The Trophic Consequences of Oyster Stock Rehabilitation in Chesapeake Bay

ROBERT E. ULANOWICZ
JON H. TUTTLE
University of Maryland System
Center for Environmental and Estuarine Science
Chesapeake Biological Laboratory
Solomons, Maryland 20688-0038

ABSTRACT: There is mounting speculation that overharvesting of oyster stocks (*Crassostrea virginica*) in Chesapeake Bay may be a factor contributing to the decline in water quality and shifts in the dominance of species inhabiting the estuary. The trophic consequences of increasing the oyster population may be addressed using a simple quasi-equilibrium, mass action model of the exchanges transpiring in the Chesapeake mesohaline ecosystem. According to output from the model, increasing oyster abundance would decrease phytoplankton productivity as well as stocks of pelagic microbes, ctenophores, medusae, and particulate organic carbon. Recently acquired field data on phytoplankton productivity, bacterioplankton, and labile organic carbon in the vicinity of rafted oyster aquaculture support model predictions. The model also indicates that more oysters should increase benthic primary production, fish stocks, and mesozooplankton densities. Hence, augmenting the oyster community by restoring beds or introducing raft culture represents a potentially significant adjunct to the goal of mitigating eutrophication through curtailment of nutrient inputs.

Introduction

Chesapeake Bay possesses the greatest areal extent of mesohaline waters in the United States. Historically, the bay has been the principal market source for the eastern oyster (*Crassostrea virginica*), and over the years the name "Chesapeake Bay" has become synonymous with the word "oyster" in the minds of many Americans. We agree with those who would argue that the pairing of these two terms is much deeper than mere word-association—that the vigor of the Chesapeake ecosystem and that of its oyster stocks are inextricably entwined (Horton 1984; Newell 1988).

Water quality and fisheries production in Chesapeake Bay both have declined dramatically over the past two decades, and intensive efforts are underway to reverse these trends (United States Environmental Protection Agency 1988). The focus of ecosystem rehabilitation has been the curtailment of nutrient inputs to the estuary–particularly those of nitrogen and phosphorous. The goal has been set by the United States Environmental Protection Agency's (EPA) Chesapeake Bay Program to reduce point-source nutrient inputs to the system about 40% by the year 2000. There is strong consensus that such reduction is vital if the bay is to return to an approximation of its former commercial and recreational productivity and to recapture its esthetic appeal. The question remains, however, whether nutrient cutbacks alone are sufficient to restore the Chesapeake ecosystem.

Recent research in aquatic systems (Power 1990; Vanni et al. 1990) has shown that primary production and water clarity are not unambiguously correlated with the amounts of inputs that enter them, but depend as well on the "top-down" influence of predators in the system. Thus, nutrient reduction goals could be achieved in the Chesapeake, but still not result in the intended recovery of the ecosystem.

In particular, attention should be paid to the influence that oysters and other filter-feeding benthos exert on the rest of the ecosystem. Newell (1988), for example, estimated that the pre-1870 oyster stocks in Maryland would have been capable of removing 77% of the 1982 daily carbon production in waters less than 9 m deep. He concluded that oysters were once abundant enough to have been the dominant species filtering carbon from the water column in Chesapeake Bay. Biggs and Howell (1984) compared the rates of water filtering by benthic organisms in Delaware Bay with those of other North American estuaries. On the average, water in Delaware Bay takes at least three times as long to be filtered by bivalves as is the case in any other estuary. Biggs and Howell (1984) speculated that attenuated filtering by bivalves in the Delaware estuary was a strong factor behind the relatively poorer water clarity.

Such evidence, both experimental and anecdotal, has led several investigators to conjecture that primary productivity and water quality in Chesa-

peake Bay could be controlled to some extent by rehabilitating the stocks of benthic filter feeders, particularly those of the oyster (Horton 1984; Tuttle et al. 1987a; Newell 1988; Gerritsen et al. 1989; Jonas and Tuttle 1990; Crosby et al. unpublished data). More recently, Jonas and Tuttle (1991) have conducted a series of experiments with an array of rafted oyster trays and have collected data that bolsters this proposition. (Some of their results will be presented and discussed below.)

Jonas and Tuttle (1991) did not begin by addressing the direct relationship between phytoplankton and oysters. As microbiologists they arrived at their hypothesis through their studies on the inordinately large stocks of pelagic bacteria found in Chesapeake waters (Tuttle et al. 1985, 1987a, b; Jonas and Tuttle 1990). Similarly, others have conjectured that strong indirect relationships might exist between the oyster and other ecosystem populations. Newell (1988), for example, cites anecdotal sources purporting that populations of ctenophores (primarily *Mnemyopsis ledyii*) and especially sea nettle medusae (*Chrysaora quinquecirrha*) historically were much lower at times when oyster stocks were many-fold higher.

It remains to establish causal links between the oyster population and other species inhabiting the Chesapeake. In particular, one wishes to know how each of the other ecosystem functional groups will be affected by changes in oyster populations and by what relative amounts? Questions like these are most frequently addressed by network analysts and ecological modelers. The issues pertain to whole system interactions and therefore require data on the full ensemble of trophic interactions (see also Diaz and Schaffner 1990). Given the considerable labor involved in assembling system-level data, it is not surprising that few collections of such extent exist.

Previous Studies

Perhaps the most complete set of information on Chesapeake trophic interactions was reported by Baird and Ulanowicz (1989). They parsed the ecosystem in the mesohaline reach of Chesapeake Bay into 36 compartments representative of the planktonic, benthic, and nektonic communities, and estimated the annual (and seasonal) exchanges of carbon among all the components. Their annual balance of carbon represents a static view of the ecosystem. Nonetheless, much information about the structure of the system and the functions of various components was obtained from a systematic analysis of the network of exchanges. For example, analysis of their network showed that the oyster population (in fact, the entire suite of benthic filter-feeders) does not engage in any substantial recycling of carbon. Rather, the benthic filter-feeders, along with filter-feeding fishes, shunt carbon (and presumably energy) out of the planktonic community and into the benthic-nektonic complex.

Ulanowicz and Puccia (1990) developed a method for estimating the asymmetric consequences of any trophic exchange to both the predator and prey species involved. Thereafter they invoked input-output analysis techniques to calculate the indirect effects of the exchanges as they ramify through the trophic network. In so doing they estimated the entire suite of indirect competitions and mutualisms as may exist in the community.

Several interesting indirect interactions arise out of this analysis, but few involve the oyster. Most interestingly, there is a three-member "autocatalytic" loop of indirect mutualisms that exists among the phytoplankton standing stock, the ctenophores, and the suspended particulate organic carbon (POC). The interactions among this triad appear to constitute a syndrome of mutualistic, esthetically displeasing components indicative of a highly-eutrophic estuarine ecosystem. A few other indirect effects bear upon the modeling analysis that will follow: The filter-feeding fishes appear to be in strong competition with the gelatinous zooplankton (ctenophores and medusae) for their common mesozooplankton resource, and the current advantage in this competition appears to lie with the gelatinous species. The analysis of Ulanowicz and Puccia (1990) further shows that many of the carnivorous fishes are mutualistically coupled to the sediment POC.

The analysis does show that the oyster population may have a slight potential to decrease phytoplankton and bacteria stocks and to augment benthic primary production, as Tuttle et al. (1987a) have speculated. Not too surprisingly, the quantitative network analysis also reveals significant competition between oysters and other benthic and epizooitic filter-feeders. There is little evidence from static calculations that oyster densities have much effect upon the gelatinous zooplankton. In fact, the macrozooplankton seem to exert a mildly beneficial indirect trophic influence upon the oyster population.

Parallel to, but entirely independent of the foregoing network analysis, a small field program has been conducted to investigate the effects of oyster filtering upon ambient water quality. The oyster raft field site, maintained by the St. George Oyster Co., was situated ca. 25 m offshore from the northwestern bank of St. George's Creek, located in southern St. Mary's County, Maryland. Individual oyster rafts consisted of rectangular, plastic commercial bread trays (ca. 0.9 m × 0.6 m × 0.15 m

deep) in which the oysters were retained by plastic-covered wire mesh. Styrofoam sheets, affixed to the open tops of the trays by mesh straps, prevented the oysters from spilling during handling and rough weather, and provided flotation. The experimental raft array consisted of four rows of 20 rafts each, moored to the bottom by rope lines parallel to the shore. The rows were separated by ca. 1 m of open water to permit passage of a small boat for sampling and oyster care. The entire array covered about 200 m^2 of water surface with an oyster population of 60,000 individuals (750 oysters per tray).

The experimental raft array was located upstream from an extensively rafted aquaculture area. To minimize the influence of these additional oyster rafts, water was sampled just after high tide when flow was from the unrafted headwater portion of the creek through the experimental rafts. Water samples were collected with a hand-operated vacuum pump from 0.1 m depth along a transect of five approximately equidistant sites, beginning at the upstream end of the experimental array between the middle rows of rafts and ending at the downstream terminus. Mean water depth along the transect was ca. 0.6 m. A second, five-site transect (ca. 1.2 m mean depth), located about 10 m offshore from and parallel to the raft area transect, served as an unrafted control area. Among the measurements made on the samples were primary production, chlorophyll, bacterial abundances and production, and biological oxygen demand. These measurements are discussed below in parallel with the results of the ecosystem model.

The Quasi-Equilibrium Model

The network analysis revealed what many had suspected: in their current depleted state the oyster stocks are not a central player in the trophic dynamics of the Chesapeake ecosystem. That, of course, is not the hypothesis under consideration, which is that oysters once were and once again can become key agents in structuring the bay's ecosystem (Newell 1988). To address that issue it becomes necessary to ask "what if" questions, for example, "What if oyster stocks were significantly increased? Would that tend to restore the historical trophic balance?" In a system that probably includes nonlinear feedback loops, it is not possible to answer such "what if" questions with any degree of confidence by analyzing only the static configuration. In addition one must assume some type of dynamics for the system and employ them in a quantitative model to give some indication how the system might respond to "what if" scenarios.

The Baird-Ulanowicz network was intended to concentrate on trophic interactions. it contains no explicit information that would allow one to model the effects of changes in temperature, light regime, or available space on trophic interactions. Accordingly, the dynamical model to be developed will address explicitly only the trophic consequences of particular changes in stocks or interactions. Of course, abiotic conditions do affect the measured stocks and exchanges, but their influences will be assumed embedded in the values of the dynamical constants calculated from these measurements.

Having thus delimited attention to only trophic interactions, we wish mathematically to describe these interchanges in as simple and nonredundant fashion as possible. Early efforts to model the Baird-Ulanowicz network revealed that the interactions among 36 species were too easily destabilized by small parameter changes. Thus, we aggregated the Baird-Ulanowicz network into the more tractable (stable) 13-compartment configuration shown in Fig. 1. All the fishes have been condensed into only two compartments—filter feeding and carnivorous. Also, all pelagic microbiota were combined into a single grouping, as were the deposit feeders (including meiofauna).

The material balance on these 13 groupings is cast around each node as

(amount of carbon in) − (amount of carbon out)
= (rate of carbon accumulation).

Or, in mathematical terms

$$\left(\sum_{j=1}^{n} T_{ji} + I_i\right) - \left(\sum_{k=1}^{n} T_{ik} + E_i + R_i\right) = \frac{dM_i}{dt} \quad (1)$$

where M_i = biomass in compartment i, T_{ji} = flow from j to i, I_i = exogenous input into i, E_i = usable export from i, R_i = dissipation (respiration) from i, i, j, k = 1, 2, 3, . . . , n, and n = the number of system components (13 in this case). Before proceeding with any type of rudimentary forecasting, it is necessary to assume how the flows on the left-hand side of Eq. 1 might be expressed in terms of the biomasses, M_i. Such mathematical assumptions are called the "constitutive relations" and prescribe the dynamics of the model.

Perhaps the simplest function that models the bidirectional propagation of trophic influence is the Law of Mass Action, originally used to model chemical reactions,

$$T_{ik} = \beta_{ik} M_i M_k \quad (2)$$

where the β_{ik} form a set of proportional constants. A model consisting of bilinear forms like Eq. 2 is usually neutral in its stability and tends to behave in oscillatory fashion. All nonfeeding flows are usually insensitive to the magnitudes of the receiving compartments. Therefore, we choose to model
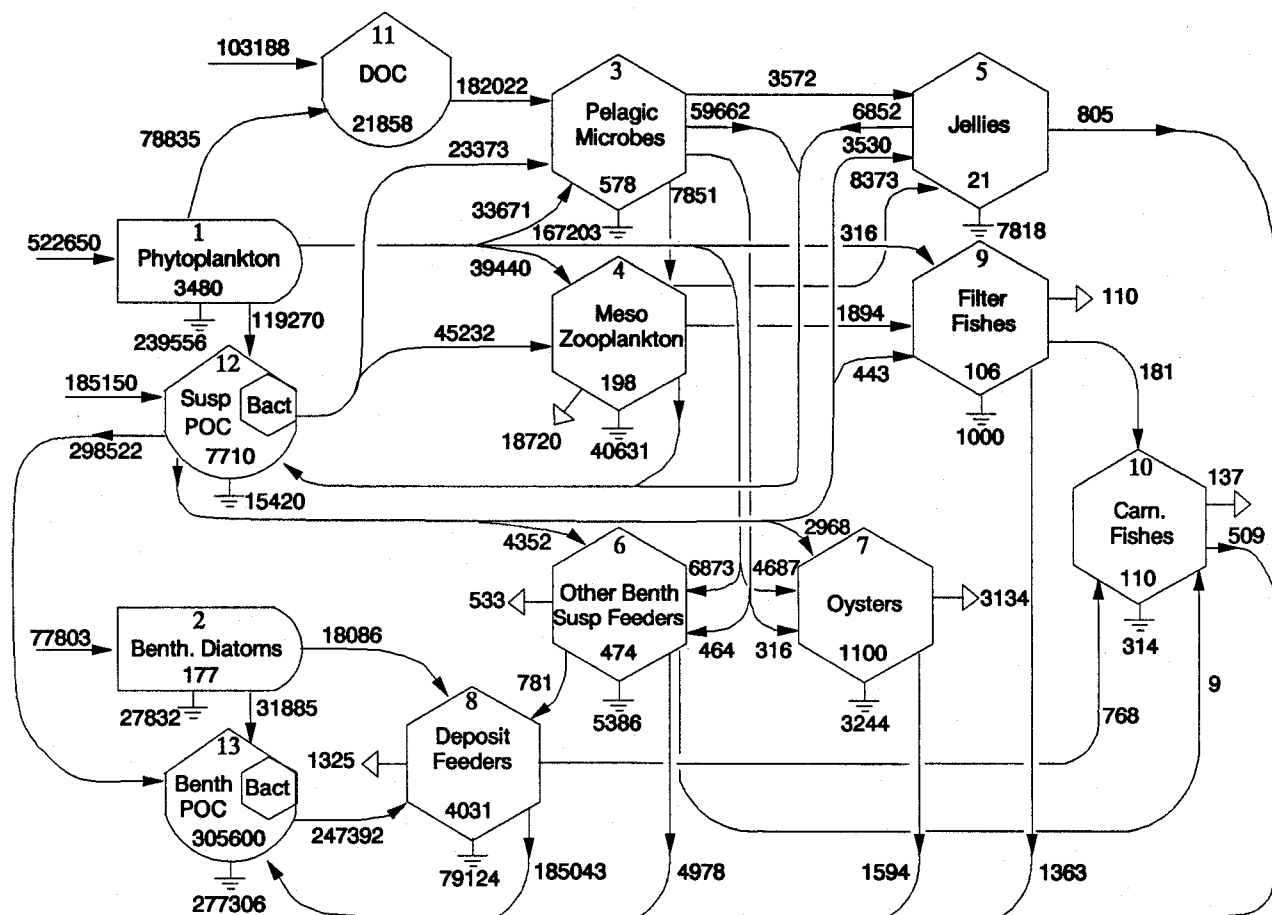
Fig. 1.   Carbon flows (mg m⁻²yr⁻¹) and stocks (mg m⁻²) for 13 components of the mesohaline Chesapeake Bay ecosystem. Ground symbols represent respirations; open arrows, exports. This network is an aggregated version of the annual budget appearing in Fig. 7 of Baird and Ulanowicz (1989).

these passive transfers using donor-controlled kinetics,

$$T_{ik} = \alpha_{ik}M_i \qquad (3)$$

Donor control terms impart a modicum of stability to a system that might otherwise remain only neutrally stable. Because the recipients of the exports are usually left unspecified, the E_i either can be assumed constant or modeled by linear, donor-controlled kinetics. The latter option will be employed here. Finally, there are the exogenous inputs. They can be assumed to be constant source flows, or else one could make them proportional to the stocks in the recipient compartment,

$$T_{ik} = \alpha'_{ik}M_k \qquad (4)$$

where α'_{ik} is a different constant than the α_{ik} in Eq. 3. Relationship Eq. 4 probably is a reasonable assumption for primary producers whenever carbon does not limit production. Recipient control does tend to destabilize the system, but in the present case it is not enough to tip the balance.

With the constitutive relations now specified, the balance (Eq. 1) now looks like:

$$\sum_{j=1}^{n} \beta_{ij}M_iM_j + \sum_{k=1}^{n} \alpha'_{ik}M_k + \sum_{m=1}^{n} \alpha_{mi}M_m + \phi_i = \frac{dMi}{dt}$$
$$(5)$$

If one has estimates for all the flows and biomasses, one can employ Eq. 2, Eq. 3, or Eq. 4 as appropriate to calculate all the nonzero β's and α's. (The ϕ's represent those net imports or exports that were assumed to remain constant.) For example. Fig. 1 shows that 39,440 mg C m⁻² y⁻¹ of phytoplankton are grazed by the mesozooplankton. As the average standing stocks of phytoplankton and zooplankton are 3,480 mg C m⁻² and 198 mg C m⁻², respectively, the value for β_{14} in Eq. 2 works out to be 5.72×10^{-2} m² mg C⁻¹ y⁻¹. (Many of the other nonzero β's and ϕ's are composites from more than one flow, but calculating them is a matter of straightforward bookkeeping.)

Manifold effects from various processes are compressed into any single parameter value in Eq. 5.

For example, the value for β_{14} calculated above includes such effects as copepod filtering rates, encounter probabilities for phytoplankton and zooplankton, patchiness, seasonal temperature pattern, etc. By holding β_{14} constant, one is thereby assuming that the overall effect of this constellation of factors affecting grazing (some of which interact in compensatory ways) remains the same.

Flows around all compartments in Fig. 1 balance over the depicted annual cycle. Accordingly, the right-hand side of Eq. 5 vanishes, and the set of first-order, quadratic, ordinary differential equations at equilibrium becomes a collection of simultaneous quadratic algebraic equations,

$$\sum_{j=1}^{n} \beta_{ij} M_i M_j + \sum_{k=1}^{n} \alpha'_{ik} M_k + \sum_{m=1}^{n} \alpha_{mi} M_m + \phi_i = 0 \tag{6}$$

that characterize that particular stationary point. (The word "equilibrium" is used here in its mathematical context and carries no thermodynamic connotations.)

One could proceed by integrating Eq. 5 under various sets of changed parameters or initial biomasses to study the "predicted" behaviors of the system. It is unclear, however, precisely what meaning any predicted intra-annual changes to an annual balance would have. Rather, at this stage of approximation, one is more interested in whether the system ultimately can accommodate a particular parameter change. The following "quasi-equilibrium" analysis should address this question. (1) Choose an appropriate change in a single parameter that one expects will mimic the desired perturbation. (2) Keep all other parameters constant, that is, all the effects incorporated in the parameters as calculated from the "typical" balance are assumed to remain unchanged. (3) Increment the chosen parameter by a small fraction (e.g., 1%) of its original value and attempt to solve Eq. 6 for the biomasses of the slightly perturbed system. (4) If a new equilibrium (solution) with all positive biomasses is found, continue to increment the given parameter either until the desired amount of parameter change has been achieved or until a major system collapse occurs. (5) During the course of the iteration in step (4), it may happen that a particular species goes extinct (falls below zero). At such point, the extinct species is decoupled from the rest of the system, and the iterative solutions are continued. Often a system will continue to yield sensible solutions after the extinction of one or two species, but eventually the point is reached where numerous extinctions occur simultaneously, signaling general system collapse.

The set of nonlinear equations (Eq. 6) is solved using the multiple Newton-Rhapson method (Press

et al. 1986). The system of 13 equations could have up to 26 distinct roots. The Newton-Rhapson method converges most quickly when one is in the vicinity of a known root, and it could happen that if a parameter value were changed too suddenly, the solution might converge to a spurious root. This explains the method of slow "deformation" employed in step (4) which keeps the system always near a known, plausible solution.

Doubtless, some readers may feel that the approximations made in this quasi-equilibrium model of trophic response are much too crude. The model has the nature of an engineering "back-of-the-envelope" type of calculation. For any particular change in the dynamics, this method yields a zero-order estimate of what the trophic implications (and *only* the trophic consequences) might be. The sole justification for such a rough approximation is that it seems to give plausible results that accord with available evidence, as will be discussed below.

Results

To apply the quasi-equilibrium model to oyster rehabilitation, we began by choosing a "strategy" to increment oyster stocks. We chose to decrease the catch per unit stock. The nominal value of the rate of exploitation is $3,134$ mg m^{-2} yr$^{-1}/1,100$ mg m$^{-2} = 2.85$ yr^{-1} (Fig. 1). As outlined in step (4), this rate was gradually decreased by 1% intervals, and the balance was recalculated after each such decrement. Very early during this iteration, compartment 6 (other benthic suspension feeders) went extinct. This unrealistic extinction is thought to be an artifact of the assumptions that Baird and Ulanowicz (1989) used in estimating in their network. They had assumed identical diet rations for all three compartments used to represent the benthic filter feeders. In retrospect, this assumption appears unrealistically to exaggerate the degree of niche competition among the benthic filter feeders.

Despite such an inauspicious beginning, further decreases in the exploitation rate did not create additional difficulties until the decrement reached 25%, at which point the gelatinous zooplankton went extinct. Further exercise of the model beyond that harvest rate resulted in progressively more improbable predictions, so the final balance was cast for a 23% reduction in exploitation rate, that is, just before the gelatinous zooplankton became extinct. The predicted biomasses and exchanges are shown in Fig. 2; all trophic parameters remain the same in both Figs. 1 and 2, save for the oyster exploitation rate.

The most obvious result of the decreased exploitation rate was that the oyster stocks (and the accompanying catch) increase by 150% over their
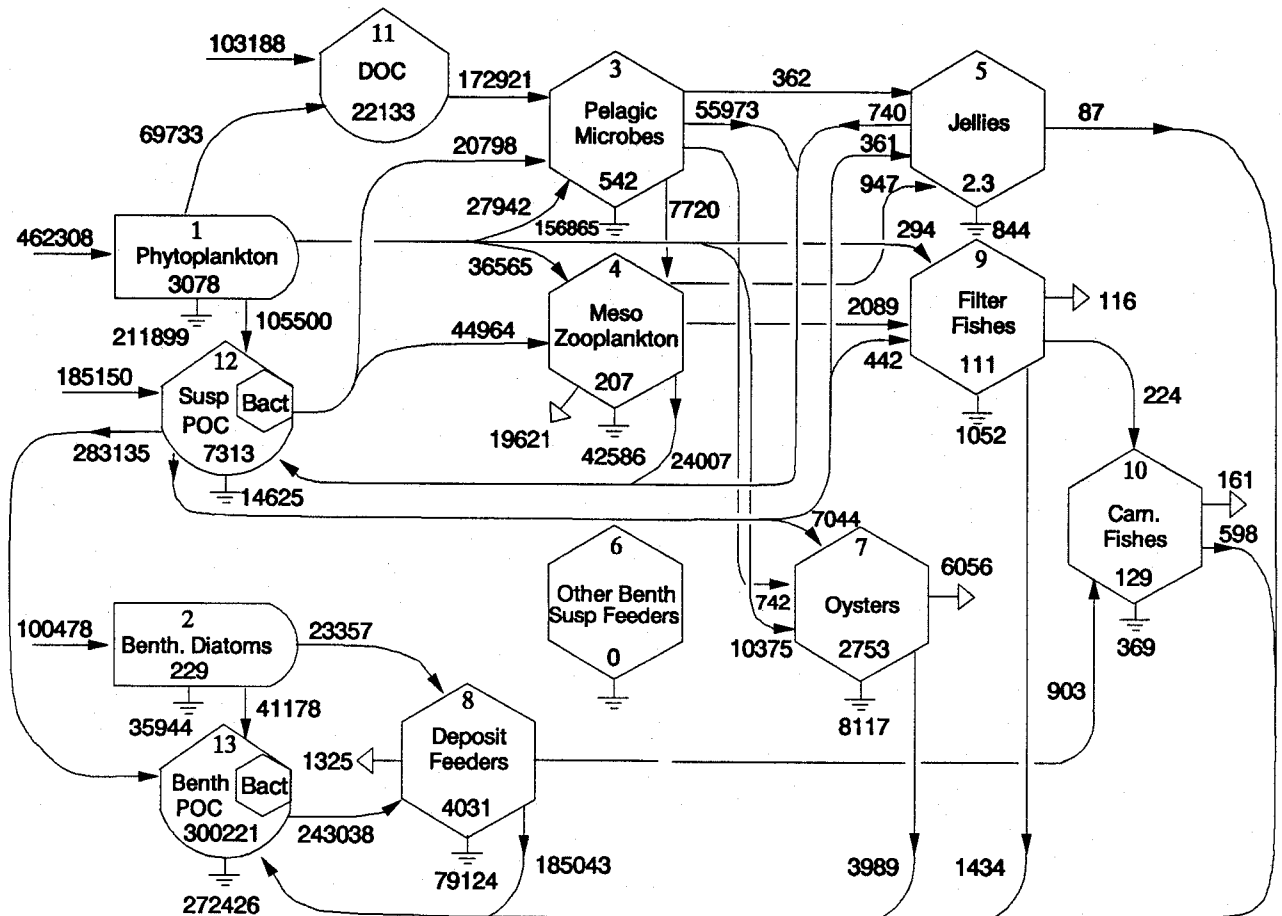
Fig. 2.   Predicted trophic consequences of decreasing the oyster exploitation rate per unit stock by approximately 23%. Carbon flows are expressed in mg m^{-2} yr^{-1}, and stocks are expressed in mg m^{-2}.

original values (Fig. 2). That a decrease in the exploitation rate should lead to an increase in yield indicates that oyster stock is being heavily overfished relative to the optimal level of exploitation that could be supported by the trophic web. This result derives only from considerations of food availability and was not influenced by the details of oyster recruitment, which likely would modify the quantitative (but probably not the qualitative) outcome.

The decrease in primary productivity (Fig. 2) accords with the predictions by Tuttle et al. (1987a) that phytoplankton biomass and production should fall as oyster stocks rise. Phytoplankton productivity fell by 12%, but was partially compensated by a 29% increase in benthic primary production. The overall primary production fell by 6%. The shift from water column productivity to benthic photosynthesis would reverse the trend that has characterized the past two decades of increasing eutrophication and has culminated in the virtual disappearance of submerged aquatic vegetation.

This vegetation was not included in the Baird and Ulanowicz network because it comprised an insignificant fraction of baywide benthic photosynthesis during the years 1984–1985. Had it been included, it likely would have increased as oyster stocks rose.

The two components most negatively affected in the simulation of oyster rehabilitation are the other benthic suspension feeders and the gelatinous zooplankton. As mentioned above, earlier network analysis indicated a potential for strong competition between oyster stocks and other benthic filterers. There is certainly no reason to believe that other bivalves actually would be driven to extinction. After all, they have managed to coexist with the oyster over the eons. One could expect, however, some competition with the oyster for sustenance.

The cropping of phytoplankton by oysters apparently interferes with the autocatalytic relationship among phytoplankton, gelatinous zooplankton, and suspended POC. The strength of this indirect mutualism decreases almost 8-fold in the

TABLE 1. Percentage changes in stocks of the compartments in Fig. 1 that are induced by a 23% reduction in the rate of oyster exploitation per unit biomass.

Compartments	Percentage Change
Increments	
Oysters	+150.2
Benthic diatoms	+29.1
Carnivorous fishes	+17.5
Filter feeding fishes	+5.2
Mesozooplankton	+4.8
DOC[a]	+1.3
Decrements	
Gelatinous zooplankton	−89.2
Phytoplankton	−11.5
Pelagic microbes	−6.2
Suspended POC[b] & bacteria	−5.2
Sediment POC[b] & bacteria	−1.8

[a] DOC = dissolved organic carbon.
[b] POC = particulate organic carbon.

oyster-augmented community. This drop in support for the gelatinous zooplankton apparently tips the competition for mesozooplankton between filter-feeding fishes and gelatinous zooplankton in favor of the former. Thus, the stocks of planktivorous fishes increase by 5% along with stocks of oyster.

The response of the mesozooplankton populations to higher oyster stocks is quite interesting. Herbivorous production by this size class actually falls by 4%, presumably in response to decreased productivity by its food source, the phytoplankton. The remaining secondary production, however, is being utilized better by the fish populations. The fraction of mesozooplankton production eventually reaching the planktivorous fishes via all pathways (as calculated by the method of Szyrmer and Ulanowicz [1987]) increases from 72% to 75% as oyster stocks rise. The corresponding increase in zooplankton carbon that reaches the carnivorous fishes is from 18% to 19%. Apparently, some of the mesozooplankton production disencumbered by the smaller reduction in macrozooplankton grazing pressure goes into stock maintenance, because the standing stock of mesozooplankton increases by 5% after oyster rehabilitation.

The conjecture by Tuttle et al. (1987a) that bacterial standing stocks and associated POC densities would diminish as oyster filtering increases accords with the output of the model. The density of pelagic microbes falls by 6% in the presence of more oysters, whereas stocks of suspended and sediment POC (as well as their associated microflora) decline by 5% and 2% respectively.

Little confidence should be attached to the quantitative magnitudes of the biomass changes induced by oyster replenishment (Table 1), but evidence supporting the qualitative nature (directions and relative magnitudes) of some of these predicted shifts is provided by recently collected field data (Table 2). Within a rafted oyster aquaculture plot, phytoplankton standing stocks and production were about half those of adjacent unrafted water (Table 2). Total pelagic bacterial abundances, as predicted by the model (Table 1), were less affected, and their production and metabolism showed hardly and differences between rafted and unrafted areas. Heterotrophic bacterioplankton growth and metabolism in the mesohaline bay appear to respond primarily to labile DOC, as assessed by measurements of dissolved biochemical oxygen demand (BOD, Jonas and Tuttle 1990). Also in agreement

TABLE 2. Changes in phytoplankton, bacteria, and organic carbon in oyster raft areas compared to open waters adjacent to the aquaculture rafts. Data are averages of transect means from five sample collections (late May to early October 1989). Methods used to measure each of the listed parameters are given in Tuttle et al. (1987a) and Jonas and Tuttle (1990). Key: (+) = increase, (−) = decrease in raft area.

Parameter	Units	Oyster Rafts	Outside Raft Area	Average Percent Change
Total chlorophyll	$\mu g\ l^{-1}$	9.7	17.3	−50
Chlorophyll <10 μm	$\mu g\ l^{-1}$	7.6	12.3	−45
Phaeopigment/chlorophyll	Percent	29.9	13.9	+417
Bacterial abundance				
Total cells	number ml^{-1} (xE6)	15.6	19.1	−19
Cells >2 μm	number ml^{-1} (xE6)	0.2	0.4	−37
Cells 1–2 μm	number ml^{-1} (xE6)	1.4	2.2	−41
Biochemical oxygen demand				
Total	mg C m^{-3}	939	1,297	−30
Particulate	mg C m^{-3}	420	708	−47
Dissolved	mg C m^{-3}	519	588	−9
Primary production	mg C $m^{-3}\ d^{-1}$	386	647	−44
Bacterial production	mg C $m^{-3}\ d^{-1}$	235	235	−1
Glucose turnover rate	Percent h^{-1}	10.5	10.8	−3

with the model, particulate BOD (labile POC) was influenced more than dissolved BOD by increased oyster stocks. As a point of reference, particulate BOD (5-d incubations) accounts for 26–44% of euphotic zone POC during the spring and summer in the mesohaline bay (Jonas and Tuttle 1990). Therefore, we expect POC differences (labile and refractory carbon) resulting from increased oyster stocks to be less than that found for particulate BOD. Unfortunately, the open creek rafted oyster aquaculture experiment was too small in areal extent and sampled over too short an interval to allow for meaningful measurements of changes in the stocks of other trophic components or for adequate determination of mass balances. Semi-enclosed model field systems need to be established to adequately refine and quantitatively test the ecosystem model.

What is most striking about the pattern of changes (Table 1) is how well it accords with a shift toward a more desirable state of the estuary. There is an undocumented but strong consensus that increases in oyster stocks, fishes, mesozooplankton, and benthic flora, when accompanied by declines in the gelatinous zooplankton, phytoplankton, bacteria, and POC would constitute a decided improvement in the trophic status of the bay. That is, most would deem the ecosystem depicted in Fig. 2 to be preferable to the present conditions portrayed in Fig. 1. Therefore, oyster rehabilitation should provide environmental benefits that extend beyond the oyster industry itself.

Conclusions

The model used here to forecast trophic changes is exceedingly simplistic. Nevertheless, it appears capable of simulating the rudiments of nonlinear feedback behavior and provides unanticipated, but qualitatively plausible results that appear to be supported by the available experimental evidence.

Although oysters currently play a minor role in the Chesapeake mesohaline ecosystem, this exercise gives yet another reason to believe that their influence on community structure was once much greater. All available indications are that the oyster population is capable of exerting top-down control on the pelagic ecosystem in such a way as to depress the level of pelagic primary productivity while at the same time amplifying the delivery of that production to those species deemed more useful to society.

The major symptom of ecosystem distress in Chesapeake Bay is its overabundant phytoplankton production. The current efforts to mitigate this problem attack it from the supply-side, that is, by trying to reduce nutrient inputs. Such a strategy is well-advised, but possibly insufficient. The results

of this exercise lend credence to Tuttle et al.'s (1987a) hypothesis that overproduction also should be attacked from the demand side. Reductions in nutrients alone very probably will not clear up Chesapeake waters and restore their commercial and recreational productivity, so long as stocks of benthic filter feeders continue to be overexploited. Artificial means of increasing oyster populations, such as raft culture, can be economically self-sustaining and also would provide much needed rehabilitation to a beleaguered ecosystem.

LITERATURE CITED

BAIRD, D. AND R. E. ULANOWICZ. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59: 329–364.

BIGGS, R. B. AND B. A. HOWELL. 1984. The estuary as a sediment trap: Alternative approaches to estimating its filtering efficiency, p. 107–129. *In* V. S. Kennedy (ed.), The Estuary As a Filter. Academic Press, Orlando, Florida.

DIAZ, R. J. AND L. C. SCHAFFNER. 1990. The functional role of estuarine benthos, p. 25–56. *In* M. Haire and E. C. Krone (eds.), Perspectives on the Chesapeake Bay 1990. Chesapeake Research Consortium, Gloucester Point, Virginia.

GERRITSEN, J., A. RANASINGHE, AND A. F. HOLLAND. 1989. Comparison of three strategies to improve water quality in the Maryland portion of Chesapeake Bay. Report to the Maryland Department of Natural Resources, Annapolis, Maryland. Appendix C. 20 p.

HORTON, T. 1984. Oysters' brief "survival season" is focus of studies, p. 1C. *Baltimore Sun* August 5, 1984. Baltimore, Maryland.

JONAS, R. B. AND J. H. TUTTLE. 1990. Bacterioplankton and organic carbon dynamics in the lower mesohaline Chesapeake Bay. *Applied Environmental Microbiology* 56:747–757.

JONAS, R. B. AND J. H. TUTTLE. 1991. Improving Chesapeake Bay water quality: Influences of rafted oyster aquaculture on microbial processes and organic carbon. p. 323–329. *In* J. A. Mihursky and A. Chaney (eds.), New Perspectives on the Chesapeake Bay. Publication #137, Chesapeake Research Consortium, Solomons, Maryland.

NEWELL, R. I. E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? p. 536–546. *In* M. P. Lynch and E. C. Krome (eds.), Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Solomons, Maryland.

POWER, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.

PRESS, W. H., B. P. FLANNERY, S. A. TUKOLSKY, AND W. T. VETTERLING. 1986. Numerical Recipes: The Art of Scientific Computing. Cambridge University Press, New York. 818 p.

SZYRMER, J. AND R. E. ULANOWICZ. 1987. Total flows in ecosystems. *Ecological Modelling* 35:123–136.

TUTTLE, J. H., R. B. JONAS, AND T. C. MALONE. 1987b. Origin, development and significance of Chesapeake Bay anoxia, p. 442–472. *In* S. K. Malumdar, L. W. Hall, Jr., and H. M. Austin (eds.), Contaminant Problems and Management of Living Chesapeake Bay Resources. Pennsylvania Academy of Sciences, Philadelphia.

TUTTLE, J. H., T. MALONE, R. JONAS, H. DUCKLOW, AND D. CARGO. 1985. Nutrient-dissolved oxygen dynamics: Roles of phytoplankton and microheterotrophs under summer conditions. Report to United States Environmental Protection Agency. University of Maryland [UMCEES] CBL 85-39. Chesapeake Biological Laboratory, Solomons, Maryland. 121 p.

TUTTLE, J. H., T. MALONE, R. JONAS, H. DUCKLOW, AND D. CARGO. 1987a. Nutrient-dissolved oxygen dynamics: Roles of phytoplankton and microheterotrophs under summer conditions, 1985. Report to United States Environmental Protection Agency. Annapolis, Maryland. CBP/TRS3/87. 158 p.

ULANOWICZ, R. E. AND C. J. PUCCIA. 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5:7–16.

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY. 1988. 1987 Chesapeake Bay Agreement, 37 p. Comprehensive Research Plan, an Agreement Commitment Report from the Chesapeake Bay Executive Council, 12 p. United States Environmental Protection Agency, Annapolis, Maryland.

VANNI, M. J., C. LUECKE, J. F. KITCHELL, Y. ALLEN, J. TENTE, AND J. J. MAGNUSON. 1990. Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335.