shell clam *Mya arenaria* in Grays Harbor, Washington. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10(4):279-303.
- Palumbi, S.R. and D. Hedgecock. 2005. The life of the sea: Implications of marine population biology to conservation policy. In *Marine Conservation Biology*, Norris, E.A. and L.B. Crowder (eds.). Island Press, Washington, DC.
- Parsons, T.R., M. Takahashi, and B. Hargrave. 1983. *Biological Oceanographic Processes (3rd Edition)*. Pergamon Press, Oxford, England, United Kingdom.

- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10(10):430.
- Peacor, S.D. and E.E. Werner. 2001. The contribution of trait mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences of the United States of America* 98(7):3904-3908.
- Pechenik, J.A., M. Blanchard, and R. Rotgan. 2004. Susceptibility of larval *Crepidula fornicata* to predation by suspension-feeding adults. *Journal of Marine Biology and Ecology* 306:75-94.
- Peterken, C. and C. Conacher. 1997. Seed germination and recolonization of *Zostera capricorni* after grazing by dugongs. *Aquatic Botany* 59:333-340.
- Peterson, B.J. and K.L. Heck, Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. *Journal of Experimental Marine Biology and Ecology* 240(1):37-52.
- Peterson, B.J. and K.L. Heck, Jr. 2001a. An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. *Marine Ecology Progress Series* 218:115-125.
- Peterson, B.J. and K.L. Heck, Jr. 2001b. Positive interactions between suspension-feeding bivalves and seagrass—A facultative mutualism. *Marine Ecology Progress Series* 213:143-155.
- Peterson, C.H. 1976. Relative abundances of living and dead molluscs in two California lagoons. *Lethaia* 9:137-148.
- Peterson, C.H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology* 43:343-359.
- Peterson, C.H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecological Monographs* 52(4):437-475.
- Peterson, C.H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist* 124(1):127-133.
- Peterson, C.H. 2002. Recruitment overfishing in a bivalve mollusk fishery: Hard clams (*Mercenaria mercenaria*) in North Carolina. *Canadian Journal of Fisheries and Aquatic Sciences* 59:96-104.
- Peterson, C.H. and R. Black. 1987. Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. *Limnology and Oceanography* 32(1):143-166.
- Peterson, C.H. and R. Black. 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. *Estuarine, Coastal and Shelf Science* 32(4):405-413.
- Peterson, C.H., H.C. Summerson, and S.R. Fegley. 1983. Relative efficiency of two clam rakes and their contrasting impacts on seagrass biomass. *Fishery Bulletin* 81(2):429-434.
- Peterson, C.H., H.C. Summerson, and S.R. Fegley. 1987. Ecological consequences of mechanical harvesting of clams. *Fishery Bulletin* 85:281-298.
- Peterson, C.H., H.C. Summerson, and J. Huber. 1995. Replenishment of hard clam stocks using hatchery seed: Combined importance of bottom type, seed size, planting season, and density. *Journal of Shellfish Research* 14:293-300.
- Peterson, C.H., F.J. Fodrie, H.C. Summerson, and S.P. Powers. 2001. Site-specific and density-dependent extinction of prey by schooling rays: Generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129(3):349-356.
- Peterson, C.H., R.T. Kneib, and C. Manen. 2003. Scaling restoration actions in the marine environment to meet quantitative targets of enhanced ecosystem services. *Marine Ecological Progress Series* 264:173-175.
- Peterson, C.H., S.R. Fegley, and D. Gaskill. 2008. Cascading trophic effects on a seasonal fishery: Decimation of bay scallop, *Argopecten irradians*, populations in North Carolina. *Journal of Shellfish Research* 27:1041.

- Pew Oceans Commission. 2003. *America's Living Ocean: Charting a Course for Sea Change*. Pew Oceans Commission, Washington, DC.
- Philippakos, E., C. Adams, A. Hodges, D. Mulkey, D. Comer, and L. Sturmer. 2001. *Economic Impact of the Florida Cultured Hard Clam Industry*. Florida Sea Grant College Program, University of Florida, Gainesville, Florida.
- Phillips, R.C. 1984. *The Ecology of Eelgrass Meadows in the Pacific Northwest: A Community Profile*. U.S. National Coastal Ecosystems Team, U.S. Fish and Wildlife Service, Washington, DC.
- 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(3):499-506.
- Piersma, T., A. Koolhaas, A. Dekinga, J.J. Beukema, R. Dekker, and K. Essink. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *Journal of Applied Ecology* 38:976-990.
- Piferferrer, F., A. Beaumont, J.C. Falguière, M. Flajšhans, P. Haffray, and L. Colombo. 2009. Polyploid fish and shellfish: Production, biology and applications to aquaculture for performance improvement and genetic containment. *Aquaculture* 293(3-4):125-156.
- Pinnix, W.D., T.A. Shaw, K.C. Acker, and N.J. Hetrick. 2004. *Fish Communities in Eelgrass, Oyster Culture, and Mudflat Habitats of North Humboldt Bay, California*. Arcata Fish and Wildlife Office, U.S. Fish and Wildlife Service, Arcata, California.
- Plus, M., J.M. Deslous-Paoli, and F. Dagault. 2003. Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany* 77(2):121-134.
- Pomeroy, L.R., C.F. D'Elia, and L.C. Schaffner. 2006. Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. *Marine Ecology Progress Series* 325:301-309.
- Posey, M.H., T.D. Alphin, C.M. Powell, and E. Townsend. 1999. Oyster reefs as habitat for fish and decapods. In *Oyster Reef Habitat Restoration: A Synopsis of Approaches*, Luckenbach, M.W., R. Mann, and J.A. Wesson (eds.). Virginia Institute of Marine Science Press, Williamsburg, Virginia.
- Poulton, V.K., J.R. Lovvorn, and J.Y. Takekawa. 2002. Clam density and scaup feeding behavior in San Pablo Bay, California. *The Condor* 104:518-527.
- Pouvreau, S., Y. Bourles, S. Lefebvre, A. Gangnery, and M. Alunno-Bruscia. 2006. Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. *Journal of Sea Research* 56:156-167.
- Powell, E.N. and J.M. Klinck. 2007. Is oyster shell a sustainable estuarine resource? *Journal of Shellfish Research* 26(1):181-194.
- Powell, E.N., E.E. Hofmann, J.M. Klinck, and S.M. Ray. 1992. Modeling oyster populations I. A commentary on filtration rate. Is faster always better? *Journal of Shellfish Research* 11:387-398.
- Powell, E.N., J. Song, M.S. Ellis, and E.A. Wilson-Ormond. 1995. The status and long-term status of oyster reefs in Galveston Bay, Texas. *Journal of Shellfish Research* 14:439-457.
- Powell, E.N., J.N. Kraeuter, and K.A. Ashton-Alcox. 2006. How long does oyster shell last on an oyster reef? *Estuarine, Coastal and Shelf Science* 69(3-4):531-542.
- Power, M.E. 2001. Prey exchange between a stream and its forested watershed elevates predator densities in both habitats. *Proceedings of the National Academy of Sciences of the United States of America* 98(1):14-15.
- Power, M.E., W.J. Matthews, and S.A. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology* 66(5):1448-1456.
- Powers, M.J., C.H. Peterson, H.C. Summerson, and S.P. Powers. 2007. Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. *Marine Ecology Progress Series* 339:109-122.
- Prins, T.C., A.C. Smaal, and A.J. Pouwer. 1991. Selective ingestion of phytoplankton by the bivalves *Mytilus edulis* L. and *Cerastoderma edule* (L.). *Aquatic Ecology* 25(1):93-100.

- Prins, T.C. and A.C. Smaal. 1994. The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde Estuary (The Netherlands). *Hydrobiologia* 282-283(1):413-429.
- Prins, T.C., A.C. Smaal, and R.F. Dame. 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquatic Ecology* 31(4):349-359.
- Prior, S., A. Segars, and C.L. Browdy. 2001. A preliminary assessment of live and frozen bait shrimp as indicators and/or vectors for shrimp viruses. In *Aquaculture 2001: Book of Abstracts*, Devoe, R. (ed.). World Aquaculture Society, Lake Buena Vista, Florida.
- Railkin, A.I. 2004. *Marine Biofouling: Colonization Process and Defenses*. CRC Press, Boca Raton, Florida.
- Raillard, O. and A. Máneguen. 1994. An ecosystem box model for estimating the carrying capacity of a macrotidal shellfish system. *Marine Ecology Progress Series* 115(1-2):117-130.
- Ralston, E.P. and H.L. Kite-Powell. In Review. An estimate of the cost of acute health effects from marine pathogens and toxins in the United States. *Environmental Health Perspectives*.
- Read, A.J., P. Drinker, and S. Northridge. 2006. Bycatch of marine mammals in U.S. and global fisheries. *Conservation Biology* 20(1):163-169.
- Reeb, C.A. and J.C. Avise. 1990. A genetic discontinuity in a continuously distributed species: Mitochondrial-DNA in the American oyster, *Crassostrea virginica*. *Genetics* 124:397-406.
- Reusch, T.B.H. and S.L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. *Oecologia* 113(3):428-441.
- Reusch, T.B.H., A.R.O. Chapman, and J.P. Groger. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Marine Ecology Progress Series* 108:265-282.
- Rice, M.A. 2000. A review of shellfish restoration as a tool for coastal water quality management. *Environment Cape Cod* 3(2):1-8.
- Richerson, K., P.S. Levin, and M. Mangel. 2009. Accounting for indirect effects and non-commensurate values in ecosystem-based fishery management (EBFM). *Marine Policy* 34(1):114-119.
- Rick, T.C. and J.M. Erlandson. 2009. Coastal exploitation. *Science* 325(5943):952-953.
- Rieser, A. 1997. Defining the federal role in offshore aquaculture: Should it feature delegation to the states? *Ocean and Coastal Law Journal* 2:209-234.
- Rieser, A. and S. Bunsick. 1999. Aquaculture in the U.S. exclusive economic zone (EEZ): Legal and regulatory concerns. In *Offshore Marine Trends and Future Challenges for U.S. National Ocean and Coastal Policy*, Cicin-Sain, B., R.W. Knecht, and N. Foster (eds.). National Oceanic and Atmospheric Administration, Silver Spring, Maryland.
- Robinson, A.M. 1997. Molluscan fisheries in Oregon: Past, present and future. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Mackenzie, C.L.J., V.G.J. Burrell, A. Rosenfield, and W.L. Hobart (eds.). U.S. Department of Commerce, Seattle, Washington.
- Rodgers, J.A. and H.T. Smith. 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildlife Society Bulletin* 25(1):139-145.
- Roslinda, R., Ø. Strand, M. Alunno-Bruscia, C. Bacher, and T. Strohmeier. 2009. Applying Dynamic Energy Budget (DEB) theory to simulate growth and bio-energetics of blue mussels under low seston conditions. *Journal of Sea Research* 62(2-3):49-61.
- Ross, B.P., J. Lien, and R.W. Furness. 2001. Use of underwater playback to reduce the impact of elders on mussel farms. *ICES Journal of Marine Science* 58:517-524.
- Ross, K.A., J.P. Thorpe, T.A. Norton, and A.R. Brand. 2002. Fouling in scallop cultivation: Help or hindrance? *Journal of Shellfish Research* 21:539-547.

- Rothschild, B.J., J.S. Ault, P. 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.
- Roycroft, D., T.C. Kelly, and L.J. Lewis. 2004. Birds, seals and the suspension culture of mussels in Bantry Bay, a non-seaduck area in Southwest Ireland. *Estuarine, Coastal and Shellfish Science* 61(4):703-712.
- Ruckelshaus, M.H., T. Klinger, N. Knowlton, and D.P. DeMaster. 2008. Marine ecosystem-based management in practice: Scientific and governance challenges. *Bioscience* 58:53-63.
- 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 and Systematics* 36:643-689.
- Ruiz, G.M., J.T. Carlton, E.D. Grosholz, and A.H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist* 37(6):621-632.
- Ruiz, G.M., P. Fofonoff, A.H. Hines, and E.D. Grosholz. 1999. Nonindigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. *Limnology and Oceanography* 44(3-2):950-972.
- Ruiz, G.M., P.W. Fofonoff, J.T. Carlton, M.J. Wonham, and A.H. Hines. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31:481-531.
- Rumrill, S.S. and V.K. Poulton. 2004. *Ecological Role and Potential Impacts of Molluscan Shellfish Culture in the Estuarine Environment of Humboldt Bay, California*. Oregon Department of State Lands, Salem, Oregon.
- Russell, E.S. 1931. Some theoretical considerations on the "overfishing" problem. *ICES Journal of Marine Science* 6(1):1-20.
- Rychlak, R.J. and E.M. Peel. 1993. Swimming past the hook: Navigating legal obstacles in the aquaculture industry. *Environmental Law* 23:837-868.
- Saavedra, C. and E. Bachere. 2006. Bivalve genomics. *Aquaculture* 256(1-4):1-14.
- Salita, J.T., W. Ekau, and U. Saint-Paul. 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. *Marine Ecology Progress Series* 247:183-195.
- Sanders, M.J. 1966. Parasitic castration of the scallop *Pecten alba* (Tate) by a bucephalid trematode. *Nature* 212:307-308.
- Sargsyan, O. and J. Wakeley. 2008. A coalescent process with simultaneous multiple mergers for approximating the gene genealogies of many marine organisms. *Theoretical Population Biology* 74(1):104-114.
- Schreffler, D. and K. Griffen. 2000. *Ecological Interactions among Eelgrass Oysters and Burrowing Shrimp in Tillamook Bay, Oregon*. Tillamook County Performance Partnership, Tillamook, Oregon.
- Schulte, D.M., R.P. Burke, and R.N. Lipcius. 2009. Unprecedented restoration of a native oyster metapopulation. *Science* 325(5944):1124-1128.
- Schulze, P.C. (ed.). 1999. *Measures of Environmental Performance and Ecosystem Condition*. National Academy Press, Washington, DC.
- Secretariat of the Convention on Biological Diversity. 2004. *Solutions for Sustainable Mariculture—Avoiding the Adverse Effects of Mariculture on Biological Diversity*, CBD Technical Series No. 12. Secretariat of the Convention on Biological Diversity World Trade Center, Montreal, Quebec, Canada.
- Selgrath, J.C., K.A. Hovel, and R.A. Wahle. 2007. Effects of habitat edges on American lobster abundance and survival. *Journal of Experimental Marine Biology and Ecology* 353(2):253-264.

- Sequeira, A., J.G. Ferreira, A.J.S. Hawkins, A. Nober, P. Lourenço, X.L. Zhang, and T. Nickell. 2008. Trade-offs between shellfish aquaculture and benthic biodiversity: A modelling approach for sustainable management. *Aquaculture* 274(2-4):313-328.
- Shatkin, G., S.E. Shumway, and R. Hawes. 1997. Considerations regarding the possible introduction of the Pacific oyster (*Crassostrea gigas*) to the Gulf of Maine: A review of global experience. *Journal of Shellfish Research* 16(2):463-477.
- Shaw, W.N. 1997. The shellfish industry of California—Past, present and future. In *The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe*, Mackenzie, C.L.J., V.G.J. Burrell, A. Rosenfield, and W.L. Hobart (eds.). U.S. Department of Commerce, Seattle, Washington.
- Shearer, L.W. and C.L. MacKenzie, Jr. 1961. The effects of salt solutions of different strengths on oyster enemies. *Proceedings of the National Shellfisheries Association* 50:97-103.
- Sheridan, A.K. 1997. Genetic improvement of oyster production—A critique. *Aquaculture* 153(3-4):165-179.
- Shull, G.H. 1908. The composition of a field of maize. *American Breeders Association Reports* 4:296-301.
- Shumway, S.E. and J. Kraeuter (eds.). 2000. Molluscan shellfish research and management: Charting a course for the future. In *Proceedings from the Workshop Held in Charleston, South Carolina, January 2000*. Charleston, South Carolina.
- Shumway, S.E., D. Card, R. Getchell, and C. Newell. 1988. Effects of calcium-oxide (Quicklime) on non-target organisms in mussel beds. *Bulletin of Environmental Contamination and Toxicology* 40(4):503-509.
- Simberloff, D.S. 2005. The politics of assessing risk for biological invasions: The USA as a case study. *Trends in Ecology and Evolution* 20(5):216-222.
- Simenstad, C.A. and K.L. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: Scales of disturbance. *Estuaries* 18:43-70.
- Sinderman, C.J. 1984. *Principal Diseases of Marine Fish and Shellfish*. Academic Press, New York.
- Sinderman, C.J., B. Steinmetz, and W. Hershberger. 1992. Introductions and transfers of aquatic species. *ICES Marine Science Symposium* 194:1-2.
- Smaal, A., M. van Stralen, and E. Schuiling. 2001. The interaction between shellfish culture and ecosystem processes. *Canadian Journal of Fisheries and Aquatic Sciences* 58(5):991-1002.
- Smaal, A.C., T.C. Prins, N. Dankers, and B. Ball. 1998. Minimum requirements for modeling bivalve carrying capacity. *Aquatic Ecology* 31(4):423-428.
- Soniati, T.M. and G.M. Burton. 2005. A comparison of the effectiveness of sandstone and limestone as cultch for oysters, *Crassostrea virginica*. *Journal of Shellfish Research* 24:483-485.
- Soto, D., J. Aguilar-Manjarrez, J. Bermúdez, C. Brugère, D. Angel, C. Bailey, K. Black, P. Edwards, B. Costa-Pierce, T. Chopin, S. Deudero, S. Freeman, J. Hambrey, N. Hishamunda, D. Knowler, W. Silvert, N. Marba, S. Mathe, R. Norambuena, F. Simard, P. Tett, M. Troell, and A. Wainberg. 2008. Applying an ecosystem-based approach to aquaculture: Principles, scales and some management measures. In *Building an Ecosystem Approach to Aquaculture*, Soto, D. and N. Hishamunda (eds.). Food and Agriculture Organization of the United Nations, Rome, Italy.
- Stachowicz, J.J., J.R. Terwin, R.B. Whitlatch, and R.W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America* 99(24):15497-15500.
- Stillman, R.A., A.D. West, R.W.G. Caldow, and S.E.A. le V. dit Durell. 2007. Predicting the effect of disturbance on coastal birds. *Ibis* 149(1):73-81.
- Stiven, A.E. 1964. Experimental studies on the host parasite system hydra and *Hydramoeba hydroxena* (Entz). II. The components of a single epidemic. *Ecological Monographs* 34:119-142.

- Stokstad, E. 2009. Oysters booming on new reefs, but can they survive disease? *Science* 325(5940):525.
- Stow, C.A., J. Jolliff, D.J. McGillicuddy, Jr., S.C. Doney, J.I. Allen, M.A.M. Friedrichs, K.A. Rose, and P. Wallhead. 2009. Skill assessment for coupled biological/physical models of marine systems. *Journal of Marine Systems* 76(1-2):4-15.
- Strathmann, M. 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. University of Washington Press, Seattle, Washington.
- Straus, K.M., L.M. Crosson, and B. Vadopalas. 2008. *Effects of Geoduck Aquaculture on the Environment: A Synthesis of Current Knowledge*. Washington Sea Grant, Seattle, Washington.
- Strayer, D.L. 2009. Twenty years of zebra mussels: Lessons from the mollusk that made headlines. *Frontiers in the Ecology and the Environment* 7(3):135-141.
- Strayer, D.L. and H.M. Malcom. 2007. Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: The beginning of the end or the end of the beginning? *Journal of the North American Benthological Society* 26(1):111-122.
- Strayer, D.L., N.F. Caraco, J.J. Cole, S. Findlay, and M.L. Pace. 1999. Transformation of freshwater ecosystems by bivalves: A case study of zebra mussels in the Hudson River. *Bioscience* 2(1):19-27.
- Strayer, D.L., K. Hattala, and A. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish populations in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 61(6):924-941.
- Sutherland, J.P. 1974. Multiple stable points in natural communities. *American Naturalist* 108(964):859-873.
- Swart, J.A.A. and J. van Andel. 2008. Rethinking the interface between ecology and society. The case of the cockle controversy in the Dutch Wadden Sea. *Journal of Applied Ecology* 45(1):82-90.
- Swearer, S.E., J.S. Shima, M.E. Hellberg, S.R. Thorrold, G.P. Jones, D.R. Robertson, S.G. Morgan, K.A. Selkoe, G.M. Ruiz, and R.R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70(1):251-271.
- Syvret, M., A. Fitzgerald, and P. Hoare. 2008. *Development of a Pacific Oyster Aquaculture Protocol for the UK—Technical Report*. Sea Fish Industry Authority, Edinburgh, Scotland, United Kingdom.
- Tallis, H.M., J.L. Ruesink, B.R. Dumbauld, S.D. Hacker, and L.M. Wisheart. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. *Journal of Shellfish Research* 28(2):251-261.
- Tallman, J.C. and G.E. Forrester. 2007. Oyster grow-out cages function as artificial reefs for temperate fishes. *Transactions of the American Fisheries Society* 136:790-799.
- Tanguy, A., N. Bierne, C. Saavedra, B. Pina, E. Bachere, M. Kube, E. Bazin, F. Bonhomme, P. Boudry, V. Boulo, I. Boutet, L. Cancela, C. Dossat, P. Favrel, A. Huvet, S. Jarque, D. Jollivet, S. Klages, S. Lapegue, R. Leite, J. Moal, D. Moraga, R. Reinhardt, J.F. Samain, E. Zouros, and A. Canario. 2008. Increasing genomic information in bivalves through new EST collections in four species: Development of new genetic markers for environmental studies and genome evolution. *Gene* 408(1-2):27-36.
- Tanner, J.E. 2005. Edge effects on fauna in fragmented seagrass meadows. *Australia Ecology* 30(2):210-218.
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16(3):284-307.
- Taylor, J.J., P.C. Southgate, and R.A. Rose. 1997. Fouling animals and their effect on the growth of silver-lip pearl oysters, *Pinctada maxima* (Jameson) in suspended culture. *Aquaculture* 153(1-2):31-40.

- Tenore, K.R., L.F. Boyer, R.M. Cal, J. Corral, C. García-Fernández, N. González, E. González-Gurriaran, R.B. Hanson, J. Iglesias, M. Krom, E. López-Jamar, J. McClain, M.M. Pamatmat, A. Pérez, D.C. Rhoads, G. de Santiago, J. Tietjen, J. Westrich, and H.L. Windom. 1982. Coastal upwelling in the Rias Bajas, N.W. Spain: Contrasting the benthic regimes of the Rias de Arosa and de Muros. *Journal of Marine Research* 40:701-772.
- Thom, R.M., A.B. Borde, S. Rumrill, D.L. Woodruff, G.D. Williams, J.A. Southard, and S.L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington and Coos Bay, Oregon, USA. *Estuaries* 26(4B):1117-1129.
- Thomas, M.B., K.D. Lafferty, and C.S. Friedman. 2008. Biodiversity, species losses and introductions. In *Biodiversity, Human Health and Sustainable Development*, Sala, O., L.A. Meyerson, and C. Parmesan (eds.). Island Press, Washington, DC.
- Thompson, D.S. 1995. Substrate additive studies for the development of hardshell clam habitat in Washington State: An analysis of effects on recruitment, growth and survival of the Manila clam, *Tapes philippinarum*, and on the species diversity and abundance of existing benthic organisms. *Estuaries* 18(1A):91-107.
- Thompson, G.R. and B. Gillis. 2001. *Sea Ducks and Mussel Aquaculture Operations in Prince Edward Island: October 2000–January 2001, Technical Report 227*. Prince Edward Island Department of Fisheries, Prince Edward Island, Canada.
- Thompson, J.K. 2005. One estuary, one invasion, two responses: Phytoplankton and benthic community dynamics determine the effect of an estuarine invasive suspension-feeder. In *The Comparative Roles of Suspension-Feeders in Ecosystems: Proceedings of the NATO Advanced Research Workshop on the Comparative Roles of Suspension-Feeders in Ecosystems, Nida, Lithuania, 4-9 October 2003*, Dame, R.F. and S. Olenin (eds.). Springer, Dordrecht, The Netherlands.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25(1):1-45.
- Travers, M.A., O. Basuyaux, N. Le Goic, S. Huchette, J.L. Nicolas, M. Koken, and C. Paillard. 2008a. Influence of temperature and spawning effort on *Haliotis tuberculata* mortalities caused by *Vibrio harveyi*: An example of emerging vibriosis linked to global warming. *Global Change Biology* 15(6):1365-1376.
- Travers, M.A., A. Barbou, N. Le Goïc, S. Huchette, C. Paillard, and M. Koken. 2008b. Construction of a stable GFP-tagged *Vibrio harveyi* strain for bacterial dynamics analysis of abalone infection. *Fems Microbiology Letters* 289(1):34-40.
- Trimble, A.C., J.L. 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.
- Troell, M., P. Tyedmers, N. Kautsky, and P. Rönnbäck. 2004. Aquaculture and energy use. In *Encyclopedia of Energy, Volume 1*, Cleveland, C. (ed.). Elsevier, Amsterdam, The Netherlands.
- Troost, K., R. Veldhuizen, E.J. Stamhuis, and W.J. Wolff. 2008. Can bivalve veligers escape feeding currents of adult bivalves? *Journal of Experimental Marine Biology and Ecology* 358(2):185-196.
- Turner, T.F., J.P. Wares, and J.R. Gold. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics* 162:1329-1339.
- Tyedmers, P. 2004. Fisheries and energy use. In *Encyclopedia of Energy, Volume 2*, Cleveland, C. (ed.). Elsevier, Amsterdam, The Netherlands.
- Tyrrell, M.C. and J.E. Byers. 2007. Do artificial substrates favor nonindigenous fouling species over native species? *Journal of Experimental Marine Biology and Ecology* 342(1):54-60.
- Underwood, J. 1997. Intertidal zone aquaculture and the public trust doctrine. *Ocean and Coastal Law Journal* 2:383-414.

- University of Maryland. 2009. *NRAC Fact Sheets*. [Online]. Available: <http://www.nrac.umd.edu/publications/factSheets.cfm> [2009, September 14].
- U.S. Army Corps of Engineers. 2009. *Record of Decision: Final Programmatic Environmental Impact Statement for Oyster Restoration in Chesapeake Bay Including the Use of a Native and/or Nonnative Oyster*. [Online]. Available: http://www.nao.usace.army.mil/OysterEIS/documents/Record_ofDecision_2009-08-13-152459.pdf [2010, January 11].
- U.S. Commission on Ocean Policy. 2004. *An Ocean Blueprint for the 21st Century*. U.S. Commission on Ocean Policy, Washington, DC.
- Vahl, O. 1980. Seasonal variations in seston and in the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Müller) from balsfjord, 70°N. *Journal of Experimental Marine Biology and Ecology* 48(2):195-204.
- VanBlaricom, G.R., J.L. Ruediger, C.S. Friedman, D.D. Woodard, and R.P. Hedrick. 1993. Discovery withering syndrome among black abalone populations at San Nicolas Island, California. *Journal of Shellfish Research* 12(2):185-188.
- Verhulst, S., K. Oosterbeek, A.L. Rutten, and B.J. Ens. 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. *Ecology and Society* 9(1):17.
- Vestal, B. 1999. Dueling with boat oars, dragging through mooring lines: Time for more formal resolution of use conflicts in state waters. *Ocean and Coastal Law Journal* 4:1-79.
- Vincenzi, S., G. Carmori, R. Rossi, and G.A. De Leo. 2006. A GIS-based habitat suitability model for commercial yield estimation of *Tapes philippinarum* in a Mediterranean coastal lagoon (Sacca di Goro, Italy). *Ecological Modelling* 193(1-2):90-104.
- Vinther, H.F., J.S. Laursen, and M. Holmer. 2008. Negative effects of blue mussel (*Mytilus edulis*) presence in eelgrass (*Zostera marina*) beds in Flensborg fjord, Denmark. *Estuarine, Coastal and Shelf Science* 77(1):91-103.
- Waddell, J.E. 1964. *The Effect of Oyster Culture on Eelgrass (Zostera marina L.) Growth*. Master of Science Thesis, Humboldt State College, Arcata, California.
- Wall, C.C., B.J. Peterson, and C.J. Gobler. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. *Marine Ecology Progress Series* 357:165-174.
- Waples, R.S. 2002. Evaluating the effect of stage-specific survivorship on the N_e/N ratio. *Molecular Ecology* 11(6):1029-1037.
- Ward, D.H., A. Morton, T.L. Tibbitts, D.C. Douglas, and E. Carrera-González. 2003. Long-term change in eelgrass distribution at Baha San Quintin, Baja California, Mexico, using satellite imagery. *Estuaries* 26:1529-1539.
- Ward, R.D. 2006. The importance of identifying spatial population structure in restocking and stock enhancement programmes. *Fisheries Research* 80(1):9-18.
- Washington Sea Grant. 2002. *Small-Scale Oyster Farming for Pleasure and Profit in Washington*. [Online]. Available: <http://www.wsg.washington.edu/mas/pdfs/smallscaleoysterlr.pdf> [2010, January 11].
- Washington Sea Grant. 2007a. *Current Geoduck Research*. [Online]. Available: http://www.wsg.washington.edu/research/geoduck/current_research.html [2009, October 23].
- Washington Sea Grant. 2007b. *Geochemical and Ecological Consequences of Disturbances Associated with Geoduck Aquaculture Operations in Washington*. [Online]. Available: http://www.wsg.washington.edu/research/geoduck/research/vanblaricom_overview.html [2009, October 23].
- Washington Sea Grant. 2007c. *Resilience of Soft-Sediment Communities after Geoduck Harvest in Samish Bay, Washington*. [Online]. Available: http://www.wsg.washington.edu/research/geoduck/research/ruesink_overview.html [2009, October 23].
- Watson, D., S.E. Shumway, and R.B. Whitlatch. 2009. Biofouling and the shellfish industry. In *Shellfish Quality and Safety*, Shumway, S.E. and G.E. Rodrick (eds.). Woodhead Publishing, Cambridge, England, United Kingdom.

- Watson-Capps, J.J. and J. Mann. 2005. The effects of aquaculture on bottlenose dolphin *Tursiops* sp. ranging in Shark Bay, Western Australia. *Biological Conservation* 124:519-526.
- Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, J.W. Kenworthy, F.T. Short, and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences Early Addition* 106(30):12377-12381.
- Wechsler, J.F. 2004. *Assessing the Relationship between the Ichthyofauna and Oyster Mariculture in a Shallow Embayment, Drakes Estero, Point Reyes National Seashore*. Master of Science Thesis, University of California, Davis, Davis, California.
- Weinstein, M.P., R.C. Baird, D.O. Conover, M. Gross, J. Keulartz, D.K. Loomis, Z. Naveh, S.B. Peterson, D.J. Reed, E. Roe, R.S. Lawrence, J.A.A. Swart, J.M. Teal, R.E. Turner, and H.J. van der Windt. 2007. Managing coastal resources in the 21st century. *Frontiers in Ecology and the Environment* 5(1):43-48.
- Weise, A.M., C.J. Crome, M.D. Callier, P. Archambault, J. Chamberlain, and C.W. McKindsey. 2009. Shellfish-DEPOMOD: Modelling the biodeposition from suspended shellfish aquaculture and assessing benthic effects. *Aquaculture* 288(3-4):239-253.
- Wells, H.W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecological Monographs* 31(3):239-266.
- Wetchateng, T. 2008. Rickettsia-like organism (RLO) infection in the abalone, *Haliotis diversicolor supertexta*: Histopathology, diagnosis and treatment. Ph.D. Dissertation, Mahidol University, Bangkok, Thailand.
- Whiteley, J. and L. Bendell-Young. 2007. Ecological implications of intertidal mariculture: Observed differences in bivalve community structure between farm and reference sites. *Journal of Applied Ecology* 44(3):495-505.
- Widdows, J., M.D. Brinsley, N. Bowley, and C. Barrett. 1998. A benthic annular flume for in situ measurement of suspension feeding/biodeposition rates and erosion potential of intertidal cohesive sediments. *Estuarine, Coastal and Shelf Science* 46:27-38.
- Wildsmith, B.H. 1982. *Aquaculture: The Legal Framework*. Edmond-Montgomery Limited, Toronto, Ontario, Canada.
- Williams, B.K., R.C. Szaro, and C.D. Shapiro. 2007. *Adaptive Management: The U.S. Department of the Interior Technical Guide*. U.S. Department of the Interior, Washington, DC.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton University Press, Princeton, New Jersey.
- Williams, S.L. and K.L. Heck, Jr. 2001. Seagrass community ecology. In *Marine Community Ecology*, Bertness, M.D., S.D. Gaines, and M.E. Hay (eds.). Sinauer Associates, Sunderland, Massachusetts.
- Winemiller, K.O. and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196-2218.
- Wisehart, L.M. 2006. Impacts of oysters on eelgrass (*Zostera marina* L.): Importance of early life history stages in response to aquaculture disturbance. Master of Science Thesis, Oregon State University, Corvallis, Oregon.
- Wisehart, L.M., J.L. Ruesink, S.D. Hacker, and B.R. Dumbauld. 2007. Importance of eelgrass early life history stages in response to oyster aquaculture disturbance. *Marine Ecology Progress Series* 344:71-80.
- Woelke, C.E. 1956. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. *Proceedings of the National Shellfisheries Association* 47:62-67.
- Woelke, C.E. 1969. *A History and Economic Evaluation of Washington State Oyster Reserves*. Washington Department of Fisheries, Olympia, Washington.
- Wong, A.C. and A.L. van Eenennaam. 2008. Transgenic approaches for the reproductive containment of genetically engineered fish. *Aquaculture* 275(1-4):1-12.

- Wootton, J.T. 1993. Indirect effects and habitat use in an intertidal community: Interaction chains and interaction modifications. *American Naturalist* 141(1):71-89.
- World Wildlife Fund. 2008. *Aquaculture Dialogues: Process Guidance Document*. World Wildlife Fund, Washington, DC.
- World Wildlife Fund. 2009. *Aquaculture: Bivalve*. [Online]. Available: <http://www.worldwildlife.org/what/globalmarkets/aquaculture/dialogues-molluscs.html> [2009, September 14].
- Würsig, B. and G. Gailey. 2002. Marine mammals and aquaculture: Conflicts and potential resolutions. In *Responsible Marine Aquaculture*, Stickney, R. and J. McVey (eds.). CAB International, Wallingford, England, United Kingdom.
- Zhang, J., P.K. Hansen, J.G. Fang, W. Wang, and Z. Jiang. 2009. Assessment of the local environmental impact of intensive marine shellfish and seaweed farming—Application of the MOM system in the Sungo Bay, China. *Aquaculture* 287(3-4):304-310.
- Zouros, E., S.M. Singh, and H.E. Miles. 1980. Growth-rate in oysters: An overdominant phenotype and its possible explanations. *Evolution* 34:856-867.
- Zouros, E. and G.H. Pogson. 1994. The present status of the relationship between heterozygosity and heterosis. In *Genetics and Evolution of Aquatic Organisms*, Beaumont, A.R. (ed.). Chapman and Hall, London, England, United Kingdom.
- Žydelis, R., D. Esler, M. Kirk, and W.S. Boyd. 2009. Effects of off-bottom shellfish aquaculture on winter habitat use by molluscivorous sea ducks. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:34-42.

Appendixes

A

Statement of Task

The committee will develop recommendations for best practices for shellfish mariculture to maintain ecosystem integrity. To this end, the committee will address the following questions:

- What are the ecological effects of mariculture, and how do they vary in magnitude by duration, operation size, harvest intensity, species cultivated, habitat type, and geographic location (e.g., effects on carrying capacity, water clarity, physical disturbance, species shifts, diseases, benthic deposition)?
 - What are the uncertainties surrounding these ecological effects?
 - How do the ecological effects of mariculture compare with the harvest of wild populations?
 - Does shellfish mariculture reduce the harvest pressure on wild populations?
 - What are the risks for the spread of nonnative species, and how could these risks be reduced?
 - What socioeconomic factors influence the size and location of shellfish mariculture activities (e.g., “not-in-my-backyard” [NIMBY] issues, economic parameters [permitting/leases for seabed, price stability, labor, transportation], local traditions)?
 - What are the most important subjects for future research to better understand and manage the ecosystem responses to mariculture operations?

The report will identify best management practices that could be employed to enhance the benefits of shellfish mariculture and minimize any negative ecological effects.

B

Committee and Staff Biographies

COMMITTEE

Charles (Pete) Peterson (*Chair*) is an alumni distinguished professor in the Institute of Marine Sciences at the University of North Carolina at Chapel Hill. Dr. Peterson earned a Ph.D. in biology from the University of California, Santa Barbara, in 1972. His research can be characterized as interdisciplinary marine conservation ecology. His specializations involve marine benthic ecology, including the importance and nature of predation and intra- and inter-specific competition in benthic communities and the role of resource limitation in suspension-feeding bivalve populations. He also conducts research in paleoecology, invertebrate fisheries management, estuarine habitat evaluation, and barrier island ecology. Dr. Peterson has served on numerous NRC committees.

Barry Costa-Pierce is the director of the Rhode Island Sea Grant College Program and a joint professor of fisheries, aquaculture and oceanography at the University of Rhode Island. Dr. Costa-Pierce earned a Ph.D. in oceanography from the University of Hawaii. His research focuses on capture-based aquaculture systems; on the environmental impacts and systems ecology of aquaculture ecosystems; and on the development of scientifically credible sustainability indices for mariculture projects worldwide. Dr. Costa-Pierce is on the Board of Directors of the World Aquaculture Society and is also one of the four international editors of *Aquaculture*.

Brett Dumbauld is an ecologist at the Agricultural Research Service of the U.S. Department of Agriculture. Dr. Dumbauld earned a Ph.D. in fisheries from the University of Washington. His research focuses on solving the problem shellfish growers have with burrowing shrimp and investigating the role of shellfish aquaculture in the estuarine environment. He is a member of the National Shellfisheries Association, the Coastal and Estuarine Research Federation, the Pacific Estuarine Research Society, and the Society for Conservation Biology.

Carolyn Friedman is an associate professor in the School of Aquatic and Fishery Sciences at the University of Washington. Dr. Friedman earned a Ph.D. in comparative pathology from the University of California, Davis. Her research focuses on the examination of infectious and non-infectious diseases of wild and cultured marine invertebrates and on the conservation of marine invertebrates, particularly abalone. More specifically, she investigates the mass mortality of the Pacific oyster (*Crassostrea gigas*) on the west coast of the United States and the herpes-like viral infection of Pacific oysters.

Eileen Hofmann is a professor of oceanography in the Center for Coastal Physical Oceanography at Old Dominion University. Dr. Hofmann earned a Ph.D. in marine science and engineering from North Carolina State University. Her research focuses on the analysis and modeling of biological and physical interactions in marine ecosystems and descriptive physical oceanography. She served on the Ocean Studies Board and on numerous NRC committees, including the Committee on Strategic Advice on the U.S. Climate Change Science Program.

Hauke Kite-Powell is a research specialist at the Marine Policy Center of the Woods Hole Oceanographic Institution. Dr. Kite-Powell earned his Ph.D. in ocean systems management from the Massachusetts Institute of Technology. His research focuses on public and private sector management issues for marine resources and the economic activities that depend on them. His current research projects include the policy issues surrounding use of ocean space for non-traditional activities, such as aquaculture and wind power; the potential of shellfish aquaculture to contribute to nutrient level management in coastal water bodies; the economics and management of marine aquaculture operations; and the environmental and ecological implications of long-term growth in marine aquaculture industries. Dr. Kite-Powell served on the NRC Committee on Assessment of Technical Issues in the Automated Nautical Chart System.

Donal Manahan is a professor of biological sciences at the University of Southern California. Dr. Manahan earned a Ph.D. in marine biology from the University of Wales, Bangor. His research focuses on animal environmental physiology; biological adaptations to temperature and food; marine biology of temperate, polar, tropical, and deep-sea species; Antarctic marine biology; hydrothermal vent biology; developmental biology; evolutionary biology; marine invertebrate life history; larval ecology; and aquaculture. Dr. Manahan has served on NRC committees and as the Chair of the Polar Research Board.

Francis O'Beirn is the benthos ecology team leader at the Marine Institute in Galway, Ireland. Dr. O'Beirn earned a Ph.D. in zoology from the University of Georgia. His research interests focus on benthic ecology and monitoring, bivalve biology, as well as finfish and shellfish mariculture. He sits on a number of advisory committees responsible for licensing of marine activities in Ireland. He is currently the Chair of the International Council for Exploration of the Seas' (ICES) Working Group on Environmental Interactions of Mariculture and is the Irish delegate to the ICES mariculture committee. Dr. O'Beirn also has experience with shellfish mariculture and habitat restoration in the Chesapeake Bay area and the southeastern United States.

Robert Paine is a professor emeritus in the Department of Biology at the University of Washington. Dr. Paine earned a Ph.D. from the University of Michigan in 1961. His research focuses on experimental ecology of organisms on rocky shores, interrelationships between species in an ecosystem, and the organization and structure of marine communities. He has examined the roles of predation and disturbance in promoting coexistence and biodiversity. Dr. Paine is a member of the National Academy of Sciences and was a member of the Ocean Studies Board. He has served on numerous NRC committees, including the Committee on Ecosystem Effects of Fishing.

Paul Thompson has a Personal Chair in Zoology in the University of Aberdeen's School of Biological Sciences, and is Director of the Lighthouse Field Station, Cromarty, Scotland, which he set up in 1989. Dr. Thompson earned a Ph.D. in marine mammal ecology from the University of Aberdeen. He has been researching marine mammal behavior and ecology, including harbor and gray seals, for 20 years. His current research aims to assess how natural and anthropogenic environmental variations influence the behavior, physiology, and dynamics of marine mammal and seabird populations. Topics of particular interest have included interactions between wildlife populations and fisheries, the impact of

disturbance and contaminants on marine mammal biology, seal foraging and breeding strategies, and the effects of changing prey stocks and climate change on the population dynamics of marine top predators. Dr. Thompson is a member of the International Union for the Conservation of Nature's Seal Specialist Group, the Scottish Association of Marine Sciences, among others.

Robert Whitlatch is a professor of marine sciences at the University of Connecticut. He earned a B.S. in zoology, an M.S. in marine sciences, and a Ph.D. in evolutionary biology from the University of Utah, the University of the Pacific, and the University of Chicago, respectively. Dr. Whitlatch is a benthic ecologist interested in animal–sediment relationships, trophic dynamics of deposit-feeding invertebrates, life history analysis, shellfish ecology, the ecology of invasive species, and community ecology. He has worked extensively on both oyster reef biology and on the ecology of non-native species in coastal New England. Dr. Whitlatch served on the NRC's Committee on Nonnative Oysters in the Chesapeake Bay.

STAFF

Jodi Bostrom is an associate program officer with the Ocean Studies Board. She earned an M.S. in environmental science from American University in 2006 and a B.S. in zoology from the University of Wisconsin-Madison in 1998. Since starting with the Ocean Studies Board in May 1999, Ms. Bostrom has worked on several studies pertaining to coastal restoration, fisheries, marine mammals, nutrient over-enrichment, ocean exploration, capacity building, and marine debris.

Susan Roberts became the director of the Ocean Studies Board in April 2004. Dr. Roberts received her Ph.D. in marine biology from the Scripps Institution of Oceanography. She worked as a postdoctoral researcher at the University of California, Berkeley and as a senior staff fellow at the National Institutes of Health. Dr. Roberts' past research experience has included fish muscle physiology and biochemistry, marine bacterial symbioses, and developmental cell biology. She has directed a number of studies for the Ocean Studies Board including *Nonnative Oysters in the Chesapeake Bay* (2004); *Decline of the Steller Sea Lion in Alaskan Waters: Untangling Food Webs and Fishing Nets* (2003); *Effects of Trawling & Dredging on Seafloor Habitat* (2002); *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems* (2001); *Under the Weather: Climate, Ecosystems, and Infectious Disease* (2001); *Bridging Boundaries Through Regional Marine Research* (2000); and *From Monsoons to Microbes: Understanding the Ocean's Role in Human*

Health (1999). Dr. Roberts specializes in the science and management of living marine resources.

Jeremy Justice is a senior program assistant with the Ocean Studies Board. He received his B.A. degree in international and area studies from the University of Oklahoma in 2008. Since joining the National Academies staff in October 2008, Mr. Justice has worked on *Science at Sea: Meeting Future Oceanographic Goals with a Robust Academic Research Fleet* in addition to this report.

