

**Shellfish Aquaculture: Ecosystem Effects,
Benthic–Pelagic Coupling
and Potential for Nutrient Trading**

Roger I. E. Newell
Horn Point Laboratory,
University of Maryland Center for Environmental Science
PO Box 775, Cambridge, MD 21613, USA
rnewell@umces.edu

and

Roger Mann
Virginia Institute of Marine Science
Gloucester Point, VA 23062 USA
rmann@vims.edu

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Summary

The processes connecting dissolved inorganic nitrogen (N) and phosphorus (P) uptake by phytoplankton from the water column and incorporation with carbon fixed by photosynthesis into organic molecules that are an essential food source for shellfish are briefly reviewed. The fate of N and P bound in shellfish biomass and voided as biodeposits are described and discussed in the context of nutrient trading. Nitrogen and P that are incorporated in tissue and shell of harvested bivalves can reliably be quantified, thereby allowing shellfish farmers in Virginia to participate in nitrogen trading should such a market become established. In 2010, the most recent year for which data are available, there were 16.9 million eastern oysters (*Crassostrea virginica*) harvested from aquaculture farms in Virginia. We estimate that this level of harvest will have removed from Chesapeake Bay a total of 2,197 Kg of N and 338 kg of P in oyster tissue and shell combined.

The fate of organic N and P ingested by bivalves but not assimilated into tissue and shell is more difficult to predict because key biogeochemical processes are influenced by season, location, and farm management practices. Although the bacterially mediated process of denitrification can achieve permanent nitrogen removal from the aquatic system to the atmosphere, this is likely to occur only in well-managed shellfish aquaculture sites that have been placed in suitable locations. At the present time there are no methods to reliably quantify and predict such nitrogen removal on a large scale and on an ongoing basis. Current research efforts are attempting to quantify the magnitude of nitrogen loss via denitrification in shellfish farms. In all probability, site-specific monitoring will be required to quantify such nitrogen removal if the intent is to include denitrification in nutrient trading; however, sufficient information is available to encourage farm Best Management Practices that will promote nitrogen loss via denitrification, thereby gaining ecosystem benefits.

Introduction

Shellfish harvesting from the Chesapeake Bay was an important food source for native people prior to the arrival of European colonists. The more recent history of shellfish harvest, especially oyster harvest, through the 19th and 20th century, is that of an industry that considered the resource limitless; however, the cumulative impacts of disease, overharvest, and environmental degradation resulted in a drastically depleted oyster stock by the end of the 20th century. Consequently, there has been a forced transition from a wild fishery exploiting public oyster bars to intensive oyster aquaculture which is now a rapidly expanding industry in the Chesapeake Bay (Murray and Hudson 2011). In concert with selective breeding for disease tolerance and ploidy manipulation that is ongoing at the Virginia Institute of Marine Science, the intensive culture of oysters' proffers hope as a major element for the resurgence of the native oyster fishery. The development of Pacific oyster culture on the U.S west coast over the last five decades provides an example of the scale of production that might be achieved in the mid-Atlantic with the native eastern oyster. The extant intensive efforts in shellfish culture in many Asian and European countries suggest that there exists enormous growth potential for the oyster aquaculture industry.

Many economic benefits are associated with developing shellfish aquaculture in Chesapeake Bay. The Bay is highly productive, with excess nutrient inputs from point and non-point

anthropogenic sources that stimulate high levels of phytoplankton primary production that is the food source for shellfish. Aquaculture can provide both employment in rural areas and a continuous supply of seafood that will reduce dependence on foreign imports. But there are ecological consequences associated with greatly enhancing stocks of bivalves in intensive aquaculture farms. These consequences can be beneficial if managed correctly or highly adverse if aquaculture farms are not sited and managed correctly (Newell 2004, Shumway 2011). Potential ecosystem benefits have been promoted, but these must be viewed with caution in that they are rarely accompanied by consideration of the impacts of intensive culture in situations with less than ideal management. Of recent interest is the possible role of intensive shellfish culture in nutrient reduction in the Bay's receiving waters, that is, the use of shellfish culture as a component of nutrient trading directed at overall improvement of Bay water quality. A balanced discussion is required.

Connecting shellfish production with the source and fates of nutrients: how does this fit with nutrient trading?

The objective of this review is to briefly summarize the ecosystem effects of shellfish aquaculture, predominantly the culture of oysters suspended near the water surface in floats or held in cages on the bottom, in the Chesapeake Bay. Additional details and supporting literature are provided in Newell (2004), Newell et al. (2005), Shumway (2011), and Dame (2012). We specifically identify areas where lack of information limits the accurate estimation of associated ecosystem benefits at the present time. We focus on the role of shellfish in connecting water column processes (the pelagic zone) where nutrients are central to the production of single cell plankton upon which oysters feed, and processes at the sediment water interface and surface sediment layers (the benthic zone). Nutrients, nitrogen N and phosphorus P, from terrestrial point and non-point sources flow into the Bay as dissolved inorganic nitrogen and phosphorus (DIN and DIP).

The first question to be addressed is how inorganic nutrients result in phytoplankton growth, and how oyster feeding on this phytoplankton may improve water quality. The entire process is summarized in a series of graphics (Figure 1). The dissolved inorganic nitrogen (DIN = ammonium $[\text{NH}_4^+]$ + nitrite $[\text{NO}_2^-]$ + nitrate $[\text{NO}_3^-]$) and phosphorus (DIP = phosphate $[\text{PO}_4^{3-}]$), together considered as the DIN and DIP pool, are taken up by the phytoplankton and incorporated as part of their growth and cell multiplication process to form particulate organic nitrogen (PON) and particulate organic phosphorus (POP), collectively termed particulate organic matter (PON + POP = POM). The production of POM is driven by photosynthesis and dependent on the availability of specific wavelengths of light (photosynthetic active radiation or PAR) passing through the water column. Turbidity reduces light penetration and PAR, and diminishes photosynthesis. Production of phytoplankton results in removal of dissolved nitrogen and phosphorus from the water column (i.e., the oysters themselves do not directly remove the inorganic nutrients).

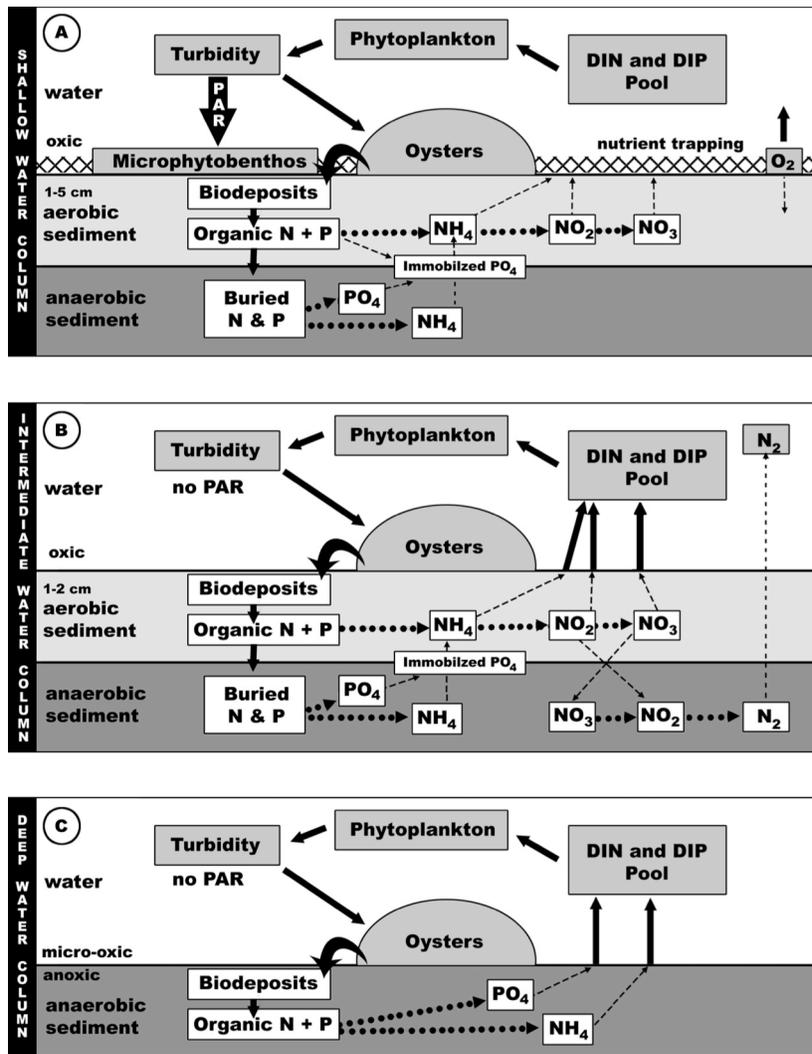


Figure 1. Role of eastern oysters in removing phytoplankton from the water column and transferring undigested particulate material as biodeposits to the sediment surface. Illustrated are benthic-pelagic scenarios for three locations (Panels A, B, and C) with different levels of photosynthetic active radiation (PAR) and dissolved oxygen concentrations. From surficial aerobic sediments (middle panel) N and P are released to the water column. The microbially mediated process of nitrification in the aerobic surface sediments coupled to denitrification within the underlying anaerobic sediments causes N to be lost from biodeposits as N₂ gas. N not regenerated is buried in accumulating sediments and P is immobilized in the aerobic sediments. In contrast, little nutrient regeneration into the water column takes place in locations with sufficient light to support active microphytobenthos that absorb regenerated N and P at the sediment surface (upper panel). Coupled nitrification-denitrification is also reduced because the microphytobenthos out-compete bacteria for NO₂, NO₃, and NH₄. In locations where the sediments are anoxic (lower panel) nitrification is inhibited and all N and P is regenerated from the sediments as NH₄ and PO₄. Some burial of N occurs but P sorption is precluded. Solid lines indicate transfer of materials; dashed lines indicate diffusion of materials; dotted lines indicate microbially mediated reactions. From Newell et al. (2005)

Nitrogen and Phosphorus in Harvested Oysters

Phytoplankton (PON + POP) are filtered from the water column by the oysters and after ingestion and digestion these nutrients are available to support the oyster's metabolism and growth. Nitrogen, and to a lesser amount phosphorus, are required to synthesize proteins used to build tissue as the oyster grows from the small, newly metamorphosed juvenile (= spat or seed) to a large market-size individual. Some of these proteins are also required to form an organic matrix along the margin of the shell that serves as a framework for the deposition of calcium carbonate as the growing oyster enlarges its shell (Carriker 1996). By the time oysters have grown to market size they have incorporated appreciable amounts of N and P into tissue and shell and so these nutrients are removed from Chesapeake Bay when the oysters are harvested.

In order to allow the process of nutrient removal by oyster harvest to be used for nutrient trading credits it is necessary to develop equations to estimate the amount of N and P removed based on the numbers and size of harvested oysters. Also, in order to have credibility, it is necessary to assess the variation in oyster nutrient content that can stem from seasonal differences in oyster tissue composition and site specific variation in oyster growth.

Shell

Oysters grown in aquaculture floats in Chesapeake Bay reach market size of 3-inch shell height almost twice as fast as oysters grown on natural oyster bottom (= reefs). This faster growth is attributable to high water flow through oyster floats that serves to provide the oysters with large amount of phytoplankton and avoid food depletion. Palmer (1981) hypothesized for bivalves in general that faster-growing individuals have thinner shells than slower-growing individuals because calcium carbonate deposition in molluscs is a rate-limited rather than an energy-limited process. This has been found to be true for oyster grown in floats in Chesapeake Bay which have thinner and lighter shells compared with oysters growing more slowly on-bottom (Paynter and Dimichele 1990, Newell et al. 2005, Higgins et al. 2011). For example, Newell et al. (2005) reported that the shell of a market size oyster grown on bottom weighed ~150 g (Table 1), which is about 5 times greater than the ~ 30 g of a similarly sized oyster grown in floats (Higgins et al. 2011). Therefore, the relative contribution of the shell to removal of N and P will typically be less in oysters grown in floating cages than for oysters grown on natural oyster bottom.

Tissue

There are seasonal differences in protein (and hence nitrogen) content in oyster tissue (meats) when expressed as percentage of total dry weight which are caused by relative changes in the amount of non-nitrogen containing glycogen that the female oyster uses as a nutrient reserve (Thompson et al. 1996). (We only need consider here the situation for females since the eastern oyster is protandric and hence market size oysters are predominately female). As the oyster builds glycogen reserves to a maximum in early winter this effectively reduces the percentage of the total weight attributable to protein in the harvested oyster meats. In the spring, these glycogen reserves are used to synthesize lipids for yolk reserves in eggs, which are eventually spawned in early summer. As a consequence of this annual reproductive cycle, female protein content varies from a maximum of ~45% immediately post-spawning (June) to ~ 35% in early winter (November) when oysters are "fattest" (Thompson et al. 1996). This 10% seasonal

variation in percent protein content must be considered when applying equations relating N and P tissue content to oyster size that have been generated from data obtained at only one season.

The most comprehensive study of Nitrogen and Phosphorus incorporation in tissues of oysters in Chesapeake Bay was undertaken by Higgins et al. (2011) at two sites near the mouth of the Potomac River. They grew oysters in aquaculture floats from seed to various shell sizes over a period of up to three years. In April and May prior to spawning, oysters of different shell sizes were collected for analysis of tissue and shell N and P content. They found quite a narrow range of 7.3% to 8.2% for N and 0.8% for P in tissue, and 0.17% to 0.26% N and 0.04% for P in shell (Table 1). These percent composition data are similar to that reported by Newell (2004) for older oysters collected from a natural oyster bar.

Table 1. Literature data for Nitrogen and Phosphorous content in tissue and shell of oysters from Chesapeake Bay grown on bottom or in floating cage culture. DW = dry weight

Shell size (mm)	Shell DW (g)	Tissue DW (g)	tissue		shell		whole oyster	
			%N	%P	%N	%P	Total N (g)	Total P (g)
<i>Wild oysters collected from natural oyster reefs (Newell 2004)</i>								
76	150	1.0	7.0	0.8	0.3	0.1	0.52	0.16
<i>Cultivated oysters grown in floating cages (Higgins et al. 2011)</i>								
43.6	4.8	0.20	8.15	0.83	0.18	0.04	0.025	0.003
64.8	24.3	0.80	8.06	0.83	0.19	0.04	0.112	0.016
85.5	37.6	1.58	7.28	0.82	0.17	0.04	0.176	0.026
117.8	71.9	3.00	7.37	0.82	0.26	0.04	0.394	0.050

Spatial variability

Oyster growth can vary widely among aquaculture sites within an estuary, probably in most cases largely due to variations in food supply and other environmental factors, such as salinity (Brown et al., 1998; Brown et al., 2005a). At six sites in the Great Bay estuarine system in New Hampshire, Grizzle and Ward (2011) studied nitrogen assimilation over a 3-month period by oysters grown in bags suspended 10-20 cm off the bottom. They reported that among the six sites the mean percent nitrogen content in tissue ranged from 4.7% to 10.6% content. This was much wider variation than observed by Higgins et al (2011) for their two aquaculture farm sites in Chesapeake Bay. Grizzle and Ward (2011) offered no explanation for their findings. It is

possible that this high spatial variability was an artifact stemming from their short three-month study period. Oysters from the sites with better growing conditions will have accumulated larger glycogen stores, thereby effectively reducing percent protein content. In contrast, oysters held at sites with less favorable conditions for growth would have less available energy to build glycogen reserves and hence protein would constitute a greater fraction of the animals total tissue weight. But if the oysters had been grown from spat to market size this longer growth period may have reduced this spatial variability in tissue composition.

Initial Estimates of N and P removal by Oyster Aquaculture

Higgins et al. (2011) developed from their floating cage-grown oyster data the following predictive equations relating total nitrogen (TN in g) and phosphorus (TP in g) contained in oyster tissue and shell to individual maximum shell size (TL in mm) (Figure 2).

$$\text{TN} = e^{(-14.1569 + 2.7994 \times \ln(\text{TL}))} \quad (\text{R}^2 = 0.76; \text{SE} = 0.47) \quad [1]$$

$$\text{TP} = e^{(-15.6926 + 2.7061 \times \ln(\text{TL}))} \quad (\text{R}^2 = 0.78; \text{SE} = 0.44) \quad [2]$$

Higgins et al. (2011) used these equations to estimate that, at harvest, the total nutrient content of one market-sized oyster (maximum shell size of 76 mm) is 0.13 g N and 0.02 g P. This is lower than the 0.5 g N and 0.16 g P reported by Newell et al. (2005) in comparably sized oysters harvested from oyster bottom due to the greater amount of N and P in the considerably heavier shell (Table 1).

We used values from Higgins et al (2011) for N and P in an individual oyster to estimate the total nutrients removed in 2010 by the aquaculture production of oysters in Virginia. The production of oysters from aquaculture farms in Virginia has been collated by Murray and Hudson (2011) who performed a detailed survey of annual harvest by all known producers (Figure 3). Their survey did not differentiate between oysters grown off-bottom in floating cages, on bottom in cages, or on cultch planted directly on-bottom. For the purpose of our calculation we assumed that the values of N and P measured for oysters grown in floating cages (Table 1) applies to all oysters grown to 3-inch market shell size in these various different ways. During 2010, the most recent year for which data are available there were 16.9 million oysters harvested. This level of harvest will have removed from Chesapeake Bay an estimated total of 2,197 Kg of N and 338 kg of P.

Benefits of Using Oysters in Nutrient Trading

The use of oyster aquaculture as a means to remove nutrients is a unique solution to helping attain water quality improvements in Chesapeake Bay because it offers the only opportunity to reduce nutrients after they have entered a receiving body of water (Newell 2004, Newell et al. 2005). This may be especially important in ameliorating the effects of non-point source inputs that are the most difficult to regulate and control. On a per-unit area basis, oyster aquaculture removes a relatively large quantity of nutrients from receiving waters compared with implementing agricultural Best Management Practices (BMP), such as cover crops (Higgins et al. 2011). In addition it should be noted that oyster aquaculture results in substantial revenues

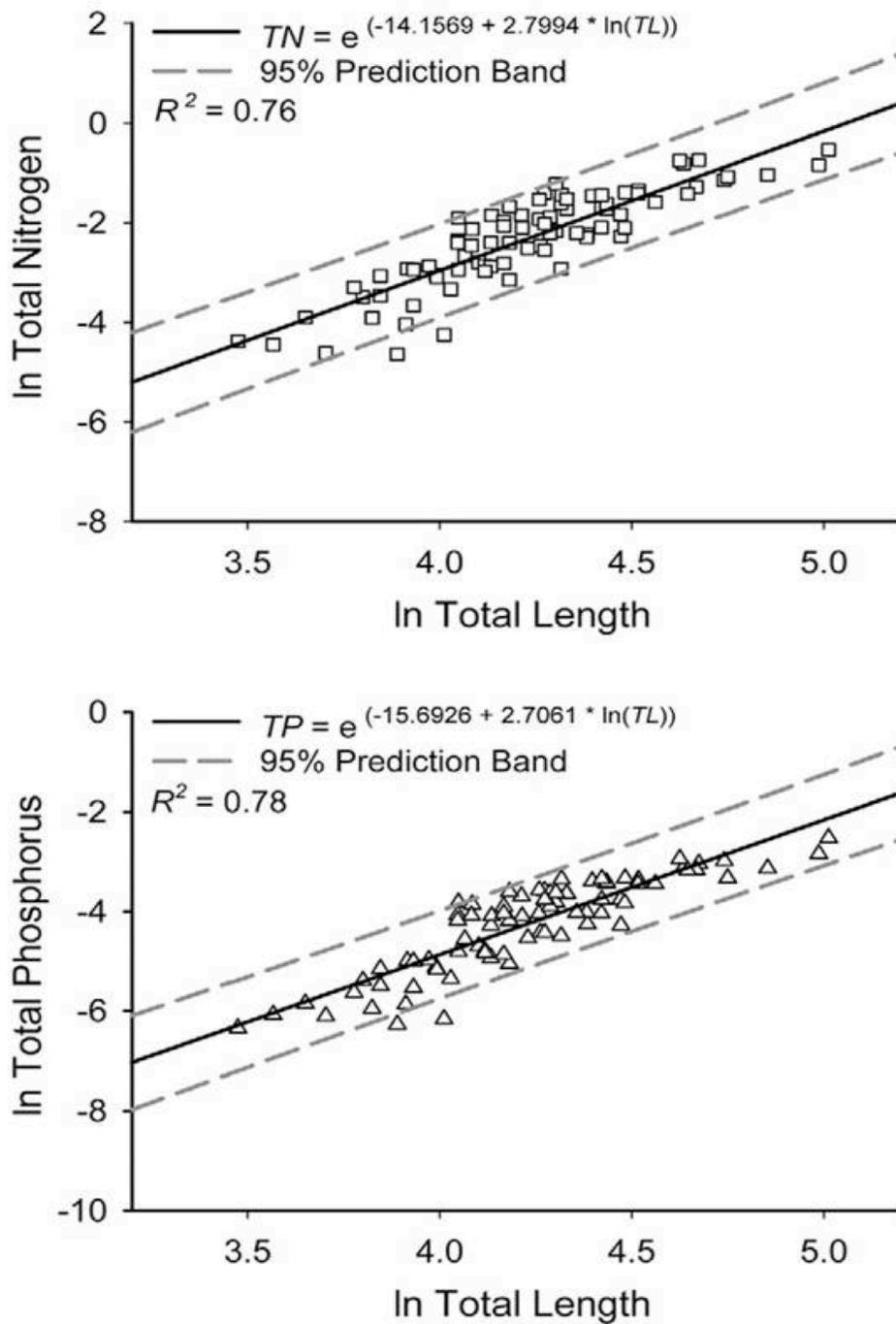
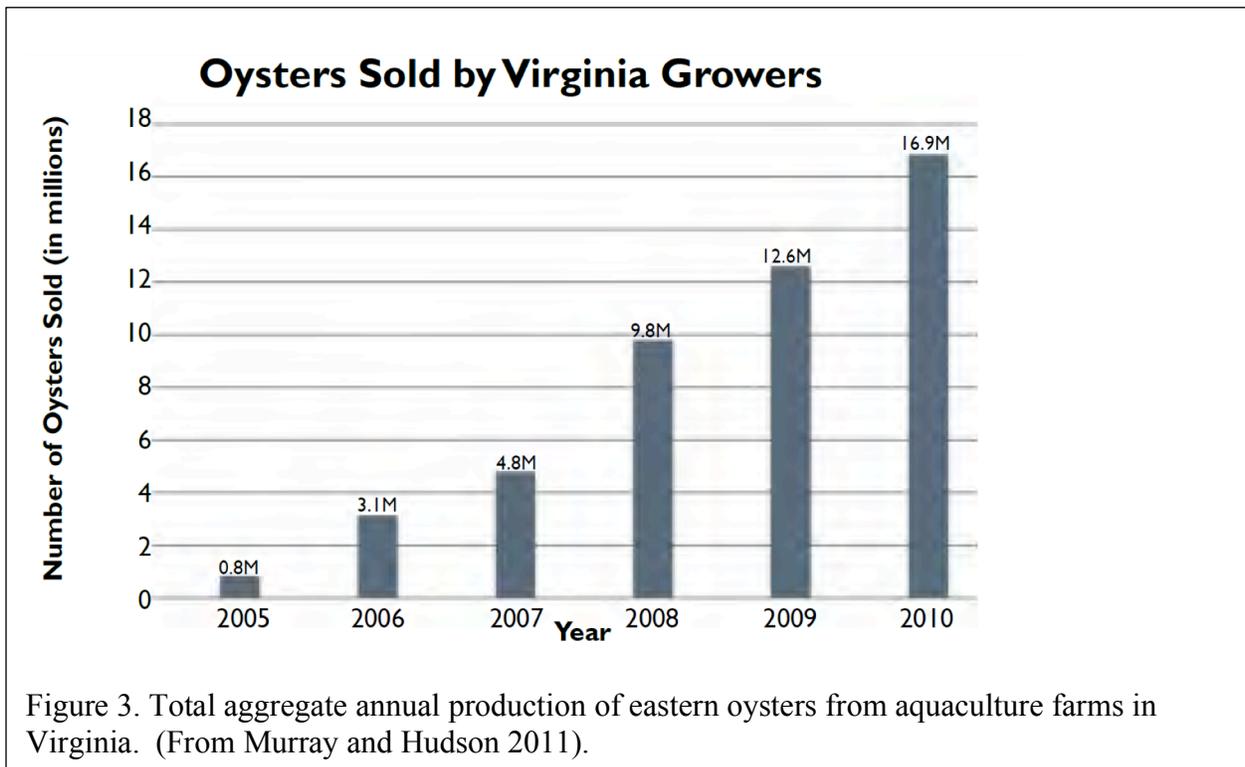


Figure 2. Linear regressions of \log_e -transformed total nutrient content [g total nitrogen (TN; squares) and g total phosphorous (TP; triangles)] against \log_e -transformed maximum shell size (TL; mm) for eastern oysters cultivated in floats in Chesapeake Bay. (From Higgins et al. 2011)



from oyster sales and ancillary economic value in economically depressed rural communities. The additional revenue provided to farms from Nutrient Trading may be sufficient to allow these farms to be economically viable over the long-term (Newell 2004)

A requirement for any nutrient-trading program is the ability to document the exact amount of nutrient removed. This can be done accurately for oysters based on periodic farm inspections to check the number and size of oysters being grown and from records of numbers and size of oysters harvested and sold. Such clear quantifiable benefits are in contrast to agricultural BMP's where the amount of nutrient removal attributable to a specific practice implemented at a particular location is based on highly extrapolated data (Higgins et al. 2011).

Validation Studies

Once oysters reared in aquaculture farms start to be used in nutrient trading schemes in Virginia it will be necessary to perform a study of the seasonal variation in total nitrogen and phosphorous content of market size oyster tissue and shell at one farm site. These data can then be used to determine if the average values (Table 1 and Figure 2) reported by Higgins et al. (2011) for oysters harvested in April and May can be applied to oyster harvested at other times of the year. If the seasonal variations observed are large then appropriate seasonal values must be developed to estimate N and P removal associated with oysters harvested at various times of the year.

For each aquaculture farm site that becomes involved in nutrient trading it will be important to take samples of the oysters being marketed to establish the relationships between shell size, tissue dry weight, and percent N and P content. These data can then be used to build a larger data set for all of Virginia to estimate the among-farm variation in these fundamental relationships. If this variability is small then the same size and seasonal conversion factors can be applied to harvest from all farms. If the site and seasonal specific differences are large among farms then location specific conversion factors will be required.

The Role of Oyster Aquaculture in Enhancing Sedimentary Nutrient Removal

A proportion of the ingested PON and POP is passed through the oyster gut and ends up on the sediment surface as feces (biodeposits). In oysters, but not clams, the possibility also exists that phytoplankton is filtered but not ingested. When the oyster gills become clogged, they are cleaned by a rapid shell closure action and the material is simply ejected onto the bottom in a mucous bound mass called pseudofeces (which are also part of biodeposits). The fate of nitrogen and phosphorus in both the fecal (ingested and processed) and pseudofecal (filtered but not ingested) biodeposits is variable, site specific, and cannot be consistently estimated as a constant for all situations.

There is a significant seasonal element to shellfish feeding because the animal's overall activity is strongly controlled by water temperature. This activity response varies with species. Oysters in Chesapeake Bay feed actively and consume phytoplankton when water temperature exceeds 8⁰C, with maximum feeding activity occurring when temperatures are between ~20 and 28⁰C. Hard clams feed maximally when temperatures are lower with decreased feeding when temperatures exceed 20⁰C. Thus the processes of nutrient removal discussed herein for oyster and clams and illustrated in Figure 1 are only important for ~6 month period each year.

There are several fates for the residual organic material and nutrients in biodeposits (Figure 1). Any particulate material that is deposited to the sediment surface is subject to degradation by bacterial and metazoa. The details of the process are particularly dependent on local conditions of light (PAR) and oxygen. Both the community of animals that feed on organic detritus (detritivores) and bacteria (aerobic and anaerobic bacteria that function in the presence and absence of oxygen, respectively) can degrade organic biodeposits in the sediments and regenerate DIN and DIP to the water column where it can support additional phytoplankton production.

Where oxygen is present in the surface sediments the bacterial metabolism of PON results in the release of ammonium ions. In the continuing presence of oxygen (aerobic or oxic sediments) bacteria oxidize ammonium first to nitrite, and then nitrate. The process of oxidation of ammonium to nitrate is termed nitrification. A portion of these dissolved inorganic forms (DIN) can be returned to the water column and a portion can diffuse deeper into the sediments to reach anoxic sediments where all oxygen has been depleted by aerobic bacterial respiration. When nitrite and nitrate enter this anaerobic zone then, in a process called denitrification, anaerobic bacteria can use the oxygen from these molecules to sustain their metabolism. The end result is that these molecules are reduced, resulting in the production of nitrogen gas [N₂] which is

released to the atmosphere and NOT retained in the system. Such denitrification is an important mechanism whereby natural bacterial processes found in sediments and marshes can lead to the net removal of nitrogen from the estuary. This is the same process that is harnessed in modern waste water treatment facilities to enhance nitrogen removal. This two-layer, aerobic over anaerobic sediment processing of organic material is illustrated in Box B in Figure 1. Note that in the scenarios illustrated in both Boxes A and B in Figure 1 phosphate is generally immobilized by binding with iron.

In shallower areas (<~ 3 m) there is often sufficient light (a region termed the euphotic zone where PAR can support photosynthesis) to allow benthic microalgae (also termed microphytobenthos) to grow at the sediment water interface. During daylight these microalgae can intercept a large proportion of inorganic nutrients before they are released back up into the water column. This is the scenario illustrated in Box A of Figure 1. These benthic microalgae are a crucial food resource for many mobile and sessile benthic animals. However, if the DIN is returned to the water column then it again becomes available for uptake by pelagic phytoplankton and the process starts all over for a second cycle. So there is an option for the DIN to end up as oyster tissue on the second, third and so on cycles. In this scenario only the nitrogen removed in harvested oysters or clams can be consistently estimated for a possible nutrient credit.

In sheltered locations, tidal and wave generated water currents may not be sufficient to widely disperse the biodeposits generated from shellfish aquaculture farms. In such locations, often characterized by fine grain "muddy" bottoms, then the accumulation of deposits may overwhelm the normal sediment biogeochemical processes. This excess organic material results in stimulation of such intense aerobic bacterial respiration that it exceeds the resupply of oxygen from the overlying water. In such situations even the surface layers of the sediment become anoxic and the resulting accumulation of hydrogen sulfide kills any remaining benthic infaunal organisms, including nitrifying bacteria. This is the scenario illustrated in Box C of Figure 1. The remaining anaerobic bacteria continue to metabolize the residual PON in the biodeposits but only ammonium is released due to the absence of the nitrifying bacteria. The PON and POP are released to the water column as dissolved inorganic forms that can again support phytoplankton production. This is a highly adverse environmental situation requiring immediate changes in farm management practices including reducing the stocking density of animals in the floats, reducing the number of floats or relocating the floats and allowing the area to recover (Newell 2004).

The practical outcome of the above discussion is that at the present time the pathways of processing nitrogen and phosphorus from biodeposits cannot be uniformly predicted for a shellfish population of defined size for a defined time period. The pathways of processing are both location and seasonally specific, and subject to modification by short-term physical disturbance by wind, tide and even storm events. When assessing a nutrient trading value for a shellfish farm the inclusion of calculations describing the fate of biodeposit nitrogen and phosphorus are highly variable – precisely what we do not need for a trading situation and a discussion with a federal agency requiring a precise budgeting approach.

A final note is worthy of consideration with respect to the location of oyster farms in shallow waters and seasonal processes in deeper waters of the Chesapeake Bay. In the summer months the waters of the Bay stratify, that is warmer and less dense water overlays deeper, colder water of higher density. There is generally insufficient wind energy to mix the water column so stable stratification characterizes the water column throughout the summer months, usually with the deeper water becoming depleted in oxygen over the time course of the summer. The depth of greatest density stratification is termed the pycnocline. When bivalves feed in the shallows and deposit PON to aerobic sediments (boxes A and B in Figure 2) this particulate material is prevented from being deposited to sediments beneath the pycnocline, which are generally anaerobic in summer months (as in Box C in Figure 1). In the absence of bivalve feeding, senescent phytoplankton sink and can be advected to the deeper channels where bottom waters are often anaerobic. In such conditions, nitrifying bacteria (that require oxygen) cannot survive and hence coupled processes illustrated in Boxes A and B are precluded. Thus, in such a situation all nitrogen is bacterially remineralized as ammonium (Box C in Figure 2) and available to support further phytoplankton production when it becomes mixed into waters above the euphotic zone. In properly located sites, cultured shellfish populations may facilitate deposition of particulate material to aerobic sediments, and hence form an important control mechanism of particulate organic regeneration, by altering the location where this material is processed (compare Boxes A and B with Box C). When natural oyster stocks were highly abundant in Chesapeake Bay this may once have been a very important ecosystem function. But today, natural stocks are so depleted, and oyster aquaculture not yet extensive, that such processes are very modest in the overall nitrogen cycling in Chesapeake Bay. Continued expansion of shellfish culture would, however, present the opportunity for positive ecosystem effects to become locally important.

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