

A framework for developing “ecological carrying capacity” mathematical models for bivalve mollusc aquaculture

Roger I. E. Newell *

Abstract Aquacultural production of suspension-feeding bivalve molluscs can profit from information on the stocking density at which commercially valuable meat production is maximized. Predicting these stocking densities in the natural environment is difficult a priori because of the complex interacting effects of environmental variables on bivalve growth (e.g., food availability varies with rates of phytoplankton production, water currents affect “food flux” to the bivalves, etc.) In an effort to integrate the influence of environmental variables on bivalve growth a number of mathematical “carrying capacity” models have been developed that estimate the standing stock at which commercial harvests are maximized. This emphasis means that other important aspects of ecosystem carrying capacity, such as the ability of the culture site to process the excrement produced by the animals, may not be adequately modeled. I recommend that an open source-code community model be developed to assess “ecological carrying capacity” for bivalve aquaculture. The overall objective should be to develop a well-parameterized model that will allow a comprehensive assessment of the major interactions between cultivated bivalves and the ecosystem. For example, in addition to predicting tissue production, this model can be used to assess the ability of suspension-feeding bivalves to exert top-down control on phytoplankton stocks, reduce turbidity, enhance nutrient removal, and provide habitat for other organisms. These secondary benefits can have economic value to the aquaculturists as part of polyculture systems, environmental remediation, and nutrient trading schemes. By modeling major aspects of ecosystem function, such as competition for food with other suspension feeding organisms, rates and location of biodeposition etc., models can be used to predict and possibly minimize potential adverse effects of bivalve aquaculture.

Key Words: Aquaculture, Bivalves, Carrying Capacity, Nutrient Removal, Polyculture

INTRODUCTION

All models are wrong. Some models are useful (DiToro 2001)

Commercial aquaculture of suspension-feeding bivalve molluscs, such as oysters and mussels, can benefit from quantitative estimates of how much production can be obtained from a location. The number of individuals that have to be stocked to

achieve this maximum production is often simply referred to as the “carrying capacity.” Carrying capacity is quite a widely-used term in biological science and, confusingly, has acquired a number of different meanings. Originally, it was a concept in ecology that was applied to the population density achieved at the asymptote in the logistic population growth equation (Odum 1983, Dame and Prins 1998). More recently, the term has broadly come to mean the maximum biomass that can be sustained

2006年6月26日受理 (Received, June 26, 2006)

* Horn Point Laboratory,
University of Maryland Center for Environmental Science
PO Box 775, Cambridge, MD 21613, USA
email: newell@hpl.umces.edu

by the available resources (Odum 1983). This ecosystem-based concept forms the basis of Carver and Mallet's (1990) definition of carrying capacity as the maximum standing stock of a particular cultured species at which production is maximized without negatively affecting growth rates. That definition may not always apply to commercial aquaculture, however, because production may be maximal even though individual growth rates are low (Smaal *et al.* 1998). Because of such inconsistencies, Smaal *et al.* (1998) proposed a definition for aquacultural production where "exploitation carrying capacity is the stock size at which a maximum yield of the marketable cohort is achieved."

Estimating "exploitation carrying capacity" for aquaculture sites in the natural environment, and thereby assessing potential economic returns prior to establishing an aquaculture operation is difficult. This is because food availability, which is one of the prime factors governing bivalve growth, is spatially and temporally variable because of changes in rates of phytoplankton production and water currents that regulate "food flux" through the grow-out sites (Wildish and Kristmanson 1997, Bacher *et al.* 2003). In an effort to integrate these complex environmental variables a number of different "carrying capacity" models have been specifically developed in order to predict optimum bivalve stocking densities (e.g., Bacher *et al.* 1997, Dowd 1997, Campbell and Newell 1998, Smaal *et al.* 1998, Chen *et al.* 1999, Bacher *et al.* 2003, Duarte *et al.* 2003, Nunes *et al.* 2003).

Restricting models to predicting the stocking density that maximize harvest yields means that there is no consideration of possibly adverse effects of the cultivated bivalves on important aspects of ecosystem function, such as the ability of the culture site to process excrement. In addition, possible ecosystem benefits are not modeled, such as bivalves feeding on phytoplankton and in the process removing nutrients from the water column (Newell 2004). This concept is the basis of integrated "ecological" or "balanced ecosystem" aquaculture operations (McVey *et al.* 2002, Neori *et al.* 2004) in which commercially valuable species from different trophic levels (e.g., algae and bivalves) are cultured so that they "extract" nutrients that are being added

elsewhere into the system (e.g., from finfish that are intensively fed). Furthermore, in some countries (e.g., USA) there is a move toward nutrient trading schemes where industries that pollute aquatic systems with nutrients pay other industries to remove nutrients from the same body of water. It is possible that shellfish aquaculture may qualify for payment under such nutrient trading schemes if the aquaculture facility is managed in such a way to maximize nutrient removal (Newell 2004). Only by developing predictive models will it be possible to design systems that maximize levels of nutrient removal.

In order to accommodate this broader ecosystem perspective, I propose that "ecological carrying capacity" for bivalve aquaculture be defined as "The standing stock of suspension-feeding bivalves where the consumption of phytoplankton, enhancement of nutrient removal, and other ecosystem services are maximized without negatively affecting water quality, sediment biogeochemistry, and overall ecosystem function." This is similar to the definition of carrying capacity proposed by Duarte *et al.* (2003) of "the level to which a process or variable may be changed within a particular ecosystem, without driving the structure and function of the ecosystem over acceptable limits." Both definitions suffer from ambiguous definitions of an unacceptable outcome (i.e., "without negatively affecting" and "over acceptable limits.") It is necessary for there to be greater discussion as to what constitutes the proper criteria and methods for assessing "ecosystem influence." It is overly optimistic to think that any aquaculture operation will have no adverse impacts whatsoever; consequently, the question becomes what level of impact is considered acceptable given the benefits accrued from that activity. Ultimately because that is a societal, and not an objective scientific question, the acceptable levels will likely vary from country to country.

Some criteria for monitoring ecosystem influences of bivalve aquaculture have been developed and can be used both as modeling criteria and then objectively measured in field situations. For example, Grant *et al.* (1995) performed a detailed study of a mussel aquaculture site and used a sophisticated benthic faunal analysis and

measurements of sediment biogeochemistry to quantify ecosystem impacts. Both of these criteria are highly sensitive to sediment redox balance. The depth of the redox potential discontinuity (RPD) in sediments can be measured directly, either in sediment cores collected in transparent acrylic plastic tubes (Grizzle and Penniman 1991), or by using a remotely operated camera system that directly photographs the sediment profile (O'Connor *et al.* 1989). This photographic technique can also provide quantitative information on changes in the infaunal macrofauna community. These criteria are similar to those adopted in Japan, where the accumulation of acid volatile sulfide in the sediment and changes in macrofauna abundance are used to monitor the influence of fin fish cultivation on the surrounding environment (Yokoyama 2003). This approach of objectively specifying certain key ecosystem processes and then monitoring these at aquaculture sites allows deviation from predetermined values for each variable to be discerned. These key ecosystem processes can also be incorporated as output parameters in a model to predict the effects of balanced aquaculture on the ecosystem.

The objective of this paper is to provide a framework to help stimulate a discussion of what should be included in future "ecological carrying capacity models" for bivalve aquaculture. This model should only include the essential elements as it would be counterproductive to develop an overly complex model, with time spent parameterizing details that do little to improve the overall accuracy of the model predications. I briefly review here some of the information that needs be included for the main four ecosystem processes that suspension-feeding bivalves influence: 1) top-down control on phytoplankton and microzooplankton; 2) sediment hypoxia; 3) inorganic nutrient cycling; 4) reduction in turbidity. I also briefly draw attention to the fact that the culture gear (rafts, cages, ropes, etc.) and the animals themselves can provide important habitat for other ecologically valuable "fouling community" organisms. Transfer of organic material to the sediment surface in biodeposits may also stimulate benthic production. Such effects on secondary production, and the likely transfer of this

production to higher trophic levels, are difficult to model but can be important ecosystem benefits of bivalve aquaculture systems.

MODEL COMPONENTS

1) Top-down control on phytoplankton and microzooplankton

Suspension-feeding bivalves remove particles $> 3 \mu\text{m}$ diameter from the water column with high efficiency when water temperatures are high enough to promote activity (Bayne and Newell 1983). This feeding activity can have the beneficial effect of exerting top-down control on phytoplankton populations that may be stimulated by nutrient inputs from point and diffuse terrestrial sources, adjacent fin-fish aquaculture sites, etc. (Newell 2004, Newell *et al.* 2005). Bivalves, by directly grazing on microzooplankton, may also reduce the dominance of carbon flow through "microbial loop" pathways (Sherr and Sherr 1988, Kreeger and Newell 1997, Kamiyama 2004).

Size selective feeding by bivalves means that larger nanoplankton cells ($>3 \mu\text{m}$ diameter) are preferentially removed in comparison with smaller and less efficiently retained picoplankton species. In order to accurately model the food resources available to suspension-feeding bivalves in any particular location, the size structure of the phytoplankton and microzooplankton community needs to be assessed. This will require models to include size-specific rates of phytoplankton production rather than use total chlorophyll *a* concentrations as a proxy for food available to bivalves, which is the approach adopted in many existing bivalve carrying capacity models (Campbell and Newell 1998, Smaal *et al.* 1998, Nunes *et al.* 2003, Duarte *et al.* 2003). Furthermore, differential grazing by bivalves can lead to the situation where picoplankton species are subject to reduced grazer control compared to larger species and hence become relatively more abundant (Olsson *et al.* 1992, Prins *et al.* 1998). Such an increase in picoplankton was documented by Vaquer *et al.* (1996) and Souchu *et al.* (2001) in a poorly flushed lagoon in the Mediterranean that has high abundances of aquacultured bivalves.

An additional reason for not simply using total chlorophyll as an estimate of food availability is that some species of phytoplankton possess toxins that reduce bivalve feeding activity (Shumway 1990). It is thought that blooms of such toxin producing algae may be increasing in distribution and frequency worldwide and anthropogenic nutrient enrichment is a likely causal factor (Cloern 2001). Even if the algal toxins do not adversely affect the bivalves directly, toxins can be bioaccumulated to levels that render the flesh unsafe for human consumption (Shumway 1990). Because the exact causes of harmful algal blooms are uncertain, it will be difficult to incorporate their occurrence into predictive ecosystem models but that does not mean that their influence should be ignored.

There can also be deleterious ecosystem effects of high rates of phytoplankton removal by suspension-feeding bivalves. At high bivalve densities there can be intraspecific competition for food that can be partially reduced by configuring the culture system to increase water through the site, thereby minimizing refiltration. This purely physical influence of water flow on food flux can now be efficiently modeled using coupled physical and biogeochemical models (e.g., Campbell and Newell 1998, Chen *et al.* 1999, Duarte *et al.* 2003). Interspecific food competition between high abundances of cultured bivalves and other ecologically valuable benthic and pelagic suspension-feeders (e.g., zooplankton) should be modeled explicitly. For example Lam-Hoai *et al.* (1997) reported that in areas with shellfish aquaculture there were appreciable differences in abundances of 40 to 300 μm diameter microzooplankton compared to areas with no aquaculture farms. They ascribed these differences in community structure to microzooplankton being directly grazed by bivalves and by other suspension-feeding invertebrates attached to the aquaculture structures. Bivalves may also out-compete some types of zooplankton for phytoplankton because bivalves overwinter as adults and are able to start feeding when water temperatures reach the threshold necessary to promote an active metabolism. In contrast, temperate copepod species, that form a dominant

component of the zooplankton, rely on a relatively small number of adults to survive overwinter that can then feed and reproduce in order to rebuild the population. As discussed above, bivalve grazing may alter phytoplankton species and size composition and thereby affect the food resources available to other benthic and pelagic suspension-feeding fauna.

2) Sediment hypoxia

Aquacultured finfish require an external food source and this feeding results in the addition to the water surrounding the aquaculture facility of "new" dissolved inorganic nutrients from fish urine and feces that can stimulate high levels of phytoplankton production. The situation is very different for bivalve aquaculture because the dissolved and particulate excrement released to the environment by bivalves is solely from them consuming autochthonous production that utilizes ambient dissolved inorganic nutrients. However, potentially adverse effects from both finfish and shellfish aquaculture facilities can result from excess deposition of fecal material that may overload the underlying sediments with particulate organic material. Bacterial decomposition of this organic material can release more inorganic nutrients and in extreme situations cause sediment anoxia, thereby reducing the biomass and species diversity of benthic fauna.

Undigested organic material in the feces and pseudofeces of bivalves are voided as mucus-bound pellets (collectively called biodeposits) that can be as long as several millimeters. As a consequence of this aggregation, biodeposits have a faster sinking velocity that is up to 40 times that of the component particles (Widdows *et al.* 1998). These biodeposits settle where the friction velocity (u^*), which is a function of current velocity and bed roughness, is below a critical velocity required to suspend particles of that particular mass (Miller *et al.* 2002). In locations with sufficient physical mixing, biodeposits can become disaggregated into smaller particles that sink more slowly and are resuspended at lower friction velocities. Where bottom friction velocities remain below the critical erosion velocity, biodeposits undergo a consolidation process and become incorporated into the sediments around the

bivalve population, hence increasing particulate and dissolved nutrient concentrations within that zone (Kaspar *et al.* 1985, Miller *et al.* 2002).

Because bivalves filter phytoplankton from large volumes of water, and these biodeposits are voided in the relatively small region around the aquaculture site, bivalves do serve to concentrate and focus nutrients (for review see Newell *et al.* 2005). Food-based carrying capacity models (e.g., Smaal *et al.* 1998, Duarte *et al.* 2003, Nunes *et al.* 2003) can predict the locations with the highest phytoplankton production that can support the greatest density of aquacultured bivalves. Unfortunately, in such productive locations bivalves can be stocked at such high densities that their biodeposits are focused onto a small area of sediments. When receiving sediments become overloaded with organic material the resulting bacterial respiration can consume oxygen at rates faster than it can be resupplied by diffusion. In such circumstances anaerobic microbial pathways dominate, and sulfur reducing bacteria produce high levels of hydrogen sulfide that are toxic to benthic infaunal species (Diaz and Rosenberg 1995). This loss of infauna exacerbates the adverse effects of excessive biodeposition on sediment biogeochemical processes because of a reduction in bioturbation processes that serve to bring oxygen into the sediments (Aller 2001, DiToro 2001). Loss of infauna also reduces food resources for carnivores at higher trophic levels.

Understanding and modeling the biotic and abiotic changes in the receiving sediments associated with organic loading from bivalve excrement is necessary in order to accurately parameterize "shellfish ecological carrying capacity models." Accurately modeling water flow is especially critical since strong water currents can distribute bivalve biodeposits widely over the bottom, hence reducing their adverse effects on sediment. Water flow is also crucial in supplying oxygenated water to hypoxic sediments.

3) Inorganic nutrient cycling

Nutrients incorporated in phytoplankton biomass are filtered from the water column by bivalves, ingested, and digested in seasons when water temperatures are warm enough to promote active

feeding. Nutrients that are digested but not assimilated are excreted and returned to the water column nutrient pool. A majority of the nitrogen is excreted in the form of ammonium and this may have a stimulative effect on local phytoplankton production (Dame 1996, Newell *et al.* 2005).

Undigested organic material is transferred to the sediment surface in biodeposits where it is degraded through complex microbial processes (DiToro 2001, Newell *et al.* 2002). A large proportion of the nitrogen (N) and phosphorus (P) is regenerated back to the water column (Newell *et al.* 2005). Inorganic nutrient regeneration from the sediments is not 100% efficient, however, which leads to the loss of some nutrients each time phytoplankton are consumed by bivalves and the resulting biodeposits transferred to the sediment surface. Where sediments remain oxygenated, some of the P that was originally incorporated in phytoplankton, but was not digested by the bivalves, can become sequestered and buried as iron-bound complexes. Where biodeposits are incorporated in aerobic surficial sediments that overlay deeper anaerobic sediments, microbially mediated coupled nitrification-denitrification can remove as N_2 gas some of the nitrogen that was originally incorporated in phytoplankton. Some N can also become buried in the accumulating sediments. In locations with sufficient light at the sediment surface, however, benthic microalgae compete with nitrifying bacteria for N regenerated from the bivalve biodeposits, thereby reducing or even precluding coupled nitrification-denitrification (Newell *et al.* 2002). If the sediments become anaerobic, coupled nitrification-denitrification is inhibited, P is mobilized and released to the water column, and the resulting build-up of H_2S can be toxic to other benthic animals. Loss of these bioturbating fauna reduces sediment irrigation that is an important mechanism for sediment oxygenation, and hence further increases the likelihood that the sediment will remain anoxic.

Duarte *et al.* (2003) suggested that spatially explicit hydrological models be used as the basis of carrying capacity models. By modeling water flow and food fluxes the optimum spatial distribution of aquaculture farms within coastal systems may be accurately predicted. The influence of the

aquaculture systems themselves (rafts, ropes, etc.) in imposing drag, and hence reducing water flow, also needs to be considered (Grant and Bacher 2001). Better information on water currents also means that the possible distribution of biodeposits over the surrounding sediment surface can be predicted. This distributional data, when linked with information on the biotic and abiotic characteristics of the receiving sediment (e.g., grain size, porosity, influence of periodic storms in scouring bottom sediment, etc.) will allow the influence of biodeposition on sediment biogeochemistry and benthic organisms to be modeled (DiToro 2001). Information on rates of nutrient regeneration, burial, and denitrification becomes even more crucial if bivalves are being cultivated as part of a polyculture system in order to enhance nutrient removal (Newell 2004).

4) Reduction in turbidity

In locations with high bivalve biomass and relatively restricted water exchange with surrounding waters, the feeding activity of bivalves can remove sufficient organic and inorganic seston particles that the amount of light reaching the sediment surface is increased. This has the effect of reducing the dominance of phytoplankton production and extending the depth to which ecologically important benthic plants, such as seagrasses and benthic microalgae, can grow. Newell and Koch (2004) developed a simple model of the effects of suspension-feeding bivalves on altering light penetration and the consequent benefits to seagrass beds. Their model showed that reestablishing seagrass beds may be facilitated by first rebuilding depleted oyster stocks to increase light penetration. It is apparent that aquacultured oysters could provide similar improvements to water clarity, therefore potentially allowing management authorities to permit aquaculture in regions generally considered too ecologically sensitive for such commercial uses. It has been shown, however, that there are severe reductions in seagrass beds in the immediate vicinity of oysters cultivated on the bottom in Oregon, USA. The causes of this seagrass loss were multifaceted, including direct shading by the aquaculture gear, enhanced biodeposition

reducing sediment suitability for seagrasses, sediment erosion associated with on-bottom racks altering bottom water currents, and severe disturbance associated with husbandry activities (Everett *et al.* 1995).

A potential adverse effect of an increase in light at the sediment surface is that nuisance macroalgae may become established, rather than a more normal flora of seagrasses and microphytobenthos. Some types of macroalgae (e.g., *Cladophora* spp.) flourish in locations that have elevated levels of inorganic nutrients and relatively low irradiances (from 18 to 175 $\mu\text{mol photons}^{-2} \text{s}^{-1}$), and under such conditions can out-compete other macroalgae (Rafaelli *et al.* 1998).

5) Provision of food resources and habitat for other organisms.

Bivalve biodeposits have a high residual organic content, with a C:N ratio similar to phytoplankton (Newell *et al.* 2005), and can therefore provide a nutritious food source for benthic deposit feeders. An increase in sediment organic N content has frequently been observed near large aggregations of bivalves (Kaspar *et al.* 1985, Kautsky and Evans 1987, Deslous-Paoli *et al.* 1992, Hatcher *et al.* 1994, Stenton-Dozey *et al.* 2001). The type of response observed in benthic communities adjacent to bivalve stocks is very dependent on the magnitude of sediment enrichment by biodeposits. The degree of enrichment is governed not only by the abundance of bivalves but also the area of bottom over which their biodeposits are distributed, which is dependent on the magnitude of water currents and wave action (Miller *et al.* 2002, Newell 2004). As discussed above, high levels of biodeposition can stimulate sediment microbial metabolism to the point that oxygen becomes limiting. At this point bacterial anaerobic metabolic pathways start to generate toxic hydrogen sulfide (Aller 2001).

In response to low to moderate organic loadings by bivalves, species diversity and biomass of meiofauna and macrofauna deposit feeders are often increased compared to areas without bivalves (Kautsky and Evans 1987, Dittmann 1990, Ragnarsson and Raffaelli 1999). Grant *et al.* (1995) reported relatively minor changes in macrobenthic

biomass and diversity associated with biodeposition from suspended mussel culture. The benthic community underlying intensive rope-cultivation of mussels has often been observed to change from one with a diverse species composition to one composed predominately of infaunal polychaetes (e.g., Kaspar *et al.* 1985, Stenton-Dozey *et al.* 2001). Increases in polychaetes can lead to enhanced bioturbation which has the beneficial effects of increasing rates of coupled nitrification-denitrification compared with the control sites (Kaspar *et al.* 1985). Tenore *et al.* (1982) reported that excessive biodeposition from a high density of mussel aquaculture rafts changed the benthic infauna from one with high species diversity and biomass to one characteristic of a pioneering community, with low species diversity and biomass. There was also reduction in bioturbation associated with the loss of the diverse infaunal community as the dominant species in the pioneering community were tube-building worms with little influence on sediment vertical mixing and sediment irrigation. These types of secondary effects from shellfish aquaculture are difficult to model because the responses are so variable between locations. In order to capture at least some of these ecosystem changes, three-dimensional physical models can be used to predict the amount and spatial distribution of organic material transferred to the sediment surface. Models of sediment biogeochemical processes (DiToro 2001) can be used to predict the depth of oxygen penetration into the sediment and this used to predict if there will be negative effect on infauna. In locations where sediments remain aerobic it will be possible to predict the amount of organic material available to be supplied to the benthic deposit feeder community and this can then be used to estimate rates of carbon transfer to higher trophic levels.

An important ecosystem benefit of natural shellfish beds is that they provide habitat for many invertebrate and vertebrate species (Coen *et al.* 1999, Ragnarsson and Raffaelli 1999, Peterson *et al.* 2003). Dealeris *et al.* (2004) have shown that both on-bottom and off-bottom aquaculture holding gear also provides the type of spatially complex habitat that is sought by many species of mobile animals. These aquaculture structures provide a surface for plant and animal colonization (Mazouni *et al.*

2001) that then provide a food source for many animals. A simplifying approach for including the provision of habitat in ecosystem models would be to calculate the amount of surface area available to be colonized by plants and animals on the aquaculture system (Dealeris *et al.* 2004). Then using simple empirically derived relationships estimate the amount of biomass that may be present for secondary consumers. Such estimates can then be refined by sampling the aquaculture system once it is in operation to quantify the biomass of plants and animals. The extreme periodic disturbances associated with cultivation and harvest practices, especially those required for on-bottom culture of infaunal bivalves (e.g., Everett *et al.* 1995, Kaiser *et al.* 1998), will negatively affect the habitat and should be included in the model.

CONCLUSIONS

I recommend that new “exploitation carrying capacity” models for suspension-feeding bivalve aquaculture be developed that can also serve as “ecological carrying capacity” models. The model should include sufficient detail of major ecosystem processes to predict possible beneficial and negative influences that the aquaculture facility may have on the environment. Properly designed models will allow regulatory authorities to assess the secondary benefits of using bivalves to provide ecosystem services, such as graze phytoplankton and thereby remove some of the excess anthropogenic inorganic nutrients present in many of the world’s coastal waters. Modeling rates of nutrient regeneration to the water column and removal is especially relevant to “ecological” or “balanced ecosystem” aquaculture operations where bivalves and seaweed are cultivated to help remove nutrients generated from finfish aquaculture (McVey *et al.* 2002, Neori *et al.* 2004).

Many different research groups have developed carrying capacity models for bivalve mollusc aquaculture. These models, some of which are cited above, have all been undertaken as independent projects and have rarely directly incorporated relationships parameterized for earlier models. I think that it would be advantageous to all concerned

if new ecosystem models are developed as open source “community models” that enable free and open access to the relevant code. Community models allow various investigators to parameterize and add in specialized sub-models that ultimately constitute a single, fully parameterized, model. For example, three-dimensional physical models have been developed by Chen *et al.* (1999) that could serve as the central core of a new bivalve aquaculture model. The complex sediment biogeochemical processes that will be affected by bivalves are included in the sophisticated sediment diagenesis model developed by DiToro (2001) which can be added as a component to an aquaculture model. The influence of bivalve on light penetration and the growth of benthic plants could be based on models developed by Alvera-Azcarate *et al.* (2003) for macroalgae and Newell and Koch (2004) for seagrasses. In this way essential elements are gradually incorporated into the core model in order to improve the overall accuracy of the model predictions.

The approach I advocate of developing an open source code “Community Model” with well-parameterized compartments has been widely adopted by physical oceanographers, who have developed the Princeton Ocean Model (www.aos.princeton.edu/WWWPUBLIC/htdocs.pom/) and the Regional Ocean Model System (www.marine.rutgers.edu/po/). This approach is also being adopted for ecosystem models. For example, a model is under development for the Chesapeake Bay watershed and estuary that will enable free and open access to source code. This is intended to be a web-based model that will include a base model as well as individual modules covering all aspects of hydrodynamics, ecosystem dynamics, trophic exchanges, and watershed interactions (<http://ccmp.chesapeake.org/CCMP/>). This approach of developing a community model is more efficient than the current situation where even the most recent and sophisticated bivalve carrying capacity models that have been developed (e.g., Dowd 1997, Campbell and Newell 1998, Chen *et al.* 1999, Duarte *et al.* 2003, Nunes *et al.* 2003) are missing some important components. Instead, if the best features from each were combined into a single model, it would provide more useful and robust model

predictions about ecosystem effects. There are significant logistical problems that have to be solved before embarking on developing such a community based model. Primarily this will require ensuring that sufficient long-term funding is committed for the support personnel who can maintain model code. Once a model is implemented it must be refined and validated using monitoring data that is frequently required to be collected by regulatory authorities to ensure that the aquaculture facility complies with permit requirements.

Acknowledgments

This paper was presented to the 33rd meeting of the United States-Japan Natural Resources Aquaculture panel symposium “Ecosystem and Carrying Capacity of Aquaculture Ground” as part of an international exchange agreement between the governments of Japan and the United States at the November 2004 meeting in Nagasaki, Japan. I am grateful to Dr. Jeff Cornwell, Dr. Tom Fisher, and Dr. Jim McVey for their scientific discussions that helped develop my thinking on this topic. Dr. Jack Rensel kindly commented on an early draft of this manuscript. This research was supported in part with funding from Maryland Sea Grant (SA07528051-F) through NOAA award NA16RG2207. NOAA kindly contributed toward my travel expenses. The US government is authorized to publish reprints of this work, and the author reserves the right to post a copy on his academic website for the private and non-commercial use of individuals, notwithstanding any copyright notations hereon.

Literature Cited

- Aller, R.C., 2001, Transport and reactions in the bioirrigated zone, in “The Benthic Boundary Layer: Transport processes and biogeochemistry” (ed. by Boudreau P.B. and Jorgensen B.B.). Oxford Press, Oxford. pp. 269-301.
- Alvera-Azcarate A., Ferreira, J.G., and Nunes J.P., 2003: Modeling eutrophication in mesotidal and macrotidal estuaries. The role of intertidal seaweeds. *Estuar. Coast. Shelf Sci.*, **57**, 715-724.
- Bacher C., Duarte P., Ferreira J.G., Heral M., and

- Raillard O., 1997: Assessment and comparison of the Marennes-Oleron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. *Aquat. Ecol.*, **31**, 379-394
- Bacher C., Grant J., Hawkins A.J.S., Jianguang F; Mingyuan Z., Besnard M., 2003. Modeling the effect of food depletion on scallop growth in Sungo Bay (China). *Aquat. Living Resour.*, **16**, 10-24.
- Bayne B.L. and Newell R.C., 1983: Physiological energetics of marine molluscs, in "The Mollusca" (ed. by Saleuddin A.S.M. and Wilbur, K.M.), Vol.4. Academic Press. New York, NY. pp. 407-515.
- Campbell D.E., and Newell C.R., 1998: MUSMOD, a production model for bottom culture of the blue mussel, *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.*, **219**, 171-203.
- Carver C.E.A., and Mallet A.L., 1990: Estimating carrying capacity of a coastal inlet for mussel aquaculture. *Aquaculture*, **88**, 39-53.
- Chen, C., Ji R., Zheng L., Zhu M., and Rawson M., 1999: Influences of physical processes on the ecosystem in Jiaozhou Bay: A coupled physical and biological model experiment. *J. Geophys. Res.*, **104**, No. C12, 29, 925-29, 949.
- Cloern J.E., 2001: Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.*, **210**, 223-253.
- Coen L.D., Luckenbach M.W, and Breitburg D.L., 1999: The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. *Amer. Fish. Soc. Symp.*, **22**, 438-454.
- Dame R.F., 1996: Ecology of marine bivalves, an ecosystem approach. CRC Press, Inc., Florida. 254pp.
- Dame R.F., and Prins T.C., 1998: Bivalve carrying capacity in coastal ecosystems. *Aquat. Ecol.* **31**, 409-421.
- Dealtheris, J.T., Kilpatrick B.D., and Rheault R.B., 2004. A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. *J. Shellfish Res.* **23**: 867-874.
- Deslous-Paoli, J.-M., Lannou, A.-M., Geairon, P., Bougrier, S., Raillard, O., and Heral, M., 1992: Effects of the feeding behaviour of *Crassostrea gigas* (Bivalve, Mollusc) on biosedimentation of natural particulate matter. *Hydrobiologia*, **231**, 85-91.
- Diaz R. J., and Rosenberg R., 1995: Marine benthic hypoxia: a review of its ecological effects and the behavioral responses of benthic macrofauna, *Oceanogr. Mar. Biol. Ann. Rev.*, **33**, 245-303.
- DiToro D.M., 2001: Sediment Flux modeling. Wiley and Sons New York 624 pp.
- Dittmann S., 1990: Mussel beds - amensalism or amelioration for intertidal fauna? *Helgoland. Meer.*, **44**, 335-352.
- Duarte P., Meneses R., Hawkins, A.J.S., Zhu M., Fang F., and Grant J., 2003: Mathematical modeling to assess the carrying capacity for multi-species culture within coastal waters. *Ecol. Model.*, **168**, 109-143.
- Dowd, M., 1997: On predicting the growth of cultured bivalves. *Ecol. Model.* **104**, 113-131.
- Everett R.A., Ruiz G.M., Carlton J.T., 1995 Effect of oyster mariculture on submerged aquatic vegetation: an experimental test in a Pacific Northwest estuary. *Mar. Ecol. Prog. Ser.*, **125** 205-217.
- Grant J, and Bacher C., 2001: A numerical model of flow modification induced by suspended aquaculture in a Chinese bay *Can. J. Fish. Aquat. Sci.*, **58**, 1003-1011.
- Grant J., Hatcher A., Scott D. B., Pocklington P., Schafer, C. T, and Winters G. V. 1995: A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. *Estuaries*, **18**, 124-144.
- Grizzle, R.E., and C. A. Penniman. 1991: Effects of organic enrichment on estuarine macrofaunal benthos, a comparison of sediment profile imaging and traditional methods. *Mar. Ecol. Prog. Ser.*, **74**, 249-262.
- Hatcher A., Grant J., and Schofield B., 1994: Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Mar. Ecol. Prog. Ser.*, **115**, 219-235.
- Kaiser M.J., Laing I., Utting S.D., and Burnell G.M. 1998. Environmental impacts of bivalve mariculture. *J. Shellfish Res.* **17**: 59-66.

- Kamiyama T., 2004: The microbial loop in a eutrophic bay and its contribution to bivalve aquaculture. *Bull. Fish. Res. Agen.* Supplement No. 1, 41-50.
- Kautsky N., and Evans S., 1987: Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar. Ecol. Prog. Ser.*, **38**, 201-212.
- Kaspar H.F., Gillespie P.A., Boyer I.C., and MacKenzie A.L., 1985: Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. *Mar. Biol.*, **85**, 127-136.
- Kreeger, D.A., and Newell R.I.E., 1997: Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa* (Dillwyn) and *Mytilus edulis* (L) (Bivalvia, Mollusca). *Aquat. Microb. Ecol.*, **11**, 205-214.
- Lam-Hoai, T., Rougier C., and Lasserre G., 1997: Tintinnids and rotifers in a northern Mediterranean coastal lagoon. Structural diversity and function through biomass estimations. *Mar. Ecol. Prog. Ser.*, **152**, 13-25.
- Mazouni N., Gaertner J-C., and Deslous-Paoli J-M., 2001: Composition of biofouling communities on suspended oyster cultures: An *in situ* study of their interactions with the water column. *Mar. Ecol. Prog. Ser.*, **214**, 93-102.
- McVey J.P., Stickney R., Yarish C., and Chopin T., 2002: Aquatic polyculture and balanced ecosystem management: new paradigms for seafood production, in "Responsible Marine Aquaculture" (ed by Stickney, R.R., and McVey, J.P.), CABI Publishing, Oxon, UK, pp. 91-104.
- Miller, D.C., A. Norkko and C.A. Pilditch. 2002: Influence of diet on dispersal of horse mussel *Atrina zelandica* biodeposits. *Mar. Ecol. Prog. Ser.*, **242**, 153-167.
- Neori A., Chopin T., Troell M., Buschmann A.H., Kraemer G.P., Halling C., Shpigel M., Yarish C., 2004: Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* **231**, 361-391.
- Nunes J.P., Ferreira J.G., Gazeau F., Lencart-Silva J., Zhang X.L., Zhu M.Y., and Fang J.G., 2003: A model for sustainable management of shellfish polyculture in coastal bays. *Aquaculture*, **219**, 257-277.
- Newell, R.I.E., 2004: Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish Res.* **23**, 51-61.
- Newell R.I.E., Cornwell J.C., and Owens M.S., 2002: Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. *Limnol. Oceanogr.*, **47**, 367-1379.
- Newell, R.I.E., Fisher T.R., Holyoke R.R., and Cornwell J.C., 2005: Influence of eastern oysters on Nitrogen and Phosphorus regeneration in Chesapeake Bay, USA., in "The comparative Roles of Suspension Feeders in Ecosystems" (ed. by Dame R and Olenin S.) Vol 47 NATO Science Series: IV- Earth and Environmental Sciences. Springer, Netherlands. pp. 93-120. PDF file at <<http://hpl.umces.edu/faculty/newellcv.html>>
- Newell R.I.E., and Koch, E.W., 2004: Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries*. In Press
- O'Connor B.D.S., Costelloe J., Keegan B. F., and Rhoads.D. C., 1989: The use of REMOTS technology in monitoring coastal enrichment resulting from mariculture. *Mar. Poll. Bull.*, **20**, 384-390.
- Odum E.P., 1983, Basic Ecology, Saunders College Publishers, Philadelphia. 613 p.
- Peterson C.H., Grabowski J. H, and Powers S.P., 2003: Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar. Ecol. Prog. Ser.*, **264**, 249-264.
- Olsson P., Graneli, E., Carlsson P., Abreu P., 1992. Structuring of a postspring phytoplankton community by manipulation of trophic interactions. *J. Exp. Mar. Biol. Ecol.*, **158**, 249-266.
- Prins T.C., Smaal A.C., and Dame R.F., 1998: A review of the feedbacks between bivalve grazing and ecosystem processes. *Aquat. Ecol.*, **31**, 349-359.

- Rafaelli, D.G., Raven J. A., Poole L. J., 1998: Ecological impact of green macroalgal blooms. *Oceanogr. Mar. Biol. Ann. Rev.*, **36**, 97-125.
- Ragnarsson S.A., and Raffaelli D., 1999: Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. *J. Exp. Mar. Biol. Ecol.*, **241**, 31-43.
- Sherr E., and Sherr B., 1988: Role of microbes in pelagic food webs: A revised concept. *Limnol. Oceanogr.*, **33**, 1225-1227.
- Shumway, S.E., 1990: A review of the effects of algal blooms on shellfish and aquaculture. *J. World Aquacult. Soc.*, **21**, 65-104.
- Smaal, A.C., Prins, T.C., Dankers, N., and Ball B., 1998. Minimum requirements for modeling bivalve carrying capacity. *Aquat. Ecol.* **31**, 423-428.
- Souchu P., Vaquer A., Collos Y., Landrein S., Deslous-Paoli J-M., and Bibent B., 2001: Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagon. *Mar. Ecol. Prog. Ser.* **218**, 141-152.
- Stenton-Dozey J, Probyn T., Busby A., 2001: Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa. *Can. J. Fish. Aquat. Sci.*, **58**, 1021-1031.
- Tenore K.R., and 19 others 1982 Coastal upwelling in the Rias Bajas, NW Spain. Contrasting the benthic regimes of the Rias de Arosa and de Muros. *J. Mar. Res.* **40**, 701-768.
- Vaquer A., Troussellier M., Courties C., and Bibent, B., 1996: Standing stock and dynamics of picoplankton in the Thau lagoon (northwest Mediterranean coast). *Limnol. Oceanogr.*, **41**, 1821-1828.
- Widdows J., Brinsley, M.D., Salkeld, P.N., and Elliott M., 1998: Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. *Estuaries*, **21**, 552-559.
- Wildish D.J., and Kristmanson D.D., 1997: Benthic Suspension Feeders and Flow. Cambridge University Press, Cambridge, UK. 409 p.
- Yokoyama, H., 2003: Environmental quality criteria for fish farms in Japan. *Aquaculture*, **226**, 45-56.