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Linking watershed loading and basin-level carrying capacity models to evaluate the effects of land use on primary production and shellfish aquaculture

Mark W. LUCKENBACH* and Harry V. WANG*

Abstract Aquaculture production of hard clams, *Mercenaria mercenaria*, in the lower Chesapeake Bay, Virginia, U.S.A., has increased dramatically within the last decade. In recent years concern has been raised that some growing areas may be approaching the exploitation carrying capacity for clam production. Preliminary calculations indicate that large-scale intensive clam aquaculture may be controlling nutrient and phytoplankton dynamics in this system. To date, carrying capacity models have not been applied to this system, but we are in the process of building models for that purpose. Moreover changing land use in the watersheds surrounding the clam-producing areas raises the need for an improved understanding of how these changes will affect water quality, primary production and shellfish production. We describe an ongoing project linking a watershed-based loading model with a physical transport-based water quality model to simulate primary production and predict carrying capacity for clam aquaculture. Extensive calibration and verification of the water quality model has demonstrated its utility for simulating primary production and water quality parameters in the Chesapeake Bay. In our present efforts, watershed loading models have been developed and tested for predicting both surface and groundwater inputs into the coastal waters. We are currently coupling the water quality and watershed loading models, and developing clam physiology and population-level sub-models. Also, under development is a sediment deposition/resuspension sub-model. Each of these components will be linked to estimate exploitation carrying capacity for clam production in this system. Our goal is to use the coupled models to predict how varying land use scenarios impact water quality, primary production and shellfish carrying capacity of coastal waters.

Key words: *Mercenaria mercenaria*, aquaculture, carrying capacity, water quality model

In many coastal ecosystems phytoplankton and suspension feeding bivalve production are tightly coupled (Dame, 1996). That suspension-feeding bivalves can play an important role in controlling phytoplankton abundance in coastal systems is well established (e.g., Officer *et al.*, 1982; Cloern, 1982; Nichols, 1985; Alpine and Cloern, 1992). Through their feeding activity bivalves can alter nutrient dynamics (Dame *et al.*, 1984; Dame and Libes, 1993), affect sediment composition and nitrogen cycling (Kaspar *et al.*, 1985), strongly affect carbon budgets (Rodhouse and Roden, 1987) and alter the composition of both benthic and planktonic

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* Virginia Institute of Marine Science, College of William and Mary. P. O. Box 350, Wachapreague, VA, USA, 23480
Email: luck@vims.edu Contribution number 2584 from the Virginia Institute of Marine Science

assemblages (Tenore *et al.*, 1982). Wild populations of bivalves have been implicated in some instances (Officer *et al.*, 1982, Cloern, 1982; Newell, 1988; Dame, 1996), but much evidence has come from bivalve aquaculture operations, including mussel culture in the Rias of northwest Spain (Tenore *et al.*, 1982) and New Zealand (Kaspar *et al.*, 1985) and oyster culture in Killary Harbor, Ireland (Rodhouse and Roden, 1987) and the Marennes-Oléron Bay in France (Bacher, 1989), that suspension-feeding bivalves affect phytoplankton dynamics on large scales.

The reciprocal is, of course, also true; phytoplankton production strongly affects bivalve production. In a review of trophic dynamics in temperate estuaries Heip *et al.* (1995) concluded that the ecological carrying capacity of bivalve populations in estuaries and coastal bays is often constrained by phytoplankton production. For bivalve aquaculture, which seeks to maximize shellfish production, phytoplankton production may determine the *exploitation carrying capacity*-the maximum yield of market-size individuals within a particular environment. Carver and Mallet (1990) showed that the exploitation carrying capacity of a coastal embayment in Nova Scotia for mussel production varied with temporal variations in food supply. A series of models developed to predict the exploitation carrying capacity for oyster aquaculture production in Marennes-Oléron Bay in France (Bacher, 1989; Héral, 1993; Bacher *et al.*, 1997) have been used to predict optimum stock size for maximizing production in this estuary. Similarly, Ferreira *et al.* (1998) developed a carrying capacity model for oyster cultivation in Carlingford Lough, Scotland. In the Oosterschelde estuary in the Netherlands, Smaal *et al.* (2001) found that mussel production was limited by phytoplankton production. They estimated the carrying capacity of the estuary for mussel culture before and after large-scale hydrographic modifications and discussed how adapting aquaculture practices in the context of food limitations helped the industry to maximize production.

Hard clam (*Mercenaria mercenaria*) aquaculture has expanded dramatically over the past decade along much of the United States' Atlantic coast and the northeast Gulf of Mexico. In Virginia, growth in this industry has been especially dramatic. A conservative estimate places the total standing stock of cultured clams in Virginia in excess of 500 million clams (estimate based upon federal crop insurance program statistics). Most of this aquaculture occurs in small tidal creeks that empty into the Chesapeake Bay and shallow embayments behind coastal barrier islands (Fig. 1). In many of these areas clam aquaculture has grown to a scale at which it may be reasonable to ask if clam production is close to the limit set by phytoplankton production, i.e., it may be at, near or even exceeding exploitation carrying capacity.

Additionally, the clam aquaculture industry faces threats from changing land use practices in the adjacent watersheds. Rapidly changing demographic trends in the region are leading to the replacement of farmland by residential and industrial uses. The potential impacts of this changing use on water quality and clam aquaculture are presently unknown.

In this paper we will (1) give a brief descrip-

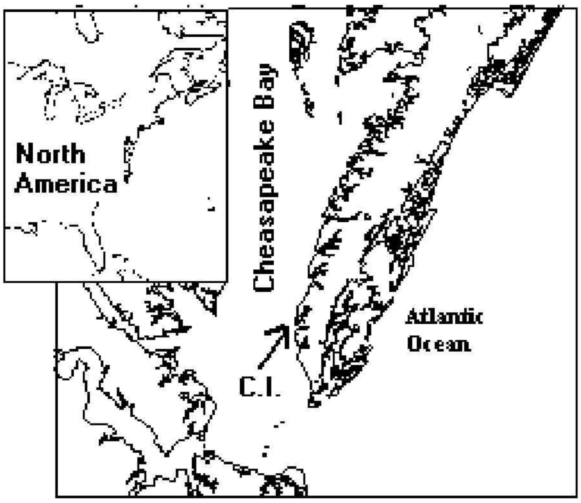

Fig. 1. Region of study. Clam aquaculture is taking place in the tributaries of the lower Chesapeake Bay and the coastal embayments on the Atlantic coast. C.I. denotes the location of Cherrystone Inlet.

tion of the farming practices for hard clams, (2) detail some preliminary calculations that reveal the potential strength of the interactions between phytoplankton production and clam production in one tributary, and (3) describe a modeling effort that is currently underway to link watershed loading, water quality and clam production models to provide a tool for predicting effects of changing land-use practices on water quality, phytoplankton production and clam aquaculture production.

Hard clam aquaculture

Detailed descriptions of the production practices for farming hard clams are given in Manzi and Castagna (1989) and Castagna (2001). Briefly, larvae are spawned and reared in hatcheries in seawater ranging from 20 to 35 ppt. Post-set juveniles are generally raised in land-based, flow-through nursery systems until they reach a size of 3-4mm in shell height. At that time they are placed into one of several types of field nursery systems-either fine mesh bags, sand-filled trays or floating upweller systems-and grown to a size range of 10-15mm. Clams are then planted in the low intertidal and subtidal zone in sand and sand-mud mix bottoms for grow-out to market size. Generally clams are planted in rows approximately 4 m ×18m at densities ranging from 550 to 1650 clams m^{-2} and covered by polyethylene netting that serves as predator protection. A typical clam farm may include several hundred such nets (Fig. 2). The grow-out period ranges from 18 to 30 months with most clams harvested within 24 months of planting.

Fig. 2. Aerial view of a clam farm in Chesapeake Bay, U.S.A. Each rectangular net is approx. 4 m× 18m and covers 50,000 clams.

In some of the most densely planted tributaries and embayments clam farmers have begun to observe declining growth rates over the past few years. One possible explanation for this observation is that these areas may have exceeded the exploitation carrying capacity and clam production may be limited by primary production in these systems.

Estimating links between clam production and water quality

To provide a first approximation of the effects of clam culture on water quality and of the possibility that clam production may be limited by phytoplankton production in these systems, we performed some simple calculations for Cherrystone Inlet, a small tidal embayment on the eastern margin of the Chesapeake Bay (see Fig. 1). From the aquaculture industry we have an estimated standing stock of cultured clams in system of 45×10^6. The volume of Cherrystone Inlet at high tide is $15.4 \times 10^6 m^3$ and the volume of the time averaged tidal prism is $5.8 \times 10^6 m^3$ (Kuo *et al.*, 1998). We used the filtration rate formula reported by Hibbert (1977a, b) for *Mercenaria mercenaria* at 25 ℃ (typical summertime water temperatures in this area): $FR = 0.063 \cdot L^{0.834}$, where L=shell length and FR has units of L $indiv^{-1}$ hr^{-1}. Multiplying by the total number of clams and dividing into the total and tidal prism volume estimates then provides rough estimates of the clams' filtration volume relative to volumes in the embayment (Table 1). Data from the clam industry indicates that annual harvest of clams from this region is approximately 20×10^6 with an average shell height of 60mm. Using a shell height to dry weight regression from Walne (1972) and value for tissue nitrogen=$0.1 \cdot$dry tissue weight (Hawkins *et al.*, 1985), we estimate the amount of nitrogen removed annually from the system

Table 1. Preliminary estimates of some of the effects of clam aquaculture on filtration on water quality in Cherrystone Inlet. (N_H=nitrogen removal from harvest, N_{ATM}=nitrogen loss as N^2 to the atmosphere, N_{EX}=nitrogen excretion rate, primarily as ammonia.

Summertime filtration rate			Nitrogen uptake and release		
Total filtration rate	% of tidal exchange	Time to filter creek volume	N_H	N_{ATM}	N_{EX}
1.6 x 10^6 m^3 day^{-1}	28%	10 days	18,000kg yr^{-1}	36,000kg yr^{-1}	900kg day^{-1}

by harvesting (Table 1). Estimates by Hibbert (1977a) on the production of feces and pseudofeces by clams and measurements reported by Newell *et al.* (2002) for rates of nitrification and denitrification of bivalve biodeposits were used to compute the amount of nitrogen lost as N_2 to the atmosphere as a result of clam feeding (Table 1). Finally, we estimate nitrogen excretion rates from these clams based on Hibbert (1977a) (Table 1).

We emphasize that all of the estimates in Table 1 are preliminary. Our intention in making these estimates was to provide an initial evaluation of whether clam aquaculture in this system might have reached a scale at which it was reasonable to hypothesize that it is near carrying capacity or that clams are having a significant effect on water quality and phytoplankton dynamics. Evaluating these hypotheses will require an integrated modeling approach. As noted above, land use in the watersheds around these small tidal creeks and embayments in which clam aquaculture is occurring is changing. It is likely that this change will affect the inputs of nutrients, sediments and freshwater into these water bodies, which in turn will have consequences for clam production. In the sections below we provide an overview of a modeling approach that we are taking to address these issues.

Model Description

Carrying capacity models

Smaal *et al.* (1998) reviewed the requirements for modeling bivalve carrying capacity in coastal ecosystems. In doing so, they outline a number of sub-models that are required to provide input to an ecosystem-level model that estimates maximum production level. In short, hydrodynamic and sediment sub-models are used to characterize movement of materials in the water column and between the sediment/water interface, respectively. A physiological sub-model incorporates bivalve feeding and energetics on a size-specific basis, while the population sub-model builds in the planting densities and harvest schedules along with cohort growth and mortality. Output from these sub-models together with data on physical characteristics (e.g., light, T & S) and nutrient loadings are then used in a system-level model to estimate production capacity. Below we discuss in greater detail how each of these sub-models are being developed for Cherrystone Inlet.

Hydrodynamic submodel

A hydrodynamic sub-model called HEM3D (Hydrodynamic Eutrophication Model 3D) has been developed at Virginia Institute of Marine Science as part of a dynamic water quality model. This model has been calibrated and verified in a number of systems such as York River, James River, Mobile Bay and Florida Bay with relative success and has been selected by the U.S. Environmental Protection Agency as one of the standard model codes for water quality application. The hydrodynamic sub-model requires a number of inputs. The geometry (shape) and bathymetry of the system is required to construct grid configuration and bathymetry (each model cell is given an average depth value). Boundary condition specifications of forcing function(s) (e.g., tidal elevation, velocity, and usually salinity) at the open boundary, as well as discharge at the upstream boundary must be specified. Runs of the model are facilitated by proper initialization values of model parameters, especially those that require a relatively long time to equilibrate, such as salinity. Finally, specification of other inputs facilitates the calibration process (e.g., bottom friction adjustment). For Cherrystone Inlet the geometry and bathymetry data have already been collected and the grid system developed (Kuo *et al.*, 1998). Boundary conditions for all forcing functions have been established and proper initialization and calibration terms incorporated. Simulation with a precursor to this model, a tidal prism water quality model conducted by Kuo *et al.* (1998), was the first attempt using coupled hydrodynamic, water quality and watershed models in the Cherrystone Inlet. The simulated results of salinity, chlorophyll, DO, total carbon, total nitrogen and phosphorus provided reasonable predictions compared to bi-monthly measured field data (Kuo *et al.*, 1998).

The state variables in this sub-model include tidal elevation at each cell in the horizontal and velocity, salinity, and temperature at cells in both the horizontal and the vertical directions. Process variables are derived from these, and include transport processes such as density driven circulation. Advection and dispersion influence the flow field as well. Pending further field verification and calibration this sub-model will be used to generate the transport features that drive the system-level model.

Resuspension/sedimentation model

This sub-model, which is currently under development, will simulate fluxes of sediments and other materials between the water column and the bottom. In order to calculate suspended sediment concentration in each cell of the model domain, flow velocities are provided to the sediment sub-model by the hydrodynamic sub-model. In addition, sediment settling velocities are specified for each size class of the sediment. Time series of sediment concentrations at the upstream and open boundaries are used as the input sediment fluxes to the model domain. The erosion and deposition rate, representing vertical sediment fluxes between the water column and the bottom, are calculated based on bottom shear stress and the critical shear stress.

The sediment sub-model is being calibrated to simulate the temporal and spatial variations of sediment concentrations within the model domain. The calculated sediment concentration in each cell will be used to determine food quality and light attenuation factors for the growth of algae. A benthic compartment in general and a clam sub-model in particular are important to include as both sink and source for nutrients and particulate matter.

Clam feeding and physiological sub-model

The purpose of the clam feeding and physiology sub-model is to link the feeding, growth, energetics and excretion by clams to the general system-level model. Data are available on the feeding, growth and energetics of wild *M. mercernaria* throughout its range (reviewed by Grizzle *et al.*, 2001). Feeding rates vary with body size, temperature and salinity; univariate relationships with each of these factors have been reported in a large number of studies (e.g., Loosanoff, 1939; Coughlan and Ansell, 1964; Hamwi, 1969; Hibbert, 1977a,b; Doering and Oviatt, 1986; Bricelj, 1984; Walne, 1972). Feeding rate also varies as a function of food concentration (Tenore and Dunstan, 1973), silt content of the seston (Hamwi, 1969; Bricelj and Malouf, 1984) and phytoplankton species composition (Rice and Smith, 1958; Walne, 1972). Relationships between respiration rate and body size (Loveland and Chu, 1969) and respiration rate and temperature (Hamwi, 1969; Hibbert, 1977b) have been published for *M. mercenaria*. Hibbert (1977a,b) developed an energy budget for this species growing on mudflats in Southampton, England.

In their extensive review of hard clam physiological ecology, Grizzle *et al.* (2001) report growth rates for *M. mercernaria* that range from 0.42-1.11mm (growth in shell height) week^{-1} and average time to market size (25.4mm shell thickness) ranging from 2.1 to 13.0 years over a geographical range from Prince Edward Island, Canada, to the Florida Gulf coast. While they observed a latitudinal gradient in growth rate, they noted that over a broad geographical range (New York to Florida) variation in growth rate within an estuary generally exceed that attributable to latitude (Grizzle *et al.*, 2001).

The basic construct of the physiology submodel is straightforward:

Growth = Consumption − Respiration − Egestion − Excretion.

Consumption is a function of filtration rate and food availability. Filtration rate and respiration vary as a function of temperature and body size as discussed above. Because the cultured clams have been artificially selected for high growth for several decades by aquaculture industry, it will be necessary to measure each of these variables for cultured animals in Cherrystone Inlet, rather than relying on published values for wild clams. When completed this sub-model will output growth rates from one size class to another that will serve as input to the population sub-model.

Clam population sub-model

For wild populations of bivalves obtaining reliable parameter estimates for the population sub-model can often be the most difficult part of developing carrying capacity model. Uncertainties surrounding estimates of reproductive output, larval survival and post-settlement mortality for field populations all make it difficult to obtain accurate predictions. For aquaculture, however, the parameter estimates are straightforward. The number and size of clams planted by the industry, the growth rate between size classes and the harvest of clams by the industry, along with a small, but defined, non-harvest related mortality are the primary parameters of interest. These values will serve as inputs to the population sub-model and the measured growth rates will be compared to predicted values based upon the linked sub-models.

System-level model

Output from the various sub-models serves as input for the system-level model that computes several state variables including primary production and bivalve biomass for each cell at the specified time step. The role of the hydrodynamic sub-model is to provide the transport quantities induced by the physical process, such as fluxes between the boxes and the mixing within a box. The sediment resuspension/deposition model calculates the suspended matter concentration, which in turn determines the food quality and light attenuation. The physiology sub-model drives the growth of clams that feeds into the clam population sub-model to drive cohort production estimates.

Because primary production varies temporally and spatially within estuaries, a dynamic modeling approach as described above is required to estimate the exploitation carrying capacity for bivalve aquaculture (Smaal *et al.*, 1998). Thus, once developed and calibrated, we will run the model under varying conditions of nutrient loading to investigate how clam production is affected by nutrient loading (either from the Bay or the watershed) and under varying clam stocking densities to evaluate aquaculture practices. Additionally, we will explore the effects of clam aquaculture on water quality within the system by running the model under various stocking densities (including no clam aquaculture) and estimating chlorophyll and light attenuation levels.

Watershed loading sub-model

A unique feature of our project to estimate carrying capacity for clam aquaculture is an ongoing effort to link a watershed loading model to the system-level water quality model. In order to understand and quantify the effects of changing basin scale land-use patterns, a watershed model is needed. The HSPC (Hydrologic Simulation Program C language) will be used for simulating the watershed hydrology and associated water quality parameters on pervious and impervious land surface and in streams and well-mixed impoundments. Sediment and nutrient loadings in the model are transported from land to the receiving coastal waters. Inputs to this model include precipitation, soil type and land-use within the watershed. Outputs will include freshwater discharge, nutrient inputs and sediment loading, each of which serves as input into the system-level water quality model. Data collected from within the watershed over the next two years will serve as initial input to the model for the purpose of modeling current conditions. Subsequently, we will vary these inputs to explore how changing conditions within the watershed affect water quality and clam production.

Discussion

Clam aquaculture is an important and growing industry in the U.S. that is replacing fisheries on over exploited wild stocks and providing economic development in traditional coastal fishing communities. Sustaining clam aquaculture in the coastal waters of the U.S. will require an improved understanding of the inter-relationships between coastal land-use, water quality, primary production and clam production. The modeling approach described here will provide an important suite of tools for advancing our understanding of these linkages.

Initial estimates from a single embayment in Virginia suggest that clam aquaculture has developed to a scale at which system-level impacts on water quality and phytoplankton dynamics may be evident (Table 1). Understanding those effects, as well as how watershed inputs and water column dynamics affect the growth and production of hard clams, requires an integrated modeling effort such as the one we described here. This effort is still underway with each of the sub-models currently being refined and field data being collected for parameterization, calibration and verification.

When complete, the model output under current conditions will provide an understanding of the relationship between current clam production levels and primary production within Cherrystone Inlet. If the model results indicate that the Cherrystone Inlet system is near or has exceeded exploitation carrying capacity, then the explanation for the reported decrease in clam growth will lie in the relationship between basin-wide phytoplankton production and clam stocking densities. Conversely, if clam production is not limited by primary production, then either local growing conditions (e.g., sediment changes) or genetic condition of the stocks may be the cause of this pattern.

The utility of this model goes beyond explaining the current growing situation in Cherrystone Inlet. It will permit us to explore various scenarios of stocking density, seasonal and inter-annual variations in primary production, and altered nutrient loading to assess their impacts on clam production in the system. Furthermore, although the specific formulation of the model in this instance will be for Cherrystone Inlet, once developed and calibrated, it should provide a useful starting point for describing the relationship between primary production and clam aquaculture in other tidal creeks and embayments throughout the mid-Atlantic region of the U.S. With the addition of basin-specific inputs on geometry, bathymetry, tidal elevations and currents, salinity and boundary conditions the model will serve to estimate exploitation carrying capacity for clam aquaculture in any system in the mid-Atlantic region.

By coupling the clam physiology and population sub-models with the hydrodynamic-based water quality model and linking it to a watershed loading model, we will achieve a powerful tool for use by natural resource managers and local governments that goes beyond traditional carrying capacity models. For instance, this region is experiencing growing development pressure, especially along the waterfronts adjacent to clam growing areas. The coupled models described here will permit us to run various hypothetical watershed development scenarios and predict the impacts on water quality and clam production. This information will be valuable in permitting informed decisions about coastal development and its impacts on a valuable aquaculture industry.

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References

Alpine S. E. and Cloern, J. E., 1992: Trophic consequences and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol Oceanogr.* **37**, 946-955.

Bacher C., 1989: Capacite trophique du basin de Marennes-Oléron: couplage d'un modele de transport pariculaire et d'un modele de criussance de l'huitre *Crassostrea gigas. Aquat. Living Resour.*, **2**, 199-214.

Bacher C., Duarte, P., Ferreira, J. G., Héral, M., and Raillard, O., 1998: Assessment and comparison of the Marennes-Oléron Bay. (France) and Carlinford Lough (Ireland) carrying capacity with ecosystem models. *Aquat. Ecol.*, **31**, 379-394.

Bricelj V. M., 1984: Effects of suspended sediments on the feeding physiology and growth of the hard clam, *Mercenaria mercenaria* L., Ph.D. Dissertation, State University of New York, Stony Brook, 157 pp.

Bricelj V. M. and Malouf, R. E. 1984: Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria. Mar. Biol.*, **84**, 155-165.

Carver C. E. A. and Mallet, A. L., 1990: Estimating the carrying capacity of a coastal inlet for mussel culture. *Aquaculture*, **88**, 39-53.

Castagna M., 2001: Aquaculture of the hard clam, in "Biology of the hard clam" (eds. by Kraeuter J. N. and Castagna M.), Elsevier, New York, pp. 675-700.

Cloern J. E., 1982: Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.*, **9**, 191-202.

Coughlan J. and Ansell, A. D., 1964: A direct method for determining pumping rate for siphonate bivalves. *J. Cons.*, **29**, 205-213.

Dame R. F., 1996: Ecology of Marine Bivalves: An Ecosystem Approach, CRC Press, Boca Raton, FL, 254 pp.

Dame R. F. and Libes S. L., 1993: Oyster reefs and nutrient retention in tidal creeks. *J. Exp. Mar. Biol. Ecol.*, **171**, 251-258.

Dame R. F., Spurrieri J. D., and Wolaver T. G., 1989: Carbon, nitrogen and phosphorus processing by an oyster reef. *Mar. Ecol. Prog. Ser.*, **54**, 249-256.

Doering P. H. and Oviatt C. A., 1986: Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. *Mar. Ecol. Prog. Ser.*, **31**, 265-275.

Ferreira J. D., Duarte P., and Ball B., 1998: Trophic capacity of Carlingford Lough for oyster culture-analysis by ecological modeling. *Aquat. Ecol.*, **31**, 361-378.

Grizzle R. E., Bricelj V. M., and Shumway S. E., 2001: Physiological ecology of *Mercenaria mercenaria*, in "Biology of the Hard Clam" (eds. by Kraeuter, J. N. and Castagna, M.), Elsevier, NY. pp. 305-382.

Hamwi A., 1969: Oxygen consumption and pumping rate of the hard clam *Mercenaria mercenaria* L., Ph.D. Dissertation, Rutgers University, 177 pp.

Hawkins A. J. S., Salkeld P. N., Bayne B. L., Gnaiger E., and Lowe D. M., 1985: Feeding and resource allocation *in the mussel Mytilus edulis*: evidence for time-averaged optimization. *Mar. Ecol. Prog. Ser.*, **20**, 273-

287.

Heip C. H. R., Goosen N. K., Herman P. M. J., Kromkamp J., Middelburg J. J., and Soetaert K., 1995: Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. and Mar. Biol. Ann. Rev.*, **33**, 1-149.

Hérral M., 1993: Why carrying capacity models are useful tools for management of bivalve mollusk culture, in "Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes" (ed. by Dame, R. F.), Springer-Verlag, Heidelberg. pp. 453-477

Hibbert C. J., 1977a: Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria mercenaria* from Southampton water. *Mar. Biol.*, **44**, 71-76.

Hibbert C. J., 1977b: Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. *Mar. Biol.*, **44**, 77-84.

Kaspar H. F., Gillespie P. A., Boyer I. C., and MacKenzie A. I., 1985: Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. *Mar. Biol.*, **85**, 127-136.

Kuo A. Y., Butt A. J. Kim S.-C., and Lin J., 1998: Application of a tidal prism water quality model to Virginia small coastal basins: Poquoson River, Piankatank River, Cherrystone Inlet and Hungars Creek, Special Report No. 348 in Applied Marine Science and Ocean Engineering, Virginia Institute of Marine Science, Gloucester Point, VA.

Loosanoff V. L., 1939: Effect of temperature upon shell movements of clams, *Venus mercenaria* (L.). *Biol Bull.*, **76**, 171-182.

Loveland R. E. and Chu D. S. K., 1969: Oxygen consumption and water movements in *Mercenaria mercenaria. Comp. Biochem. Physiol.*, **29**, 73-184.

Manzi J. J. and Castagna M. (eds.), 1989: Clam mariculture in North America, Elsevier, New York,461 pp.

Newell R. I. E., 1988: Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? in "Understanding the Estuary: Advances in Chesapeake Bay Research" (eds. by Lynch, M. P. and Krome E. C.), Chesapeake Research Consortium, Solomons, Maryland, pp. 536-546.

Nichols F. H., 1985: Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay during the 1976-1977 drought. *Estuar. Coast. Shelf Sci.*, **21**, 379-388.

Officer C. B., Smayda T. J., and Mann R., 1982: Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.*, **9**, 203-210.

Rice T. R. and Smith R. J., 1958: Filtering rates of the hard clam (*Venus mercenaria*) determined with radioactive plankton. *Fish. Bull.*, **58**, 71-82.

Rodhouse R. R. and Roden C. M., 1987: Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve mollusks. *Mar. Ecol. Prog. Ser.*, **36**, 225-236.

Smaal A. C., Prins T. C., Dankers N., and Ball B., 1998: Minimum requirements for modeling bivalve carrying capacity. *Aquatic Ecology*, **31**, 423-428.

Smaal A., van Stralen M., and Schuiling E., 2001: Interaction between shellfish culture and ecosystem processes. *Can. J. Fish. Aquat. Sci.*, **58**, 991-1002.

Tenore K. R., Boyer L. F., Cal R. M., Corral J., Garcia-Fernandez C., Gonzalez N., Gonzalez-Gurrianan E., Hanson R. B., Iglesias J., Krom M., Lopez-Jamar E., McClain J., Pmamtmat M. M., Perez A., Rhoads D. C., de Santiago G., Tiejen J., Westrich J., and Windom H. L., 1982: Coastal upwelling in the Rias Bajas, NW Spain: contrasting the benthic regimes in the Rias de Arosa and de Muros. *J. Mar. Res.*, **40**, 701-772.

Tenore K. R. and Dunstan W. M., 1973: Comparison of feeding and biodeposition of three bivalves at different food levels.

Mar. Biol., **21**, 190-195.

Walne P. R., 1972: The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. Mar. Biol. Assoc. U.K.*, **52**, 345-374.