

ECOSYSTEM INFLUENCES OF NATURAL AND CULTIVATED POPULATIONS OF SUSPENSION-FEEDING BIVALVE MOLLUSCS: A REVIEW

ROGER I. E. NEWELL*

*Horn Point Laboratory, University of Maryland Center for Environmental Science,
Cambridge, Maryland 21613*

ABSTRACT Suspension-feeding bivalves serve to couple pelagic and benthic processes because they filter suspended particles from the water column and the undigested remains, ejected as mucus-bound feces and pseudofeces, sink to the sediment surface. This biodeposition can be extremely important in regulating water column processes where bivalves are abundant in coastal waters and in seasons when water temperatures are warm enough to promote active feeding. Bivalves under these conditions can exert “top-down” grazer control on phytoplankton and in the process reduce turbidity, thereby increasing the amount of light reaching the sediment surface. 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. Nitrogen and phosphorus, excreted by the bivalves and regenerated from their biodeposits, are recycled back to the water column and support further phytoplankton production. In some situations, however, bivalves can also exert “bottom-up” nutrient control on phytoplankton production by changing nutrient regeneration processes within the sediment. Some of the N and P that was originally incorporated in phytoplankton, but was not digested by the bivalves, can become buried in the accumulating sediments. Where biodeposits are incorporated in aerobic surficial sediments that overlay deeper anaerobic sediments, microbially mediated, coupled nitrification–denitrification can permanently remove N from the sediments as N₂ gas. Consequently, natural and aquaculture-reared stocks of bivalves are potentially a useful supplement to watershed management activities intended to reduce phytoplankton production by curbing anthropogenic N and P inputs to eutrophic aquatic systems. Environmental conditions at bivalve aquaculture sites should be carefully monitored, however, because biodeposition at very high bivalve densities may be so intense that the resulting microbial respiration reduces the oxygen content of the surrounding sediments. Reduction in sediment oxygen content can inhibit coupled nitrification–denitrification, cause P to become unbound and released to the water column, and the resulting buildup of H₂S can be toxic to the benthos.

KEY WORDS: benthic–pelagic coupling, bivalves, denitrification, eutrophication, extractive aquaculture, nutrient cycling, nutrient enrichment, nutrient trading, suspension-feeders

INTRODUCTION

Coastal waters worldwide are increasingly enriched with nitrogen and phosphorus as a consequence of agricultural fertilizer run-off and sewage inputs from growing human populations along coastal margins (Malone 1992, Conley 1999, Cloern 2001). This anthropogenic nutrient overenrichment is causing fundamental changes in the patterns and magnitude of primary production, including enhanced phytoplankton production and blooms of both toxic and nontoxic microalgae (Shumway 1990, Cloern 2001). In locations where this enhanced phytoplankton production exceeds the demands of metazoan herbivores, the excess phytoplankton carbon is metabolized by bacteria and protists and is not efficiently transferred to higher trophic levels (Pomeroy & Wiebe 1993). These high levels of microheterotrophic respiration frequently generate hypoxic or anoxic conditions in estuarine bottom waters. For example, in Chesapeake Bay, USA, water beneath the pycnocline in the deepest channel becomes anoxic most summers when the level of bacterial respiration, supported by the carbon produced during the spring phytoplankton bloom, exceeds the rate of oxygen resupply from the surface (Kemp & Boynton 1992, Diaz & Rosenberg 1995). In an effort to curb phytoplankton production in Chesapeake Bay, actions have been taken throughout the watershed to control inputs of nutrients from point and non-point sources, such that there will be an overall reduction by 40% of controllable inputs from the maximum levels recorded (D’Elia et al. 1992).

Phytoplankton concentrations increase not only as a result of

enhanced nutrient inputs—the so called “bottom-up” influence—but similarly increase when there is a reduction in the abundance of grazer organisms that normally exert “top-down” control (Newell 1988, Dame 1996). Thus, in eutrophic waters, consumption of particulate organic matter (POM) by abundant stocks of bivalve suspension-feeders in shallow and well-oxygenated conditions will directly reduce the amount of POM remineralized by bacteria beneath the pycnocline where oxygen resupply is restricted. Verwey (1952) was the first to identify the important ecological role of bivalves that are often the dominant component of the macroinvertebrate community in many coastal ecosystems. He recognized that bivalves serve as key agents in benthic–pelagic coupling because they feed on seston and transfer undigested organic and inorganic material in their feces and pseudofeces to the sediment surface.

The diverse influences that populations of suspension-feeding bivalves exert on marine ecosystem processes have comprehensively been reviewed by Dame (1996). I review here only those aspects of bivalve suspension-feeding ecology that pertains to their ability to alter water quality in eutrophic temperate estuaries and that may change the environment in a manner that affects other species. It is likely that some of these ecosystem effects will be a linear function of bivalve density, even at the rather high population densities associated with aquaculture farms, unchecked growth of an exotic species, and so forth. Other effects may be positive at low and moderate population densities but these beneficial changes can be reduced or lost at extremely high densities, as could result from overintensive aquaculture. I do not discuss the important secondary benefits of natural and cultivated shellfish beds as habitat for many invertebrate and vertebrate species (Coen et al. 1999). There is little known about such habitat benefits that

*Corresponding author. Fax: +1-410-221-8490; E-mail: newell@hpl.umces.edu

may derive from bivalves commercially cultured in various holding gear (e.g., rack and bag culture, attached to suspended ropes, held in floating trays, and so forth). These aquaculture structures are likely to provide a surface for fouling growth that serves as a food source for many animals and to some extent provide the type of spatially complex habitat that is sought by many species of animals. More research is required to determine to what extent the extreme periodic disturbances associated with cultivation and harvest practices, especially those required for on-bottom culture of infaunal bivalves, positively or negatively affect the habitat (Simenstad & Fresh 1995).

BIVALVE FEEDING

Suspension-feeding bivalves clear seston particles greater than $\sim 3\text{-}\mu\text{m}$ diameter from the water column with high efficiency during times of the year when water temperatures are sufficient to promote activity (Bayne & Newell 1983, Bayne & Hawkins 1992). Captured particles are sorted on pallial organs prior to ingestion, with the less nutritious and excess particles being immediately rejected as pseudofeces (Newell & Jordan 1983, Newell & Langdon 1996, Ward et al. 1997). In some situations, pseudofeces, which have not been exposed to any type of digestive degradation, can account for as much as 80% to 90% of the total volume of filtered particulate material (Tenore & Dunstan 1973, Bayne & Hawkins 1992).

The feeding response of bivalves to changes in seston concentration varies considerably among species. Some species, such as the eastern oyster, *Crassostrea virginica*, and the blue mussel, *Mytilus edulis*, maintain relatively high clearance rates even when seston concentrations increase (Newell & Langdon 1996, Hawkins et al. 1998). By maximizing the number of particles captured and subjected to efficient preingestive sorting and selection processes, such species can maximize their ingestion of nutritious particles (Newell & Langdon 1996, Ward et al. 1997). The maintenance of high feeding rates appears to be an adaptation to living in estuarine systems that historically supported low concentrations of phytoplankton in relation to less nutritious detrital and mineral particles. Today, throughout the majority of the estuaries and coastal waters of North America and western Europe, phytoplankton production has increased due to anthropogenic nutrient enrichment (Cloern 2001). Therefore, once the bivalve's nutritional needs are satisfied, excess phytoplankton cells, in addition to less nutritious detrital and silt particles, are rejected in pseudofeces. In response to increasing seston concentrations, other species of suspension-feeding bivalves, such as cockles, clams, and scallops, mainly regulate their ingestion rates by reducing clearance rates and not so much by rejecting excess particles as pseudofeces (Hawkins et al. 1998, Grizzle et al. 2001). Consequently, the species of bivalves that can exert the greatest influence on benthic-pelagic coupling are those that maintain high clearance rates and reject large numbers of particles as pseudofeces.

Ingested material is subject to extracellular and intracellular digestion, and the remains are defecated within ~ 24 h. Bivalves digest and assimilate different sources of POM with efficiencies that can vary from $\sim 20\%$ to 90% (Bayne & Newell 1983, Kreeger & Newell 2001). This efficiency varies depending on how susceptible the particles are to enzymatic breakdown; for example, many chlorophyte algal species are poorly digested because of their characteristically thick cellulosic cell walls (Langdon & Newell 1996). Assimilation efficiencies of bivalve molluscs for some particles,

including phytoplankton, also varies seasonally (Kreeger & Newell 2001). This high variability in assimilation efficiency, together with the substantial amounts of POM in pseudofeces that is not even subject to digestion, means that large amounts of undigested particulate organic nitrogen (PON) and phosphorus are transferred to the sediment surface in feces and pseudofeces (collectively called biodeposits). Newell & Jordan (1983), working with eastern oysters fed on natural seston ranging in concentration from 5 to 20 mg L^{-1} , reported that $\sim 50\%$ of the PON cleared from the water column was assimilated, and the remainder was voided in biodeposits.

Of the N absorbed by bivalves from the ingested food, the majority is used for tissue growth and some is excreted as urine (70% of which is NH_4^+ , 0% to 13% urea, and 5% to 21% amino-N; Bayne et al. 1976, Bayne & Hawkins 1992). This excreta increases the water column dissolved nitrogen pool and hence can support new phytoplankton and microphytobenthos production (Kaspar et al. 1985, Asmus & Asmus 1991, Swanberg 1991). Feces and pseudofeces are voided from bivalves as mucus-bound aggregates; consequently, they have a faster sinking velocity than nonaggregated particles and settle at rates up to 40 times that of nonaggregated particles (Kautsky & Evans 1987, Widdows et al. 1998). In locations where bottom water currents are below the critical erosional bottom shear stress (Newell et al. 2005), the biodeposits undergo a de-watering process and gradually become incorporated into the sediments (Haven & Morales-Alamo 1966, Haven & Morales-Alamo 1968, Kaspar et al. 1985, Jaramillo et al. 1992, Widdows et al. 1998) leading to an increase in sediment nitrogen content (Kaspar et al. 1985, Kautsky & Evans 1987, Deslous-Paoli et al. 1992, Hatcher et al. 1994). It should be noted, however, that resuspension of biodeposits from intertidal or shallow-water bivalve populations (Dame et al. 1991a) is more likely than those from bivalves living in either deeper water or grown in suspended aquaculture systems, where the underlying sediments are isolated from frequent disturbance by wave action.

ECOSYSTEM EFFECTS OF BIVALVE FEEDING

The complex relationships among some benthic and pelagic processes that may be influenced by benthic bivalve suspension-feeders during seasons when they are actively feeding are summarized in a conceptual model (Fig. 1). This diagram highlights the role of bivalve feeding in removing both phytoplankton and inorganic particles from the water column, thereby reducing turbidity. The resulting increased light penetration to the sediment surface can potentially enhance the production of benthic plants, such as seagrasses and microphytobenthos (Newell & Koch 2004). Reductions in turbidity will be directly proportional to the abundance of bivalves. Consequently, there is likely to be a linear decline in turbidity as bivalve stocks increase in a location from low to high abundances (Fig. 2).

A number of studies [for a review, see Dame (1996)] have provided strong evidence that natural populations of suspension-feeding bivalves can exert top-down control on phytoplankton in coastal waters [e.g., ribbed mussels, *Geukensia demissa* (Dillwyn), in salt marshes of the eastern United States (Jordan & Valiela 1982) and blue mussels, *Mytilus edulis* (Linné), in the North Sea (Asmus & Asmus 1991, Dame et al. 1991)]. Similar ecosystem changes have been observed where bivalve stocks have been either experimentally increased to higher than normal abundances [e.g., blue mussels stocked in experimental enclosures (Riemann et al.

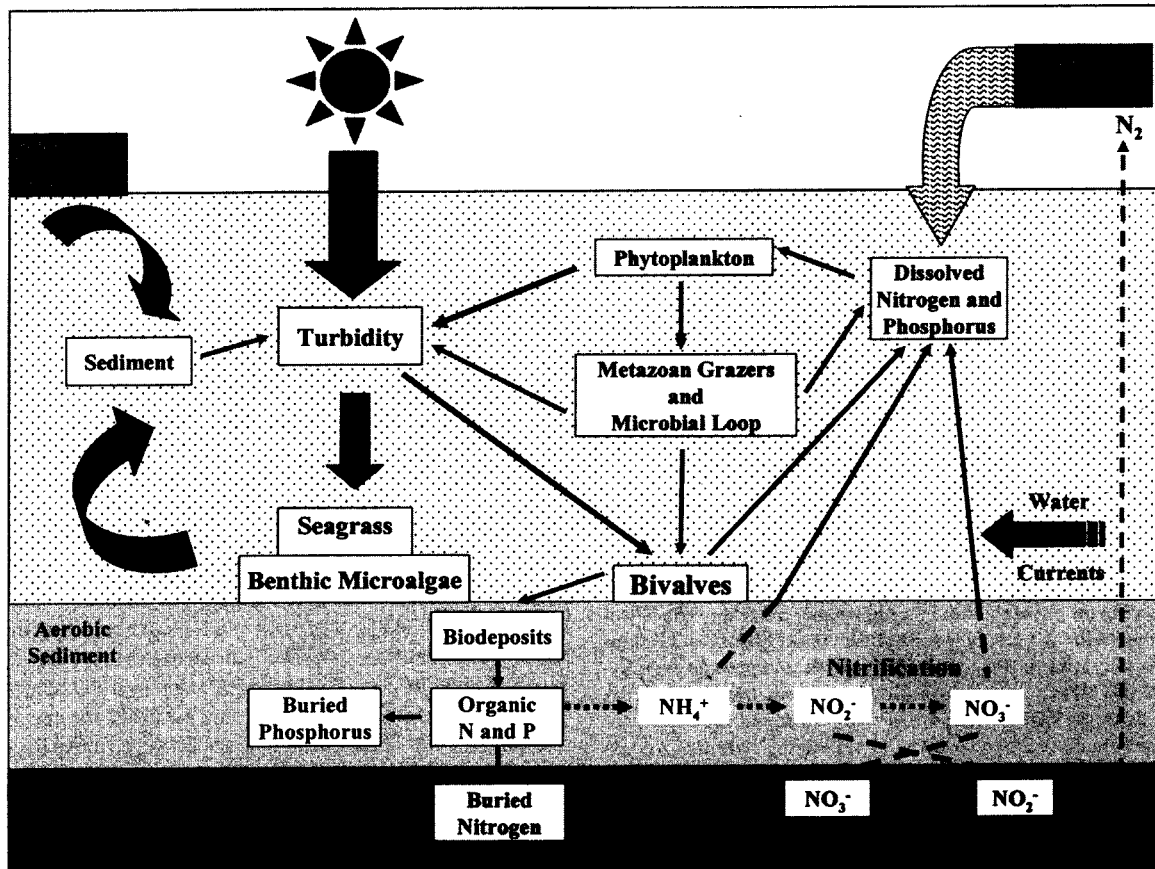


Figure 1. Conceptual diagram of the ecosystem effects of suspension-feeding bivalves in removing organic and inorganic particles from the water column and transferring undigested particulate material in their biodeposits to the sediment surface. Burial of P in aerobic sediments, and N throughout the sediment, leads to N and P removal from the water column. Within the aerobic sediment layers, the microbially mediated process of nitrification occurs, which when linked to denitrification within the underlying anaerobic sediment, leads to the further loss of N as N_2 gas. The growth of benthic microalgae (MPB) may be enhanced by increased light penetration to the sediment. The MPB can absorb regenerated nutrients, thereby out-competing phytoplankton. Solid lines indicate transfer of materials; dashed lines indicate diffusion of materials; dotted lines indicate microbially mediated reactions (adapted from Newell et al. 2002).

1988, Prins et al. 1995)] or as part of bivalve aquaculture, such as adjacent to rafts holding blue mussels in Spain (Tenore et al. 1982) and off-bottom aquaculture of Pacific oysters, *Crassostrea gigas*, in France (Souchu et al. 2001). The most dramatic ecosystem changes have been observed, however, in areas after the rapid population growth of an exotic species of bivalve. In San Francisco Bay, California, for example, phytoplankton has been shown to be controlled by non-native bivalves, including *Tapes japonica* and *Musculus senhousia* (Cloern 1982, Officer et al. 1982), and *Potamocorbula* spp. (Carlton et al. 1990). In freshwater systems of North America, non-native zebra mussels, *Dreissena polymorpha*, have increased to such an abundance that they have greatly reduced turbidities by consuming high levels of phytoplankton (MacIsaac et al. 1999, Strayer et al. 1999).

Seagrasses were once a very abundant ecotype in many locations worldwide, where they provided spatially heterogeneous habitat used by sessile and mobile fauna (Orth et al. 1984). These beds of submerged aquatic vegetation (SAV) have declined in many locations due to the adverse effects of anthropogenic nutrient enrichment (Twilley et al. 1985, Cloern 2001). Enhanced turbidity associated with high phytoplankton biomass can reduce the photosynthetically active radiation (PAR) to below the level required to enable SAV to grow (Twilley et al. 1985, Taylor et al. 1995).

Bivalves, by filtering phytoplankton and other particles from the water column, may increase PAR penetration to the point where SAV beds can become reestablished. The importance of suspension-feeding bivalves in promoting the reestablishment and growth of SAV has been demonstrated in the Potomac River, MD, USA. There, freshwater asiatic clams, *Corbicula fluminea*, reduced phytoplankton stocks (Cohen et al. 1984) and helped SAV to once again become dominant primary producers in freshwater locations (Phelps 1994). After a crash in the asiatic clam population of the Potomac River, there was a concomitant decline in SAV abundance (Phelps 1994). Increased water clarity will also promote the growth of microphytobenthos (MPB). These benthic algae are an important food source for both sessile and mobile benthic herbivorous meiofauna and macrofauna (Miller et al. 1996) that, in turn, are eaten by many carnivorous fish. Consequently, an abundant MPB community can support higher trophic levels.

Two modeling exercises support the idea that bivalve suspension-feeders can improve water clarity to the point that production of benthic plants is enhanced. Ulanowicz and Tuttle (1992) used an ecosystem model to predict that an important consequence of an increase in eastern oyster stocks in Chesapeake Bay would be to increase light penetration to bottom sediments to such an extent that MPB production would be greatly enhanced. Newell and Koch

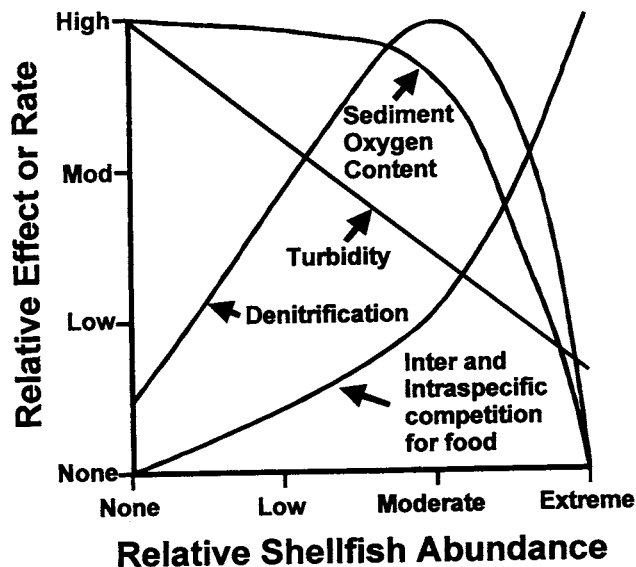


Figure 2. Conceptual figure illustrating how increasing abundances of bivalves feeding on phytoplankton and inorganic particles reduce water column turbidity in eutrophic coastal waters. At high bivalve abundances, this may lead to intra- and interspecific competition for phytoplankton with other suspension-feeding herbivores. Biodeposits, containing undigested POM, are deposited to the sediment surface where they are microbially metabolized, thereby affecting sediment oxygen content. In locations where there is either extremely heavy biodeposition or little water flow and mixing, sediment oxygen content may decline, thereby reducing coupled nitrification-denitrification.

(2004) developed a numerical model to simulate the interaction between wave-induced sediment resuspension, bivalve filtration, and seagrass growth. This model, which is parameterized based on direct measurements of eastern oyster filtration and seagrass wave dampening effects, shows that the presence of eastern oysters can reduce suspended sediment concentrations by nearly an order of magnitude. This resulted in an increase in water clarity and, hence, the depth to which seagrasses could grow. It should be noted, however, that in coastal waters and tidally flushed estuaries, the exchange of suspended particles from adjacent waters means that the localized enhancement of bivalve stocks may not reduce turbidities sufficiently to permit seagrasses to grow.

A potential adverse effect of an increase in PAR at the sediment surface is that macroalgae may become established, rather than a more normal flora of seagrasses and MPB. Some types of macroalgae (e.g., *Ulva* spp., *Enteromorpha* spp., and *Cladophora* spp.) flourish in locations that have elevated levels of inorganic nutrients and relatively low irradiances (from 18 to 175 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$), and under such conditions can out-compete other macroalgae (Peckol & Rivers 1995, Taylor et al. 2001). In some locations, these nuisance species grow so profusely that they restrict water flow and cause sediment hypoxia when they decay (Peckol & Rivers 1995, Raffaelli et al. 1998).

INFLUENCE OF EUTROPHICATION ON BIVALVE POPULATIONS

It is conceivable that increased phytoplankton biomass associated with nutrient enrichment may be beneficial to bivalve suspension-feeders. However, it is now recognized that anthropogenic inputs of N and P alter the ratio of these inorganic nutrients from

the typical Redfield ratio of 16:1 (Malone 1992, Conley 1999, Cloern 2001). Although subject to substantial variation, N:P ratios of agricultural run-off are of the order 50:1 to 70:1, whereas sewage input is closer to 10:1. The optimal ratio of N:P for algal growth is species specific, so changes in the N:P ratio alters the competitive interaction between phytoplankton species (Rhee 1978). For example, Terry (1982) demonstrated that *Pavlova lutheri*, which is considered a nutritious species for bivalves, has a high rate of P uptake and storage, but NO_3^- uptake is inhibited by increased amounts of P in the water. Consequently, a low N:P ratio might not stimulate the growth of *P. lutheri*, hence causing it to be out-competed by less nutritious species in which NO_3^- uptake is unaffected by P concentrations.

In coastal waters subject to anthropogenic nutrient loading, dissolved silicate frequently becomes depleted in relation to N and P, thereby leading to a reduction in the proportion of total primary production contributed by diatoms (Conley et al. 1993). Diatom species are generally considered to be a highly nutritious class of microalgae, and many species have been shown to promote survival and growth of bivalves (Langdon & Newell 1996). In Chesapeake Bay after the crash of the spring diatom bloom, other less nutritionally valuable classes of phytoplankton, including cyanobacteria and dinoflagellates, become dominant possibly due to the lack of available silica (Malone 1992, Conley 1999, Cloern 2001).

In addition to the ratio of inorganic nutrients, the chemical form of a nutrient can have a profound effect on phytoplankton species composition. Ryther (1954) concluded that eastern oyster stocks in the South Shore Bays of Long Island, NY, were adversely affected in the 1950s by extensive blooms of picoplanktonic algae, including *Nannochloris atomus* and *Stichococcus* spp., that were stimulated by duck farm fecal effluent containing high levels of ammonia and uric acid. These picoplanktonic species displaced nanoplanktonic algae that are more nutritious for oysters, with the consequence that the overall food quality of the phytoplankton for eastern oysters was reduced. Currently within the same South Shore Bays there are periodic blooms of the harmful picoplankton *Aureococcus anophagefferens* that causes "brown tide" (Bricelj & Lonsdale 1997). Gobler et al. (2002) reported that this species has a competitive advantage over other phytoplankton species because it can metabolize the high ambient levels of dissolved organic nitrogen and carbon that today are derived from human rather than duck farm waste. *Aureococcus anophagefferens* is toxic to bivalves as it has been shown to reduce the feeding and growth of all life stages of many species of bivalves [reviewed by Bricelj & Lonsdale (1997)]. It is thought that such blooms of toxin-producing algae are increasing in distribution and frequency worldwide, and anthropogenic nutrient enrichment is a likely causal factor (Shumway 1990, Cloern 2001). Even if the algal toxins do not adversely affect the benthic suspension-feeders themselves, they can be bioaccumulated in commercially valuable shellfish to levels that are unsafe for human consumption (Shumway 1990).

INFLUENCE OF BIVALVES ON PHYTOPLANKTON

As summarized above, suspension-feeding bivalves can serve to improve water quality in eutrophic estuaries by exerting top-down control on phytoplankton populations. In waters with substantial rates of bivalve grazing, however, larger nanoplankton cells will be preferentially removed in comparison with smaller (<3- μm diameter) picoplankton species that are retained less efficiently on the gill of most bivalve species. Furthermore, it appears

as if the growth of picoplankton compared with nanoplankton species is favored by warmer waters and changes in the relative abundance of inorganic and organic nitrogen (Malone 1992, Gobler et al. 2002). Hence, selective bivalve feeding, which is most intense during warmer months when bivalves are feeding actively, reinforces seasonal successional cycles in phytoplankton species composition, leading to the situation where picoplankton, including cyanobacteria, become relatively more abundant than larger species in areas with shellfish populations (Prins et al. 1998). Interestingly, Souchu et al. (2001) reported that high levels of bivalve aquaculture in a poorly flushed lagoon in the Mediterranean favored the production of picoplankton in all seasons except summer. Even though bivalve grazing was most intense in summer, high levels of DIN regenerated by the bivalves were sufficient to allow even the relatively slow growing nanoplankton to grow fast enough to overcome grazer control. Based on these observations, it is apparent that even though the exact seasonal changes in phytoplankton species composition are difficult to predict, bivalve grazing may possibly adversely affect food quality for other suspension-feeders.

In nutrient-enriched systems with consequent high levels of primary production, intra- and interspecific competition for food will likely be minimal at low and intermediate levels of bivalve abundance (Fig. 2). However, in systems that are either less productive, have limited water circulation, or have very high levels of bivalve biomass, intra- and interspecific competition for food may occur between natural and aquaculture stocks of bivalves. Interspecific food competition between high abundances of bivalves and zooplankton is also possible. Lam-Hoai et al. (1997) and Lam-Hoai and Rougier (2001) reported that in areas with shellfish aquaculture, there were appreciable differences in microzooplankton (cells 40- to 300- μm diameter) community structure compared with areas with no aquaculture farms. They ascribed these differences to microzooplankton being directly grazed by bivalves and also by the suspension-feeding invertebrates attached to the aquaculture structures. Bivalves may also out-compete zooplankton for phytoplankton because bivalves over-winter 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, which form a dominant component of the zooplankton, rely on a relatively small number of adults to survive over-winter and which can then feed and reproduce to rebuild the population. Copepod fecundity is directly related to food availability (White & Roman 1992), and consequently, if the majority of the phytoplankton is being consumed by adult bivalves, then copepod populations will diminish. This suggests that there is likely to be an exponential increase in interspecific competition for food as bivalve stocks increase in a location from low to high levels (Fig. 2).

NUTRIENT REGENERATION

In addition to the direct "top-down" control that bivalves can exert on phytoplankton stocks, they may also exert "bottom-up" control by changing rates and processes of nutrient regeneration (Fig. 1). Bivalves, by virtue of their high clearance rates, filter phytoplankton from large volumes of water. This has the effect of focusing nutrients that are then regenerated in the sediments around the population, hence increasing nutrient concentrations within that zone. Nonetheless, the total amount of nutrients regenerated directly by bivalve excretion and the microbial degradation

of their biodeposits cannot be any greater than if the phytoplankton was being degraded solely by pelagic organisms. Consequently, maximum phytoplankton standing stock supported by the nutrients regenerated through bivalve populations cannot exceed the level that can be sustained by ambient nutrients (Newell et al. 2005). This is in distinct contrast to fin-fish aquaculture, where new nutrients in the form of fish food are continually being added to the aquaculture site. Dissolved N and P excreted by fin-fish, together with that regenerated from their fecal waste and uneaten food, can stimulate excessive phytoplankton biomass. Furthermore, residual POM from the fin-fish food and feces settling to the sediment surface can cause sediment anoxia, thereby altering benthic community composition (Gowen & Bradbury 1987, Tsutsumi 1995).

Measured rates of NH_4^+ flux from natural bivalve communities (direct excretion plus regeneration from biodeposits in the sediments) can be substantial, ranging from ~ 1 to $5 \text{ mmol N m}^{-2} \cdot \text{h}^{-1}$ (Dame et al. 1989, Asmus & Asmus 1991, Dame et al. 1991a, Dame et al. 1992), with rates being greater in summer than in winter months (Dame et al. 1992). The nitrogen released comes not only from ingested phytoplankton but also non-phytoplankton material, such as N-rich bacteria and flagellates (Asmus & Asmus 1991), that are readily captured by bivalves (Bayne & Hawkins 1992, Kreeger & Newell 2001). These high levels of NH_4^+ regeneration have been used by some investigators as evidence that bivalve populations may not be able to exert long-lasting top-down control on phytoplankton populations. Instead, it has been suggested that bivalves serve to recycle rapidly nutrients, thereby enhancing rates of primary production and phytoplankton biomass. Such conclusions are based either on direct measurements of phytoplankton production or production potentially supported by measured rates of N flux (e.g., Dame et al. 1984, Doering et al. 1986, Doering et al. 1987, Dame & Dankers 1988, Dame et al. 1989, Prins & Smaal 1990, Asmus & Asmus 1991, Dame et al. 1991b, Dame et al. 1992, Dame & Libes 1993, Yamamuro & Koike 1993, Nakamura & Kerciku 2000, Souchu et al. 2001).

What is frequently overlooked in such studies is that the burial of N and P and removal of N from the ecosystem via denitrification is enhanced by bivalve biodeposition (Newell et al. 2002, Newell et al. 2005). When bivalve biodeposits settle to the sediment surface, any remaining PON is subject to microbial degradation that can lead to some NH_4^+ being regenerated to the water column (Fig. 1). Some N that is not microbially metabolized can become buried in the accumulating sediments (Kaspar et al. 1985, Kautsky & Evans 1987, Deslous-Paoli et al. 1992, Hatcher et al. 1994). If the surficial sediments contain sufficient oxygen, then aerobic nitrifying bacteria can oxidize nitrogen compounds within the biodeposits to NO_2^- and NO_3^- . Some of this NO_2^- and NO_3^- diffuses out of the sediment and enters the water-column dissolved inorganic nitrogen (DIN) pool and some diffuses down into the underlying anaerobic sediments. Within the anaerobic sediments, denitrifying bacteria reduce the NO_2^- and NO_3^- to N_2 gas (Henriksen & Kemp 1988, Risgaard-Petersen et al. 1994). Absent N-fixation, this gaseous N_2 is in a form unavailable to plankton and so it passes to the atmosphere without stimulating further primary production. Denitrification can only occur where there is a close juxtaposition between oxygenated conditions that support nitrifying bacteria and anaerobic conditions that support denitrifying bacteria (Kaspar et al. 1985, Kristensen 1988).

The influence of bivalve feeding and biodeposition on denitrification rates under natural field conditions have not yet been fully characterized. This is mainly due to the fact that a suitable method

for easily measuring denitrification in undisturbed sediments has only been recently devised (Cornwell et al. 1999). Newell et al. (2002) used this new method in a laboratory-based experimental system to study nitrogen regeneration from bivalve biodeposits under different scenarios typical of eutrophic estuaries. This involved using algal paste as an experimental analog of oyster biodeposits that was added to the surface of defaunated and homogenous natural sediments held in tubular cores. This was considered a realistic approach because bivalves only digest and absorb ~50% of the filtered particulate nitrogen, and hence the voided biodeposits contain a large proportion of residual PON (Newell & Jordan 1983). In these experiments, when PON was regenerated aerobically in the absence of light, 17% to 24% of the total PON added to the sediments was released as N_2 gas and hence would be unavailable to support further phytoplankton production. Newell et al. (2002) found that when the same amount of PON was degraded aerobically in incubations with sufficient light to sustain an active MPB community, little nitrogen was released to the water column and there was net N_2 fixation. It is widely recognized that an actively growing MPB community can limit nitrogen fluxes across the sediment-water interface (e.g., Sundbäck & Graneli 1988, Krom 1991, Rysgaard et al. 1995, Cerco & Seitzinger 1997, Sundbäck et al. 2000). Nitrogen fixation within MPB communities has previously been reported in many shallow-water environments when N requirements of benthic algal photosynthesis exceeds that supplied from the water column and regenerated from the sediment (Joye & Paerl 1994).

In addition to the role of MPB in intercepting DIN being regenerated from the sediments, the oxygen produced from MPB photosynthesis can alter sediment biogeochemistry. Some of this oxygen diffuses down into the sediment, thereby inhibiting the buildup of reduced inorganic compounds (Epping et al. 1999). In sediments subject to bivalve biodeposition, oxygen released by MPB can be used by bacteria in the micro-zone at the sediment-water interface to maintain nitrification, which is the critical precursor to denitrification (Sundbäck et al. 1991, Risgaard-Petersen et al. 1994, Rysgaard et al. 1994, An & Joye 2001). This pattern changes when MPB growth is high, such as may occur when turbidities are reduced by bivalve feeding in shallow-water locations. Under such circumstances, the demand for inorganic nutrients by MPB can be so great that they out-compete the nitrifying bacteria in the aerobic sediments for NH_4^+ . This results in a decline in the production of NO_2^- and NO_3^- , thereby curtailing the coupled nitrification-denitrification (Risgaard-Petersen et al. 1994, Rysgaard et al. 1995, An & Joye 2001, Newell et al. 2002).

In one of the few field studies of the role of bivalves in nutrient cycling in which denitrification was evaluated, Kaspar et al. (1985) found appreciably higher denitrification in sediments underlying rope-cultured mussels than at reference sites. [Note that denitrification was measured in this study using the acetylene block technique that provides information on denitrification potential rather than absolute rates (Cornwell et al. 1999)]. Kaspar et al. (1985) discovered that biodeposition from aquacultured mussels not only increased PON in the sediment but also changed the benthic community from a diverse assemblage, including epibenthic species, to one composed solely of infaunal polychaetes that enhanced bioturbation and hence increased coupled nitrification-denitrification. Hatcher et al. (1994) reported enhanced sedimentation under mussel aquaculture ropes that caused an increase in N accumulation in the sediment, a shallowing of the Redox Potential Discontinuity layer, and enhanced the NH_4^+ efflux from the sediment compared

with adjacent control areas. Such changes in sediment biogeochemistry do not preclude the possibility that there was enhanced denitrification in the sediments. Rather, as Hatcher et al. (1994) state, they could not make any definitive statements concerning the influence of bivalve biodeposition on ecosystem nitrogen balance because they did not have the techniques available to measure denitrification.

Souchu et al. (2001) studied how bivalve aquaculture altered water column nutrient cycling in a poorly flushed lagoon in the Mediterranean. They reported that for all seasons, except when phytoplankton were growing most rapidly in summer, bivalve grazing controlled phytoplankton biomass. Consequently, for most of the year the regenerated NH_4^+ from the aquaculture farms was not used by phytoplankton for new production. Instead it became available to be oxidized to NO_3^- by pelagic nitrifying bacteria, hence explaining their observation of elevated NO_3^- in the water column within the shellfish aquaculture farms. It is likely that this NO_3^- will diffuse into the sediments where it will be subject to denitrification, hence leading to N removal from these coastal lagoons.

Although bivalves are clearly important mediators of N cycling, their role in P cycling is less clear. For example, some studies demonstrate that P regeneration from bivalve stocks does not increase (Dame et al. 1989, Dame et al. 1991) or increases by ~50% (Asmus & Asmus 1991, Souchu et al. 2001). The balance between binding and release of P from oyster biodeposits is highly dependent on sediment oxygenation and the development of a redox gradient within the sediments. In estuarine sediments, P fluxes are controlled by interfacial adsorption and desorption processes, often involving iron and sulfur cycling (Krom & Berner 1981). Iron oxides at the sediment-water interface are a diffusive barrier to P fluxes across the sediment-water interface. Under fully oxygenated conditions, any P remaining in the biodeposits will be buried in the accumulating sediments. If the depth of the oxygenated zone in the surficial sediments decreases, the P-adsorbing iron oxide surface area can be reduced to iron monosulfides, thereby allowing the release of sedimentary inorganic P (Boynton & Kemp 1985).

The ecosystem effects of an increase in bivalves on sediment nutrient regeneration, and hence on phytoplankton production, will vary depending on bivalve population density and the rate of mixing of oxygenated water down to the sediment surface. Excess biodeposition, especially in low water flow environments, has the potential to stimulate bacterial respiration to such an extent that sediments become anoxic, thereby inhibiting coupled nitrification-denitrification (Fig. 2) and causing sediment-bound P to be mobilized. Such local adverse effects can be ameliorated by moderate water currents or wave action that allows biodeposits to be spread across a larger bottom area and that mix oxygen from the surface to the bottom waters (Haven & Morales-Alamo 1968, Dame et al. 1991).

The adverse effects of sediment overenrichment by bivalve biodeposits have often been observed in sediments underlying bivalves in suspended raft culture. For example, Ito and Imai (1955) reported that intensive oyster aquaculture resulted in underlying sediments becoming anoxic, and these effects appeared cumulative because the longer oysters were cultivated in a location, the more frequently sediment anoxia occurred. Such reductions in sediment oxygen content will reduce rates of bacterially mediated nitrification and increase the proportion of N released as NH_4^+ . When sediments become completely anoxic, the buildup of H_2S can kill

the aerobic nitrifying bacterial community. Consequently, even if aerobic conditions in the surface sediments are restored, nitrification will only recommence following the regeneration of the nitrifying bacterial community (Henriksen & Kemp 1988, Sloth et al. 1995). Similarly, sediments underlying intensive mussel raft aquaculture in a Spanish Ria exhibited rates of sulfate reduction, indicative of anaerobic microbial processes, that were 63% greater than in sediments outside the raft area (Tenore et al. 1982). Tuttle and Jonas (1992) also observed elevated amounts of microbially labile organic matter in surficial sediments beneath eastern oysters grown in floats in Chesapeake Bay. This led to about a 4-fold increase in sulfate reduction rates, although this increase was short-lived and confined to sediments in the immediate vicinity of the floats. These findings suggest that extremely dense bivalve communities can adversely affect sediment microbial processes by shifting them from aerobic to anaerobic metabolism as a result of increased POM loading (Fig. 2).

The development of anoxic sediments associated with intensive bivalve aquaculture can increase hydrogen sulfide to levels that are toxic to benthic animals (Diaz & Rosenberg 1995). For example, Dinét et al. (1990) studied bivalve aquaculture sites and observed that as biodeposition by *Crassostrea gigas* and *Mytilus edulis* increased, there was a commensurate decline in meiofaunal populations associated with sediment anoxia and elevated NH_4^+ in sediment pore water. Declines have also been observed (Tenore et al. 1982, Rodhouse & Roden 1987) in the abundance and species diversity of the burrowing and deposit-feeding macrobenthic organisms (bioturbators) that actively mix surficial sediments as a result of their feeding and burrow irrigation activity. Bioturbation serves to increase the surface area to volume ratio of the oxic-anoxic sediment interface both by forming anoxic microenvironments within the upper aerobic zone and by driving the redox potential discontinuity deeper into the sediments (Kristensen 1988). In this spatially complex interface between aerobic and anaerobic zones, denitrification rates are enhanced compared with sediments without bioturbators (Kaspar et al. 1985, Henriksen & Kemp 1988, Kristensen 1988, Pelegri et al. 1994).

Dense assemblages of bivalves do not always cause adverse changes in benthic community structure. For example, Dittmann (1990) reported that biodeposition from beds of blue mussels leads to an enhanced and more diverse benthic invertebrate assemblage that will promote bioturbation. In addition, POM remaining in biodeposits provides a major source of food to benthic meio- and macrofauna and serves as a food resource for secondary consumers. Grant et al. (1995) found relatively minor changes in macrobenthic biomass and diversity associated with biodeposition from suspended mussel culture. In contrast, Kaspar et al. (1985) found that the benthic community underlying rope-cultured mussels changed from one with a diverse species composition to one composed solely of infaunal polychaetes. As noted earlier, however, this increase in bioturbating polychaetes was responsible for enhancing the coupled nitrification-denitrification found in the aquaculture sediments compared with the control sediments.

THE POSSIBLE USE OF BIVALVES IN EXTRACTIVE AQUACULTURE

Current management strategies for curtailing the adverse effects of eutrophication in coastal waters depend on upgrading sewage treatment facilities, reducing agricultural run-off, and control-

ling atmospheric inputs (D'Elia et al. 1992). It is now recognized that a possible supplement to such nutrient controls is "extractive aquaculture" in which macroalgae are grown both for their biomass and the concomitant removal of the nutrients from that impaired water body (Chopin et al. 2001). The harvested biomass can be used either for food (e.g., the food additive carrageenan and *Porphyra* spp. used to make "nori") or as agricultural compost for fertilizer and biogas production (Gao & McKinley 1994).

Another heretofore not widely recognized form of extractive aquaculture is the growth of suspension-feeding bivalves. On a dry-weight basis, eastern oyster tissue and shell contains nitrogen (~7% and ~0.3%, respectively) and phosphorus (~0.8% and ~0.1%, respectively) (Galtsoff 1964; Newell, unpublished data) that is removed from the ecosystem at harvest. For example, a market-size eastern oyster of shell length 7.6 cm has a shell that weighs ~150 g and ~1 g dry tissue and which combined removes a total of 0.52 g N and 0.16 g P at harvest. Much of this N and P is in the relatively large shell and so when species with lighter shells, such as blue mussels, are harvested, less N and P will be removed.

In addition to the direct removal of N and P by harvesting, microbially mediated denitrification of PON transferred to the sediment surface in bivalve biodeposits has the beneficial effect of permanently removing N in the form of N_2 gas from the ecosystem. Burial of residual N and P from bivalve biodeposits in sediments also enhances nutrient removal from the water column. Consequently, suspension-feeding bivalves potentially offer this additional mechanism for N and P removal compared with extractive aquaculture of algae. Newell et al. (2005) estimated that the biodeposition activity of an adult eastern oyster (shell height 7.6 cm; ~1 g dry tissue weight) feeding under natural conditions in the Choptank River, a mesohaline tributary to Chesapeake Bay, caused 0.27 g P to be buried and 0.75 g N to be buried and denitrified annually. These estimates did not take into account the reduced levels of N and P removal during the time it takes oysters to grow from juvenile to adult size nor the enhanced levels of N and P removal as oysters grow larger than 7.6 cm.

One of the reasons for the increasing interest in extractive aquaculture is the possibility of a nutrient trading system being implemented in coastal waters, such as Chesapeake Bay (www.chesapeakebay.net/trading.htm). Nutrient trading schemes allow industry and municipal waste-water treatment facilities to purchase at market value extra nutrient removal capacity from others on the same receiving water body, rather than directly reducing their own nutrient inputs. This is becoming an important issue in the United States, where the Environmental Protection Agency is mandated by the Clean Water Act to improve water quality. One mechanism devised to help reduce phytoplankton production and thereby enhance water quality is the total maximum daily load (TMDL), which is the maximum daily amount of nutrients allowed to be discharged into a water body from all sources (www.epa.gov/waterscience/standards/nutrs.html). Nutrient trading will allow aquaculturists, who can document the amount of N and P removed by their farms, to be paid by those industries that find it less expensive to purchase nutrient removal rather than upgrade their own facilities to meet the TMDL. The use of extractive animal and plant aquaculture is actually a unique solution to helping attain these water-quality standards because it offers the only opportunity to reduce nutrients once they have entered a receiving body of water. This may be especially important in ameliorating the effects

of non-point source inputs that are the most difficult to regulate and control.

Aquaculture farms will have to undertake some procedures beyond those required for successful shellfish production to obtain remuneration for the amounts of N and P removed beyond those incorporated in bivalve tissue and shell. Such changes are necessary because sediment nutrient regeneration is extremely dependent on how the aquaculture facility is operated, including the species of bivalve being cultivated and the stocking densities. Furthermore, seasonal and physical characteristics of the aquaculture site, such as sediment porosity, water flow, abundance of bioturbators, and so forth, can directly and indirectly influence sediment biogeochemical processes. Consequently, any financial gain associated with nutrient trading will have to be balanced against possible increased operating costs associated with obtaining the targeted rates of nutrient removal.

The maximum top-down control on phytoplankton and enhancement of N and P removal only comes from species of bivalves, such as oysters, that maintain high clearance rates even when seston concentrations increase. Other species, such as hard clams, because of their comparatively low clearance rates (Grizzle et al. 2001, Newell & Koch 2004), have less influence on benthic pelagic coupling. In eutrophic conditions, the most active suspension-feeders will reject large amounts of phytoplankton as part of their copious pseudofeces that are then transferred to the sediment surface. These receiving sediments must always remain fully oxygenated because microbially mediated nitrification only occurs under aerobic conditions, and this is the crucial precursor to denitrification in the underlying anaerobic sediments. Similarly, in fully oxygenated sediments, but not anaerobic sediments, phosphorus can become bound to iron and remain buried in the accumulating sediments. Therefore, bivalve stocking densities must be constrained to prevent local overenrichment of the sediments by the biodeposits that can lead to such intense microbial activity that even the surface sediment becomes anoxic (Fig. 2). Ideally, bivalves should be cultivated in locations with moderate current flow because the continual supply of oxygenated water reduces the likelihood of bottom sediments becoming anaerobic. Water currents also cause the biodeposits to be distributed across a larger bottom area (Haven & Morales-Alamo 1968), further reducing the likelihood that the surface receiving sediments will become anoxic. Water flow also increases seston flux through the aquaculture site, thereby ensuring an adequate food supply to the bivalves (Wildish & Kristmanson 1997).

Because some of the ecological benefits associated with aquaculture of bivalve suspension-feeders are so dependent on having aerobic sediments, the degree of sediment oxygenation around the aquaculture site must be regularly monitored. This can be performed routinely by measuring the depth of the redox potential discontinuity (RPD), either in sediment cores collected in transparent acrylic plastic tubes (Grizzle & Penniman 1991) or by using a remotely operated camera system that directly photographs the sediment profile (O'Connor et al. 1989). If the depth of the RPD is found to be moving progressively shallower, it indicates that the dynamic balance between aerobic and anaerobic sediments is shifting toward less oxygenated sediment. In such a situation, remedial actions should be taken to maintain the aerobic conditions needed to sustain both nitrifying bacteria and the benthic bioturbator community. This might require the use of a paddle-wheel system to increase the rate of mixing of surface oxygenated water to the bottom. Alternatively, if off-bottom aquaculture systems are being

used, these could possibly be relocated until the normal depth of the RPD at the original site is restored.

The reduction in turbidity associated with bivalve feeding may be sufficient to increase PAR penetration to the sediment surface to a level that can sustain MPB production. Actively growing MPB absorb inorganic nutrients released from bivalve biodeposits at the sediment water interface and compete with the sediment microbial community for N remaining in the biodeposits. Consequently, in locations where sufficient PAR reaches the sediment surface to permit active MPB growth, bivalve biodeposition may not result in appreciable nitrogen removal via denitrification (Newell et al. 2002). Therefore, if enhanced denitrification is a desired ecosystem service, aquaculture stocks of bivalves should be cultivated in deeper locations where the biodeposits will be transferred to sediments beneath the euphotic zone.

In any nutrient trading scheme involving suspension-feeding bivalves, it will be relatively easy to account for N and P removed in shell and flesh based on the annual harvest levels. Unfortunately, the factors that govern the magnitude of N removal and P immobilization (Newell et al. 2005) that are by-products of rearing bivalves are too complex and variable to allow the use of fixed removal rates that can be applied across all shellfish aquaculture facilities. For example, seasonal and physical characteristics of the aquaculture site, such as sediment porosity, current flow, abundance of bioturbators, and so forth, can directly and indirectly influence sediment biogeochemical processes. The magnitude of these possible variations are illustrated in a study by Sundbäck et al. (2000) of two different grain size sediments. They reported that coupled nitrification-denitrification rates were about an order of magnitude higher annually in finer grain sediments with active bioturbators than in sediments of higher porosity and with a slightly lower biomass of bioturbators. Because of such complex interactions, aquaculturists participating in nutrient trading will have to document the actual N and P removal at the specific locations. Appropriate N and P flux measurements can be made in sediment cores collected seasonally from the aquaculture sites and adjacent control sites. For shallow-water sites, these incubations will have to be made both in darkness and in the light to account for the influence of MPB on sediment biogeochemistry. Membrane inlet mass spectrometry can be used to obtain precise measurements of denitrification rates in relation to the release into the water column of other forms of inorganic nitrogen (Cornwell et al. 1999, Newell et al. 2002). The accumulation and burial of N and P into the sediment can be measured in separate sediment cores. These measured N and P removal rates can then be used as the basis of deciding what level of remuneration may be obtained from nutrient trading.

ACKNOWLEDGMENTS

I am grateful to Dr. Jeff Cornwell and Dr. Tom Fisher for their scientific discussions. I would like to thank Ray Grizzle, Becky Holyoke, Carter Newell, and Bob Rheault for their reviews of an early draft of this manuscript. This research was supported with funding from Maryland Sea Grant (SA07528051-F) through NOAA award NA16RG2207. The U.S. government is authorized to publish reprints of this work, and the author reserves the right to post a copy on his academic Web site for the private and noncommercial use of individuals, notwithstanding any copyright notations hereon.

LITERATURE CITED

- An, S. & S. B. Joye. 2001. Enhancement of coupled nitrification-denitrification by benthic photosynthesis in shallow estuarine sediments. *Limnol. Oceanogr.* 46:62-74.
- Asmus, R. M. & H. Asmus. 1991. Mussel beds, limiting or promoting phytoplankton. *J. Exp. Mar. Biol. Ecol.* 148:215-232.
- Bayne, B. L., R. J. Thompson & J. Widdows. 1976. Physiology II. In: B.L. Bayne, editor. Marine mussels, their ecology and physiology. New York: Cambridge University Press. pp. 207-260.
- Bayne, B. L. & A. J. S. Hawkins. 1992. Ecological and physiological aspects of herbivory in benthic suspension-feeding molluscs. In: D. M. John, S. J. Hawkins & J. H. Price, editors. Plant-animal interactions in the marine benthos. Systematics Association Special Volume No. 46. Oxford: Clarendon Press. pp. 265-288.
- Bayne, B. L. & R. C. Newell. 1983. Physiological energetics of marine mollusca. In: A. S. M. Saleuddin & K. M. Wilbur, editors. The Mollusca, vol. 4. New York: Academic Press. pp. 407-515.
- Boynton, W. R. & W. M. Kemp. 1985. Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. *Mar. Ecol. Prog. Ser.* 23:45-55.
- Bricelj, V. M. & D. J. Lonsdale. 1997. *Aureococcus anophagefferens*: causes and ecological consequences of brown tides in US mid-Atlantic coastal water. *Limnol. Oceanogr.* 42:1023-1038.
- Carlton, J. T., J. K. Thompson, L. E. Schemel & F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Mar. Ecol. Prog. Ser.* 66:81-94.
- Cerco, C. F. & S. P. Seitzinger. 1997. Measured and modeled effects of benthic algae on eutrophication in Indian River-Rehoboth Bay, Delaware. *Estuaries.* 20:231-248.
- Chopin, T., A. H. Buschmann, C. Halling, et al. 2001. Integrating seaweeds into marine aquaculture systems: A key toward sustainability. *J. Phycol.* 37:975-986.
- Cloern, J. E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9:191-202.
- Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210:223-253.
- Coen, L. D., M. W. Luckenbach & D. L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *Am. Fish. Soc. Symp.* 22:438-454.
- Cohen, R. R. H., P. V. Dresler, E. J. P. Phillips, et al. 1984. The effect of the asiatic clam *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.* 29:170-180.
- Conley, D. J. 1999. Biogeochemical nutrient cycles and nutrient management strategies. *Hydrobiologia* 410:87-96.
- Conley, D. J., C. L. Schelske & E. C. Stoermer. 1993. Modifications of the biogeochemical cycle of silica with eutrophication. *Mar. Ecol. Prog. Ser.* 101:179-192.
- Cornwell, J. C., W. M. Kemp & T. M. Kana. 1999. Denitrification in coastal ecosystems: methods, environmental controls, and ecosystem level controls, a review. *Aquat. Ecol.* 33:41-54.
- Dame, R. F. 1996. Ecology of marine bivalves, an ecosystem approach. Boca Raton, FL: CRC Press. 254 pp.
- Dame, R. F. & N. Dankers. 1988. Uptake and release of materials by a Wadden Sea mussel bed. *J. Exp. Mar. Biol. Ecol.* 118:207-216.
- Dame, R. F. & S. Libes. 1993. Oyster reefs and nutrient retention in tidal creeks. *J. Exp. Mar. Biol. Ecol.* 171:251-258.
- Dame, R. F., J. D. Spurrier & T. G. Wolaver. 1989. Carbon, nitrogen and phosphorus processing by an oyster reef. *Mar. Ecol. Prog. Ser.* 54: 249-256.
- Dame, R. F., J. D. Spurrier & R. G. Zingmark. 1992. In situ metabolism of an oyster reef. *J. Exp. Mar. Biol. Ecol.* 164:147-159.
- Dame, R. F., R. G. Zingmark & E. Haskin. 1984. Oyster reefs as processors of estuarine materials. *J. Exp. Mar. Biol. Ecol.* 83:239-247.
- Dame, R. F., N. Dankers, T. C. Prins, et al. 1991a. The influence of mussel beds on nutrients in the western Wadden Sea and eastern Scheldt estuaries. *Estuaries.* 14:130-138.
- Dame, R. F., J. D. Spurrier, T. M. Williams, et al. 1991b. Annual material processing by a salt marsh-estuarine basin in South Carolina, USA. *Mar. Ecol. Prog. Ser.* 72:153-166.
- D'Elia, C. F., L. W. Harding, Jr., M. Leffler, et al. 1992. The role and control of nutrients in Chesapeake Bay. *Water Sci. Technol.* 26:2635-2644.
- Deslous-Paoli, J.-M., A.-M. Lannou, P. Geairon, et al. 1992. Effects of the feeding behaviour of *Crassostrea gigas* (Bivalve Mollusc) on biosedimentation of natural particulate matter. *Hydrobiologia* 231:85-91.
- Diaz, R. J. & R. Rosenberg. 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.
- Dinet, A., J.-M. Sornin, A. Sabliere, et al. 1990. Influence de la biodeposition de bivalves filtreurs sur les peuplements meiobenthiques d'un marais maritime. *Cahiers de biologie marine. Paris* 31:307-322.
- Dittmann, S. 1990. Mussel beds—amelioration or amelioration for intertidal fauna? *Helgoländ. Meer.* 44:335-352.
- Doering, P. H., C. A. Oviatt & J. R. Kelly. 1986. The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. *J. Mar. Res.* 44:839-861.
- Doering, P. H., J. R. Kelly, C. A. Oviatt, et al. 1987. Effect of the hard clam *Mercenaria mercenaria* on benthic fluxes of inorganic nutrients and gases. *Mar. Biol.* 94:377-383.
- Epping, E. H. G., A. Khalili & R. Thar. 1999. Photosynthesis and the dynamics of oxygen consumption in a microbial mat as calculated from transient oxygen microprofiles. *Limnol. Oceanogr.* 44:1936-1948.
- Galtsoff, P. S. 1964. The American Oyster. *Fish. Bull.* 64:1-480.
- Gao, K. & K. R. McKinley. 1994. Use of macroalgae for marine biomass production and CO₂ remediation—a review. *J. Appl. Phycol.* 6:45-60.
- Gobler, C. J., M. J. Renaghan & N. J. Buck. 2002. Impacts of nutrients and grazing mortality on the abundance of *Aureococcus anophagefferens* during a New York brown tide bloom. *Limnol. Oceanogr.* 47:129-141.
- Gowen, R. J. & N. B. Bradbury. 1987. The ecological impacts of salmonid farming in coastal waters: a review. *Oceanogr. Mar. Biol. Ann. Rev.* 25:563-575.
- Grant, J., A. Hatcher, D. B. Scott, et al. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. *Estuaries.* 18:124-144.
- Grizzle, R. E. & 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.
- Grizzle, R. E., S. E. Shumway & V. M. Bricelj. 2001. Physiology and bioenergetics of *Mercenaria mercenaria*. In: J. N. Kraeuter & M. Castagna, editors. The hard clam, *Mercenaria mercenaria*. Amsterdam: Elsevier. pp. 305-382.
- Hatcher, A., J. Grant & B. Schofield. 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.
- Haven, D. S. & R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol. Oceanogr.* 11: 487-498.
- Haven, D. S. & R. Morales-Alamo. 1968. Occurrence and transport of faecal pellets in suspension in a tidal estuary. *Sediment. Geol.* 2:141-151.
- Hawkins, A. J. S., B. L. Bayne, S. Bougrier, et al. 1998. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. *J. Exp. Mar. Biol. Ecol.* 219:87-103.
- Henriksen, K. & W. M. Kemp. 1988. Nitrification in estuarine and coastal marine sediments. In: T. H. Blackburn & J. Sorensen, editors. Nitrogen cycling in coastal marine environments. Chichester, England: Wiley and Sons. pp. 205-249.
- Ito, S. & T. Imai. 1955. Ecology of oyster bed I. On the decline of productivity due to repeated cultures. *Tohoku J. Agric. Res.* 4:9-26.

- Jaramillo, E., C. Bertran & A. Bravo. 1992. Mussel biodeposition in an estuary in southern Chile. *Mar. Ecol. Prog. Ser.* 82:85-94.
- Jordan, T. E. & I. Valiela. 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnol. Oceanogr.* 27:75-90.
- Joye, S. B. & H. W. Paerl. 1994. Nitrogen cycling in microbial mats, rates and patterns of denitrification and nitrogen fixation. *Mar. Biol.* 119: 285-295.
- Kaspar, H. F., P. A. Gillespie, I. C. Boyer et al. 1985. Effects of mussel aquaculture on the nitrogen cycle and benthic communities in Kenepuru Sound, Marlborough Sounds, New Zealand. *Mar. Biol.* 85: 127-136.
- Kautsky, N. & S. Evans. 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.
- Kemp, W. M. & W. R. Boynton. 1992. Benthic-Pelagic interactions: nutrient and oxygen dynamics. In: D. E. Smith, M. Leffler, & G. Mackiernan, editors. Oxygen dynamics in the Chesapeake Bay. College Park, MD: Maryland Sea Grant Publication. pp. 49-221.
- Kreeger, D. A. & R. I. E. Newell. 2001. Seasonal utilization of different seston carbon sources by the ribbed mussel, *Geukensia demissa* (Dillwyn) in a mid-Atlantic salt marsh. *J. Exp. Mar. Biol. Ecol.* 260: 71-91.
- Kristensen, E. 1988. Benthic fauna and biogeochemical processes in marine sediments, microbial activities and fluxes. In: T. H. Blackburn & J. Sorensen, editors. Nitrogen cycling in coastal marine environments. Chichester, England: Wiley and Sons. pp. 275-299.
- Krom, M. D. 1991. Importance of benthic productivity in controlling the flux of dissolved inorganic nitrogen through the sediment-water interface in a hypertrophic marine ecosystem. *Mar. Ecol. Prog. Ser.* 78: 163-172.
- Krom, M. D. & R. A. Berner. 1981. The diagenesis of phosphorus in a nearshore marine sediment. *Geochim. Cosmo. Acta* 45:207-216.
- Lam-Hoai, T. & C. Rougier. 2001. Zooplankton assemblages and biomass during a 4-period survey in a northern Mediterranean coastal lagoon. *Water Res.* 35:271-283.
- Lam-Hoai, T., C. Rougier & G. Lasserre. 1997. Tintinnids and rotifers in a northern Mediterranean coastal lagoon. Structural diversity and function through biomass estimations. *Mar. Ecol. Prog. Ser.* 152:13-25.
- Langdon, C. J. & R. I. E. Newell. 1996. Digestion and nutrition of larvae and adults. In: V. S. Kennedy, R. I. E. Newell & A. Eble, editors. The Eastern Oyster, *Crassostrea virginica*. College Park, MD: Maryland Sea Grant Publication. pp. 231-270.
- MacIsaac, H. J., O. E. Johannsson, J. Ye, et al. 1999. Filtering impacts of an introduced bivalve (*Dreissena polymorpha*) in a shallow lake: application of a hydrodynamic model. *Ecosystems.* 2:338-350.
- Malone, T. C. 1992. Effects of water column processes on dissolved oxygen, nutrients, phytoplankton and zooplankton. In: D.E. Smith, M. Leffler, & G. Mackiernan, editors. Oxygen dynamics in the Chesapeake Bay. College Park, MD: Maryland Sea Grant Publications. pp. 61-112.
- Miller, D. C., R. J. Geider & H. L. MacIntyre. 1996. Microphytobenthos, the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. *Estuaries.* 19:202-212.
- Nakamura, Y. & F. Kerciku. 2000. Effects of filter-feeding bivalves on the distribution of water quality and nutrient cycling in a eutrophic coastal lagoon. *J. Mar. Syst.* 26:209-221.
- Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay, are they the result of overharvesting the Eastern oyster (*Crassostrea virginica*)? In: M. P. Lynch & E. C. Krome, editors. Understanding the estuary, advances in Chesapeake Bay research. Gloucester Point, VA: Chesapeake Research Consortium Publication 129 (CBP/TRS 24/88). pp. 536-546.
- Newell, R. I. E. & S. J. Jordan. 1983. Preferential ingestion of organic material by the American Oyster, *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 13:47-53.
- Newell, R. I. E. & C. J. Langdon. 1996. Mechanisms and Physiology of Larval and Adult Feeding. In: V. S. Kennedy, R. I. E. Newell & A. Eble, editors. The Eastern Oyster, *Crassostrea virginica*. College Park, M.D.: Maryland Sea Grant Publication. pp.185-230.
- Newell, R. I. E., J. C. Cornwell & M. S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics, a laboratory study. *Limnol. Oceanogr.* 47:1367-1379.
- Newell, R. I. E. & E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries.* In press.
- Newell, R. I. E., T. R. Fisher, R. R. Holyoke, et al. 2005. Influence of eastern oysters on N and P regeneration in Chesapeake Bay, USA. In: R. Dame and S. Olenin, editors. The comparative roles of suspension-feeders in ecosystems. NATO Science Series: IV - Earth and Environmental Sciences. Dordrecht: Kluwer. In press.
- O'Connor, B. D. S., J. Costelloe, B. F. Keegan, et al. 1989. The use of REMOTS technology in monitoring coastal enrichment resulting from mariculture. *Mar. Poll. Bull.* 20:384-290.
- Officer, C. B., T. J. Smayda & R. Mann. 1982. Benthic filter feeding, a natural eutrophication control. *Mar. Ecol. Prog. Ser.* 9:203-210.
- Orth, R. J., K. L. Heck & J. Van Montfrans. 1984. Faunal communities in seagrass beds, a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries.* 7:339-350.
- Peckol, P. & J. S. Rivers. 1995. Physiological responses of the opportunistic macroalgae *Cladophora vagabunda* (L.) van den Hoek and *Gracilaria tikvahiae* (McLachlan) to environmental disturbances associated with eutrophication. *J. Exp. Mar. Biol. Ecol.* 190:1-16.
- Pelegri, S. P., L. P. Nielsen & T. H. Blackburn. 1994. Denitrification in estuarine sediment stimulated by the irrigation activity of the amphipod *Corophium volutator*. *Mar. Ecol. Prog. Ser.* 105:285-290.
- Phelps, H. L. 1994. The asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac river estuary near Washington, D.C. *Estuaries.* 17:614-621.
- Prins, T. C. & A. C. Smaal. 1990. Benthic-pelagic coupling, the release of inorganic nutrients by an intertidal bed of *Mytilus edulis*. In: M. Barnes & R. N. Gibson, editors. Trophic relationships in the marine environment. Aberdeen University Press, Scotland: Proceedings 24th European Marine Biology Symposium. pp. 89-103.
- Prins, T. C., V. Escaravage, A. C. Smaal, et al. 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. *Ophelia* 41:289-315.
- Prins, T. C., A. C. Small & R. F. Dame. 1998. A review of the feedbacks between grazing and ecosystem processes. *Aquat. Ecol.* 31:349-359.
- Pomeroy, L. R. & W. J. Wiebe. 1993. Energy sources for microbial food webs. *Mar. Micro. Food Webs.* 7:101-118.
- Rafaelli, D. G., J. A. Raven & L. J. Poole. 1998. Ecological impact of green macroalgal blooms. *Oceanogr. Mar. Biol. Ann. Rev.* 36:97-125.
- Rhee, G-Yull. 1978. Effects of N and P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake. *Limnol. Oceanogr.* 23:10-25.
- Riemann, B., T. G. Nielsen, S. J. Horsted, et al. 1988. Regulation of phytoplankton biomass in estuarine enclosures. *Mar. Ecol. Prog. Ser.* 48: 205-215.
- Risgaard-Petersen, N., S. Rysgaard, L. P. Nielsen, et al. 1994. Diurnal variation of denitrification and nitrification in sediments colonized by benthic microphytes. *Limnol. Oceanogr.* 39:573-579.
- Rodhouse, P. G. & C. M. Roden. 1987. Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs. *Mar. Ecol. Prog. Ser.* 36:225-236.
- Rysgaard, S., N. Risgaard-Petersen, N. P. Sloth, et al. 1994. Oxygen regulation of nitrification and denitrification in sediments. *Limnol. Oceanogr.* 39:1643-1652.
- Rysgaard, S., P. B. Christensen & L. P. Nielsen. 1995. Seasonal variation in nitrification and denitrification in estuarine sediment colonized by benthic microalgae and bioturbating infauna. *Mar. Ecol. Prog. Ser.* 126:111-121.
- Ryther, J. H. 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.* 106:198-209.

- Simenstad, C. A. & K. L. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. *Estuaries*. 18:43-70.
- Shumway, S. E. 1990. A review of the effects of algal blooms on shellfish and aquaculture. *J. World Aquacult. Soc.* 21:65-104.
- Sloth, N. P., T. H. Blackburn, L. S. Hansen, et al. 1995. Nitrogen cycling in sediments with different organic loadings. *Mar. Ecol. Prog. Ser.* 116:163-170.
- Souchu, P., A. Vaquer, Y. Collos, et al. 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. *Mar. Ecol. Prog. Ser.* 218:141-152.
- Strayer, D. L., N. F. Caraco, J. J. Cole, et al. 1999. Transformation of freshwater ecosystems by bivalves, a case study of zebra mussels in the Hudson River. *BioScience* 49:19-27.
- Sundbäck, K. & W. Graneli. 1988. Influence of microphytobenthos on the nutrient flux between sediment and water, a laboratory study. *Mar. Ecol. Prog. Ser.* 43:63-69.
- Sundbäck, K., A. Miles & E. Goransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments, an annual study. *Mar. Ecol. Prog. Ser.* 200:59-76.
- Sundbäck, K., V. Enoksson, W. Graneli, et al. 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water, a laboratory continuous-flow study. *Mar. Ecol. Prog. Ser.* 74:263-279.
- Swanberg, I. L. 1991. The influence of the filter-feeding bivalve *Cerastoderma edule* L. on microphytobenthos, a laboratory study. *J. Exp. Mar. Biol. Ecol.* 151:93-111.
- Taylor, D. I., S. W. Nixon, S. L. Granger, et al. 1995. Responses of coastal lagoon plant-communities to different forms of nutrient enrichment—a mesocosm experiment. *Aquat. Bot.* 52:19-34.
- Taylor, R., R. L. Fletcher & J. A. Raven. 2001. Preliminary studies on the growth of selected "green tide" algae in laboratory culture: effects of irradiance, temperature, salinity and nutrients on growth rate. *Bot. Marina*. 44:327-336.
- Tenore, K. R. & W. M. Dunstan. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.* 21:190-195.
- Tenore, K. R., L. F. Boyer, & R. M. Cal. 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.
- Terry, K. L. 1982. Nitrate and phosphate interactions in a marine prymnesiophyte. *J. Phycol.* 18:79-86.
- Tsutsumi, H. 1995. Impact of fish net pen culture on the benthic environments of a cove in south Japan. *Estuaries*. 18:108-115.
- Tuttle, J. H. & R. B. Jonas. 1992. Influence of rafted oyster aquaculture on sediment processes. Final Report to Maryland Department of Natural Resources Tidewater Administration, Maryland Coastal Research Division. 112 pp.
- Twilley, R. R., W. M. Kemp, K. W. Staver, et al. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* 23:179-191.
- Ulanowicz, R. E. & J. H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries*. 15:298-306.
- Verwey, J. 1952. On the ecology of distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation, and the source of their food supply. *Arch. Neerl. Zool.* 10:171-239.
- Ward, J. E., J. S. Levinton, S. E. Shumway, et al. 1997. Site of particle selection in a bivalve mollusc. *Nature* 390:131-132.
- White, J. R. & M. R. Roman. 1992. Egg production by the calanoid copepod *Acartia tonsa* in mesohaline Chesapeake Bay, the importance of food resources and temperature. *Mar. Ecol. Prog. Ser.* 86:239-249.
- Widdows, J., M. D. Brinsley, P. N. Salkeld, et al. 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. & D. D. Kristmanson. 1997. Benthic suspension-feeders and flow. Cambridge, UK: Cambridge University Press. 409 pp.
- Yamamuro, M. & I. Koike. 1993. Nitrogen metabolism of the filter-feeding bivalve *Corbicula japonica* and its significance in primary production of a brackish lake in Japan. *Limnol. Oceanogr.* 38:997-1007.