

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Oyster food supply in Delaware Bay: Estimation from a hydrodynamic model and interaction with the oyster population

by **Eric N. Powell^{1,2}, Danielle A. Kreeger^{3,4}, Jason M. Morson¹, Dale B. Haidvogel⁵, Zhiren Wang⁵, Roger Thomas⁴ and Jennifer E. Gius¹**

ABSTRACT

To evaluate oyster food supply, water samples were collected at fifteen sites in Delaware Bay near-monthly in 2009 and 2010. Food was estimated as the sum of particulate protein, labile carbohydrate, and lipid. Delaware Bay shows a typical spring bloom, centered in March and April, with declining food supply thereafter into early fall, followed sporadically by a minor fall bloom. The geographic and temporal structure of food was more predictable in summer to early fall, and considerably less predictable in spring. Five variables each based on temperature and the spatial and temporal variability of temperature were significant contributors to a multiple regression ($R^2 = 0.28$). Cluster analysis on residuals identified two large groups of sites, one comprising most sites on the eastern side of the bay including all of the sites on the New Jersey oyster beds downestuary of the uppermost beds and one including most of the sites along the central channel and waters west. Food values over the New Jersey oyster beds were often depressed by as much as 50% relative to the bay-wide mean. Food values did not follow an upestuary-downestuary trend anticipated from the salinity gradient. Rather, the differential was cross-bay and was distinctive throughout the estuarine salinity gradient, thus explaining the lack of significance of any salinity-related variable in the multiple regression. The consequence is that food supply cannot be sufficiently predicted or modeled based on observed environmental variables or those predicted from a hydrodynamic model. The cross-bay differential cannot be extracted from such datasets. The oyster reefs of Delaware Bay are dominantly sited on the New Jersey side, where food supply was most depressed and where passive particle residence times were longest. While not conclusive, this dataset suggests that oysters can influence food values on the New Jersey side of the bay at present biomass, and this would explain the cross-bay gradient in food values as an outcome of oyster feeding.

1. Rutgers University, Institute of Marine and Coastal Sciences and The New Jersey Agricultural Experiment Station, Haskin Shellfish Research Laboratory, Port Norris, New Jersey, 08349, U.S.A.

2. Corresponding author. *email: eric@hsrl.rutgers.edu*

3. Partnership for the Delaware Estuary, Wilmington, Delaware, 19801, U.S.A.

4. Patrick Center for Environmental Science, Academy of Natural Sciences, Philadelphia, Pennsylvania, 19103, U.S.A.

5. Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey, 08901, U.S.A.

1. Introduction

The importance of food supply for larval and adult bivalves is widely recognized; however, little direct evidence exists for food limitation within estuaries, either for adult or larval stages. The influence of food quantity and quality on larvae is strongly influenced by the recognized importance of lipids in larval diets to permit successful growth and metamorphosis (e.g., Gallagher and Mann, 1986; Pernet *et al.*, 2003; Nevejan *et al.*, 2003; Fernández-Reiriz *et al.*, 2006). Modeling work has provided support for the belief that food quantity and food quality are very important for larval success (e.g., Bochenek *et al.*, 2001; Powell *et al.*, 2002, 2004; Hofmann *et al.*, 2004) and these modeling studies have drawn upon a range of experimental literature (e.g., Thompson and Harrison, 1992; Strathmann *et al.*, 1993; Thompson *et al.*, 1996; Baldwin and Newell, 1995; Hendriks *et al.*, 2003) in aggregate supporting this contention, but direct field evidence is limited (e.g., Bos *et al.*, 2006).

Research focused on the adult stage has centered much more on food quantity rather than quality in most estuarine situations (Frechette and Bourget, 1985; Smaal *et al.*, 1986; Peterson and Black, 1987; Powell *et al.*, 1995; Wilson-Ormond *et al.*, 1997), although food quality likely plays a role (e.g., Kreeger 1993; Kreeger and Newell, 2000; Pernet *et al.*, 2003; Hendricks *et al.*, 2003; Carmichael *et al.*, 2004). Although the fact that bivalves may compete for food is well known, the management of stocks has not often included food supply as an input variable beyond the obvious issue of carrying capacity in aquaculture applications (e.g., Honkoop and Bayne, 2002; Hadley and Manzi, 1984; Crenshaw *et al.*, 1996; Gargnery *et al.*, 2001). The ability of bivalves, in sufficient quantity, to exert top-down control on phytoplankton in estuarine environments is well established, however (e.g., Officer *et al.*, 1982; Cloern, 1982; Hily, 1991; Newell, 2004; Freitas *et al.*, 2009) and leads one to consider classic carrying capacity-based biological reference points in managing bivalve fisheries (Powell *et al.*, 2009a,b).

The population dynamics of oysters has been considered mostly as a product of the influence of temperature and salinity. These environmental conditions dominantly modulate the mortality rate of juveniles, primarily through predation (e.g., Engle, 1953; Carriker, 1955; Stickle, 1985), and adults, primarily through disease (Soniati, 1985; Andrews, 1988; Burreson and Ragone Calvo, 1996). Some consideration has been given to population processes, particularly the relationship between broodstock and recruitment and population abundance and mortality (Southworth and Mann, 1998; Kimmel and Newell, 2007; Powell *et al.*, 2009b). Very little consideration has been given to the influence of food supply, beyond the suggestion that food supply may modulate the disease process (Powell *et al.*, 1996; Soniati *et al.*, 1998; Ford *et al.*, 1999). Consideration of the food resource in management has rarely if ever occurred, nor has environmental planning often included a rigorous evaluation of the potential for changes in food supply to impact oyster population dynamics. We consider here the adequacy of the “environmental-only” assumption in modeling oyster population dynamics, in which environmental change is considered solely from the standpoint of temperature and salinity and ask the question: should we and can we easily include food supply in such an evaluation?

To do so, bivalve food supply was monitored for two years in Delaware Bay over a geographically distributed set of sampling sites in order to develop information from which to assess the potential of such data in informing the stock assessment program for the oyster industry (Powell *et al.* (2008) provide a description of the assessment dataset). The program interfaced with an ongoing modeling program for the bay that included the implementation and verification of the ROMS (Regional Ocean Modeling System) hydrodynamic model [Wang *et al.* (this issue); see Shchepetkin and McWilliams (2005) and Haidvogel *et al.* (2008) for additional information on ROMS]. The abundance of oysters has varied at least 5-fold in Delaware Bay over the last 50 years (Powell *et al.*, 2008), with the suggestion that food supply has been limiting for at least some of that period (Powell *et al.*, 2009b). Concerns have been raised as to the influence of climate change on this system. One obvious approach would be to examine the hydrodynamics under future conditions of higher sea level and warmer temperatures and estimate that influence on the success of oyster larvae and the adult populations. Bay-wide modeling of this type remains in its infancy; however, a number of recent efforts have shown that certain changes in hydrodynamics may trigger substantive changes in oyster population structure, while others do not (e.g., Klinck *et al.*, 2002; Powell *et al.*, 2003). Outcomes from these models are inhibited, however, by the necessity of using a static food resource, even if geographically and temporally variable (e.g., Deksheniaks *et al.*, 2000), in that the spatial and temporal relationships of the food resource do not vary with future environmental outcomes established by the changing hydrodynamics and hydrologies.

Here we ask two related questions. First, can the bivalve food supply be inferred from variables predicted by the hydrodynamic model without recourse to a more complex food-web model? If so, then food supply can be allowed to vary according to the outcome of hydrodynamic simulations and a more realistic evaluation of the influence of differential hydrodynamics on bivalve success will be possible. Second, does evidence exist to suggest that bivalve (oyster) populations exert a significant top-down control on phytoplankton stocks in Delaware Bay today? If so, then the management of the bay's oyster populations and the inferences from simulations of future climatologies must take into account the interaction between the bivalve resource and its food supply.

2. Methods

a. Field sampling program

To examine food availability and water quality, water samples were collected at fifteen sites in Delaware Bay once every month in 2009 and 2010, with the exception of February and December (Fig. 1). Sites were accessed via the F/V *Dredge Monster*. At each site, three replicate 1-gallon jugs of water were retrieved from 30.5 cm below the surface with an *Eheim Universal Model 1048* submersible pump and flexible rubber tubing. In addition, using a YSI 85 thermistor and a refractometer, data were collected on temperature and salinity at all sites. Jugs of water were kept at ambient temperature in coolers while being transported back to the laboratory.

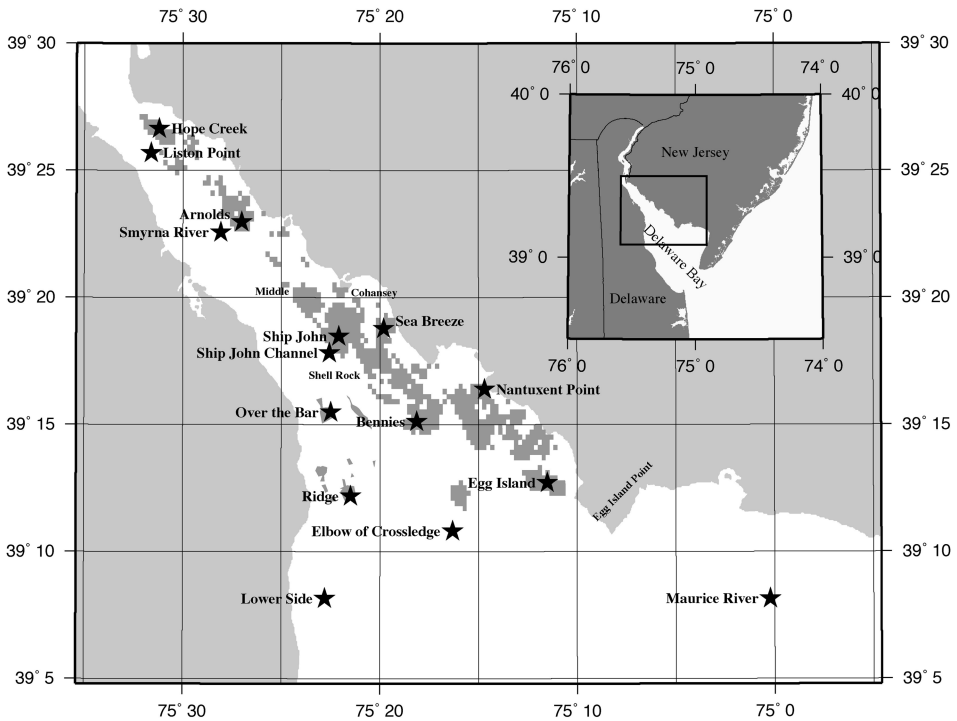


Figure 1. Map of Delaware Bay showing the location of the 15 sampling sites, names in large font, and the location of other oyster beds and locales mentioned in the text, names in small font.

b. Laboratory analyses

The concentration of particulate protein, labile carbohydrate, and lipid was measured using various published methods as adapted by Kreeger *et al.* (1997). Particulate matter was first passed through a 53- μm sieve and then collected on a pre-combusted (450° for 24 hr) 47-mm glass fiber filter having a retention efficiency of 0.7 μm . To avoid filter clogging, and maximize sample volume, a volume of water was filtered through a test filter until clogging occurred. Then, sample volume was set at 90% of clogging volume. Sample volume varied between 100 and 1,000 ml in most cases. Filters were stored at -20°C until analysis.

Protein content was measured spectrophotometrically using the bicinchonic acid modification of the procedure of Lowry *et al.* (1951), standardized with bovine serum albumen. A microplate reader was used for spectrophotometry at a wavelength of 640 nm. Carbohydrates were quantified spectrophotometrically (wavelength 480 nm) using the method of Dubois *et al.* (1956), standardized with potato starch. Lipids were measured gravimetrically according to a modification of the technique of Folch *et al.* (1957), whereby dried seston filters were suspended in 10 ml of 2:1 v/v chloroform/methanol, ground for 1 min using a Potter Elvehjem tissue grinder with PTFE pestle, and then centrifuged at 1000 x g for 5 min.

The supernatant (containing lipid) was collected and brought to 20% v/v with 0.88% KCl to promote phase separation. The bottom layer was transferred by pipette to a pre-weighed vial, dried at 60°C until constant weight was achieved, and weighed. Hexadecanone was used as the standard.

c. Food estimator

For this study, food was defined as the sum of particulate lipid, labile carbohydrate, and protein in seston retained on a 0.7- μm filter after passing through a 53- μm sieve. This characterization of food was chosen to be consistent with modeling requirements in population dynamics models. Soniat *et al.* (1998) examined the applicability of a range of options for food time series in models of oyster post-settlement population dynamics. They determined that measures based on total seston, such as total organic carbon, consistently and substantially overestimated food for oysters (see also Ren and Ross, 2001). This result is consistent with observations of seston in Delaware Bay that show that the sum of particulate protein, lipid, and labile carbohydrate is a better estimate of bioavailable food for oysters than total particulate organic matter because seston contains refractory organic carbon that often comprises half of the total particulate organic matter (Huang *et al.*, 2003a,b). Alternate measures based on chlorophyll consistently underestimate available food during certain periods of the year (e.g., Powell *et al.*, 1992, 1995; Hofmann *et al.*, 2006), and thus offer a better, but still inadequate, time series of food supply.

Food quality is undoubtedly also important (Wikfors *et al.*, 1984; Langdon and Newell, 1990; McCausland *et al.*, 1999) and preferential retention and differential sorting of food particles are well documented (e.g., Haven and Morales-Alamo, 1970; Ward *et al.*, 1998; Cognie *et al.*, 2001). Such details have yet to be implemented in population dynamics models, although Hyun *et al.* (2001) included a parameter for retention efficiency, for example. Perusal of lipid-carbohydrate-protein time series show periods of time when the ratios of the three constituents are highly biased, typically towards protein or lipid (e.g., Soniat and Ray, 1985; Hyun *et al.*, 2001; Versar, 2001; our unpublished data for Delaware Bay). Larvae have proven amenable to modeling approaches based on biochemical transformation of food inputs in the form of lipid, protein, and carbohydrate (e.g., Bochenek *et al.*, 2001; Powell *et al.*, 2002; Hofmann *et al.*, 2004; Fach *et al.*, 2008). Biochemical-based models have not been developed yet for post-settlement stages, as the biochemical milieu is considerably more complicated than for larvae which still provide substantive challenges (Powell *et al.*, 2004). Thus, this analysis is focused upon a measure of food that presently is the best estimate available for modeling purposes for oyster post-settlement population dynamics rather than one that can support the more complex biochemical-based models for bivalve larvae.

d. Statistical analysis

Monthly average values of protein, lipid, and labile carbohydrate were compiled for each station for 2009 and 2010. Total food available was estimated as the sum of the three

values, in keeping with previous investigations (Soniati *et al.*, 1998; Hyun *et al.*, 2001; see also Fach *et al.*, 2008). These data include 10 monthly samplings in each year, November and February being purposefully unsampled. For variables defined as 1-month or 2-month lags. November and February values were interpolated as the average of the adjacent months, with the December prior to the initial January value being obtained as the average of January and the following interpolated November value.

We conducted a multiple regression analysis with independent variables restricted to those available simultaneously from ROMS simulations (Wang *et al.*, this issue) and field measurements. This constraint was imposed because one goal of the study was to determine whether food supply values could be estimated from ROMS simulations of future climatologies. The following variables were included in the regression: sampling time relative to the high tide as the time differential in hours, surface temperature at sampling, surface salinity at sampling, the salinity and temperature anomalies (*22-month mean – observed value*), the absolute value of the salinity and temperature anomalies, the within-site salinity and temperature anomalies (*22-month site mean – observed value*), the within-year salinity and temperature anomalies (*11-month mean – observed value*), the 1-month and 2-month lagged temperature and salinity, and the rate of change of temperature and salinity ($\frac{\text{lag value} - \text{value}}{\text{lag value}}$). As field current velocity measurements were not available, this information otherwise provided by the hydrodynamic model was not used. Some of the variables included in the multiple regression are themselves correlated. We performed an analysis of multicollinearity to evaluate the degree to which correlation among independent variables influenced the final regression results (Freund and Littell, 2006).

Preliminary analyses showed that a 5-variable model encompassed most of the variance explained by the environmental dataset. We calculated the residuals between the expected and observed values for each site and sampling month ($R_s = \text{expected value} - \text{observe value}$). We allocated data to four half-year periods (e.g., January–June, 2009). For each group, we counted the number of site residuals exceeding 1.5, the number of site residuals less than -1.5 , and the number falling near zero ($-1.5 < R_s < 1.5$). Stations were clustered by the distribution of their residuals among these three ranks for each of the four half-year periods using an unweighted pair-group cluster algorithm with Euclidean distance as the similarity index (Boesch, 1977). We also clustered sampling periods based on the fractional deviation of each site's food value for each sampling relative to the average for all 20 samplings for that site and for the average of all 15 samplings for that month calculated as $\left(\frac{\text{value} - \text{average value}}{\text{average value}}\right)$ using the same cluster algorithm.

3. Results

a. Regression analysis

Five variables provided significant input in explaining the temporal and spatial variation in the 2009–2010 food dataset. The regression, though significant, achieved a modest R^2 of 0.28. The five variables and their significance in the regression were the temperature anomaly

($P = 0.0002$), the absolute value of the temperature anomaly ($P = 0.05$), the site-specific temperature anomaly ($P = 0.0015$), the year-specific temperature anomaly ($P = 0.0002$), and the one-month lagged temperature ($P < 0.0001$). Analysis of multicollinearity revealed a condition index (*sensu* Freund and Littell, 2006) exceeding 30 as a result of the anticipated correlation between the temperature anomaly and the year-specific temperature anomaly. Deletion of the latter from the regression reduced the R^2 to 0.25, but did not otherwise influence the outcome. Both variables were retained for subsequent analyses. No salinity-dependent variable was found to be significant. Analysis of multicollinearity revealed the expected correlation between the salinity anomaly and the year-specific salinity anomaly. Deletion of the year-specific salinity anomaly, did not raise the importance of the salinity anomaly in the regression. The one-month lagged temperature proved superior to the two-month lagged variable. No longer lags were investigated, as the dataset was only 22 months in length. Restriction of the set of independent variables to only those representing salinity returned a paltry R^2 of 0.11, confirming the limited influence of salinity in explaining variation in the food dataset. The regression equation used for subsequent analyses was:

$$\begin{aligned}
 \text{Food} = & 4.899 + (1.007x \text{ Temperature Anomaly}) \\
 & + (0.051x \text{ abs(Temperature Anomaly)}) \\
 & - (0.849x \text{ Site-specific Temperature Anomaly}) \\
 & - (0.227x \text{ Year-specific Temperature Anomaly}) \\
 & + (0.156x \text{ Temperature Lagged 1 Month}).
 \end{aligned} \tag{1}$$

A cluster analysis identified three primary clusters of sites (Fig. 2). Nantuxent Point separated from all of the rest. A large cluster of sites included all of the Delaware oyster bed sites, the remaining downestuary sites on the Delaware side, and all but one of the ship channel sites: Ridge, Liston Point, Elbow of Crossledge, Over the Bar, Smyrna River, and Lower Side of Delaware. This cluster also included the two most upestuary New Jersey oyster bed sites, Arnolds and Hope Creek. The third cluster included all the remaining oyster beds on the New Jersey side, plus the site immediately downestuary of them off the Maurice River and one channel site nearest the primary New Jersey oyster beds: Bennies, Egg Island, Maurice River, Sea Breeze, Ship John Channel, and Ship John. Sites in these three clusters differed substantially in the pattern of their residuals.

Time series of food values for similar sites based on cluster groupings are shown in Figures 3–5. Delaware Bay is characterized by relatively high food values in the March–May period. The spring bloom was distinctly more pronounced in 2009 than in 2010. Food values fell more or less continuously from bloom highs, typically reaching nadirs in August–October. A late fall/early winter bloom was recorded at some sites. The Delaware and channel group of sites, including the two upestuary New Jersey oyster bed sites, had relatively high food values, 4–8 mg DW L⁻¹, during the spring bloom, with the sites over the oyster beds, Ridge and Over the Bar, tending to be higher than the others (Fig. 3). A fall

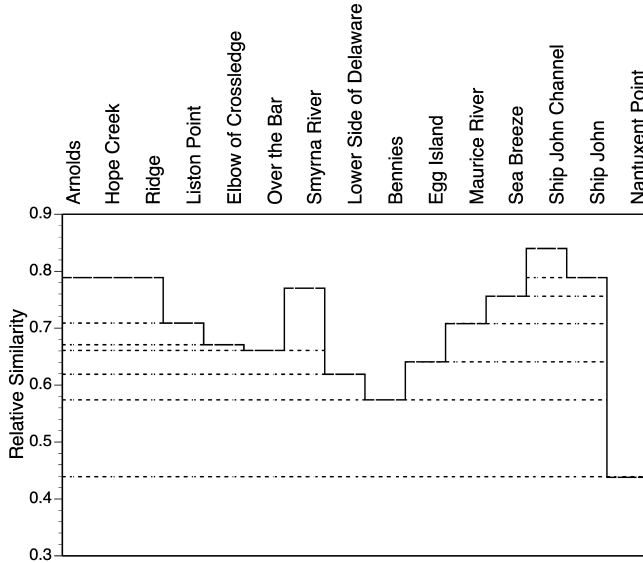


Figure 2. Cluster analysis of regression residuals by sampling location. Stations were clustered by the frequency of residuals $R_s > 1.5$, $R_s < -1.5$, and $-1.5 < R_s < 1.5$.

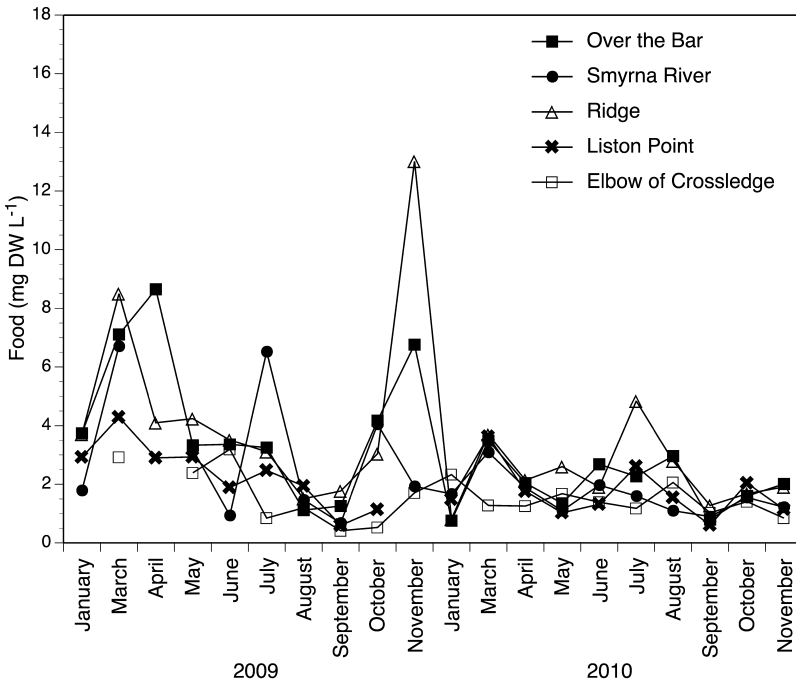


Figure 3. Time series of average food values in the Delaware Bay at selected sites representative of the Delaware and channel group of stations that clustered together based on their residuals (Fig. 2).

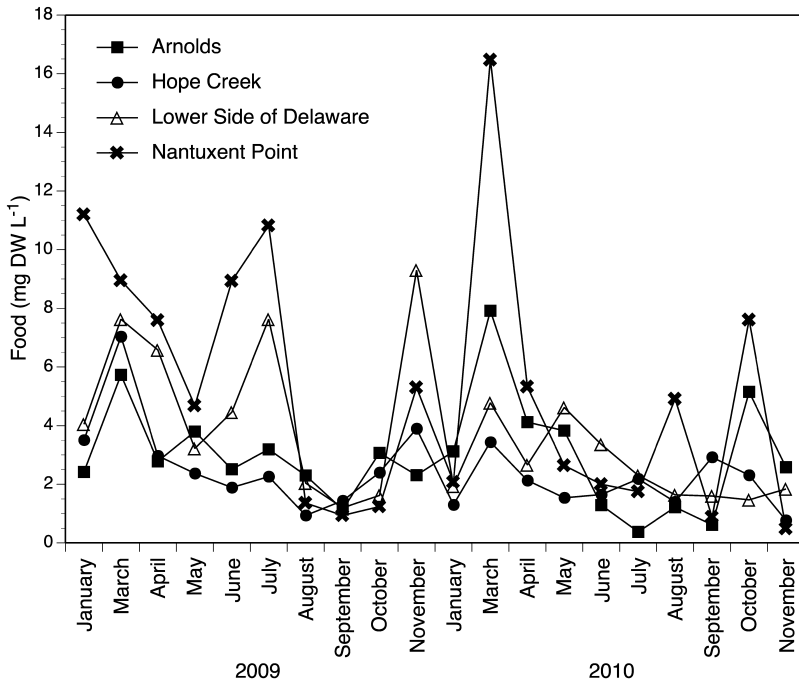


Figure 4. Time series of average food values in the Delaware Bay at Nantuxent Point and at selected sites that clustered together with the sites depicted in Figure 3 based on their residuals (Fig. 2).

bloom was apparent, particularly in 2009. The two upestuary New Jersey sites, Arnolds and Hope Creek, followed this same pattern, with a fall bloom in 2010 being more pronounced (Fig. 4). Nantuxent Point is a site obviously following a trajectory relatively different from the remaining sites, either in magnitude (e.g., March, 2010) or timing (e.g., June, 2009) (Fig. 4). In contrast, most New Jersey oyster bed sites, while demonstrating a spring bloom, had food values no higher than about 6 mg DW L⁻¹. A fall bloom was meager (2010) or absent (2009) (Fig. 5). Food values in summer to early fall fell around 2 mg DW L⁻¹ (Fig. 5), averaging lower overall than at the Delaware, channel, and upestuary sites (Figs. 3–4).

We examined this difference in residual pattern. The largest cluster of sites encompassing all the Delaware sites and a few upestuary New Jersey sites (Figs. 3–4) showed a pattern of residuals in which most residuals fell within a factor of 2 of the observed values; both negative and positive values were relatively common (Figs. 6–7). Outliers were normally high and not obviously biased towards any one of these sites. The cluster encompassing most of the New Jersey oyster beds showed a distinctly different pattern (Fig. 8). Negative residuals were vastly more common than positive residuals and residuals more negative than -2 were frequently observed. Few positive outliers occurred (Fig. 8). On the average, the expected value exceeded the observed value throughout the study at each of these sites.

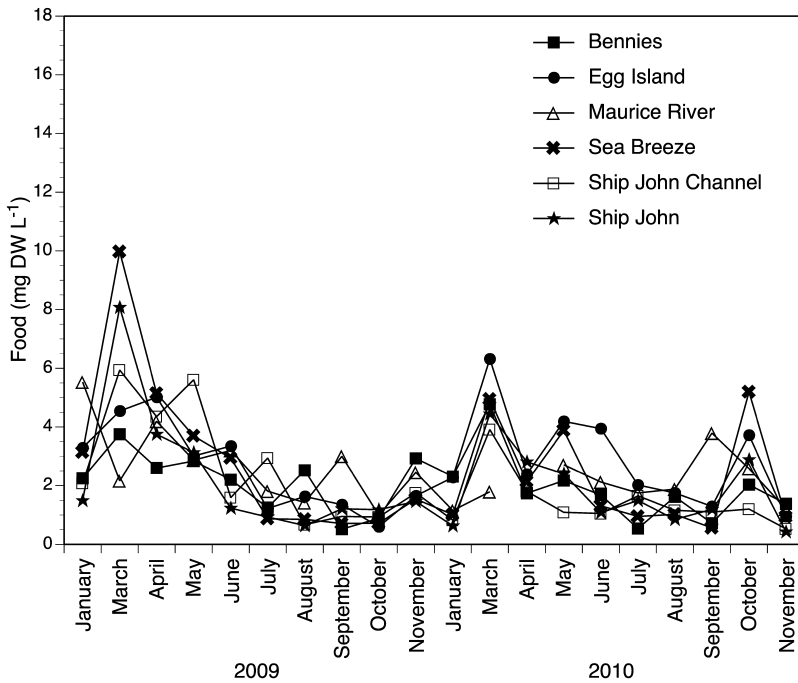


Figure 5. Time series of average food values in the Delaware Bay at New Jersey oyster bed and downestuary sites that clustered together based on their residuals (Fig. 2).

Nantuxent Point is the diametric opposite (Fig. 7), being distinguished from all other sites in having most residuals positive, the observed value exceeding the expected value, with about half of the residuals exceeding a value of +2.

We divided the dataset into four half-year sections because some residual patterns showed trends towards higher values over the 2009-2010 time period (e.g., most sites in Fig. 6). An ANOVA with half-year and site as main effects revealed a significant influence of site on residual pattern ($P < 0.0001$), with mildly significant influences of half-year ($P = 0.04$) and the interaction term ($P = 0.06$). A Tukey's *a posteriori* test repeated the pattern shown by the cluster analysis (Table 1), with most sites in the larger Delaware and channel cluster having average residuals slightly negative to mildly positive, with Nantuxent Point showing the highest average residual, and with the New Jersey beds downestuary of Arnolds and Hope Creek all having average residuals that were negative.

b. Temporal and spatial trends

We also clustered sampling periods by the relationship of each sampling site's values to the 20-month average value for the site to identify months with similar geographic and temporal trends in food. The sampling periods fell into two large clusters, with a series of sampling periods as outliers (Fig. 9). The largest cluster consisted of sampling periods

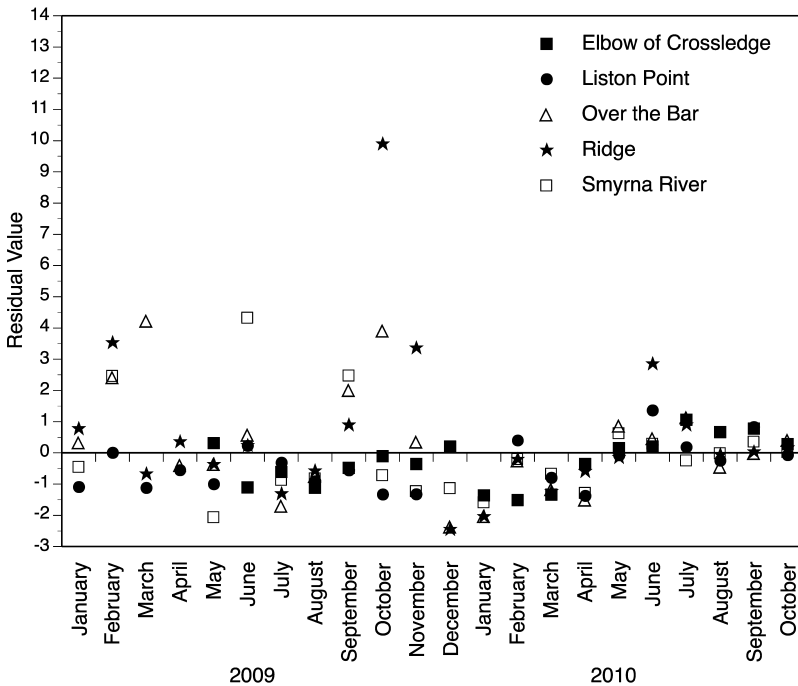


Figure 6. Pattern of residuals calculated from the observed value and the expected value derived from the best 5-variable regression equation ($R_s = \text{expected value} - \text{observed value}$) for representative sites in Delaware and along the ship channel that clustered together (Fig. 2).

when food values were relatively low over much of the bay in comparison to the 20-month mean at most sites (Fig. 10). These time periods fell dominantly during the late summer and fall, but included a few earlier summer periods in 2010, when food supply overall was lower than in 2009. A second cluster included time periods with near-average food content over much of the bay (Fig. 9). During these months, the food values for the Delaware and channel sites were consistently lower than the 20-month site average in comparison to the more chaotic New Jersey sites (Fig. 11). These periods were dominantly late spring to early summer, during the period that food supply was declining from yearly highs set during the spring bloom. The remaining sites, though falling into apparent clusters, clustered at distinctly lower similarity levels (Fig. 9). These, with one exception (November, 2009) were all bloom months in the early to late spring. The lower similarity between these time periods suggests that high-food time intervals generate highly variable food values over the bay and even between adjacent months, in comparison to the greater uniformity in food supply throughout the remainder of the year. The plot of the proportional contribution from each site shows wide and inconsistent variations from site to site during these months (Fig. 12). Thus, overall, site-to-site variation spatially and in time are highest during bloom times, with predictability improving consistency as time passes.

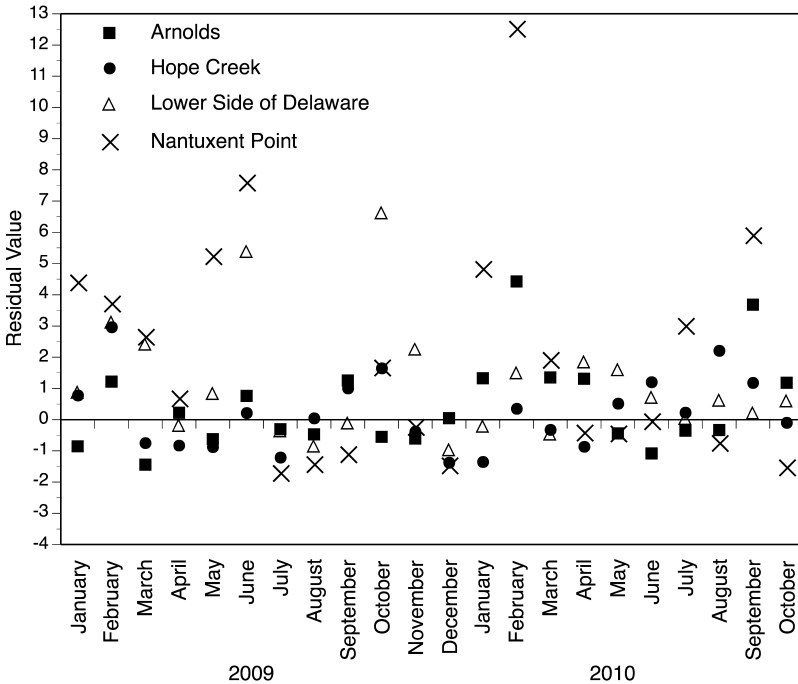


Figure 7. Pattern of residuals calculated from the observed value and the expected value derived from the best 5-variable regression equation ($R_s = \text{expected value} - \text{observed value}$) for Nantuxent Point and representative sites in Delaware and along the ship channel not shown in Figure 6.

An ANOVA reported a significant month effect ($P < 0.0001$). A Tukey’s *a posteriori* test repeated the pattern shown by the cluster analysis (Table 2) nearly identically and confirms the similarity of the sampling times during periods when food supply is average to low and during the months following the spring bloom when food supply is declining, in comparison to the much more variable bloom times.

Clustering stations by their monthly proportional deviations from the bay-wide mean yielded one large and two smaller station groups with a few outliers (Fig. 13). The largest group comprised all of the New Jersey oyster bed sites downestuary of Arnolds except Nantuxent Point (see Fig. 1) plus most of the channel sites. These sites consistently recorded lower food values at each sampling than the bay-wide mean (Fig. 14). Food values were often depressed by 50% relative to the bay-wide mean. This reduction was noticeable in all months and was particularly strong in the summer to fall of 2009. A second cluster included all of the Delaware oyster bed sites. Food values were routinely above the bay-wide mean at these sites (Fig. 15), particularly during the summer months. A third cluster comprised Hope Creek and the site off the Maurice River. (Fig. 16). Like nearly all of the remaining New Jersey oyster bed sites, these sites routinely had food values below the bay-wide mean. However, food values were distinctly above the bay-wide mean in the September–October

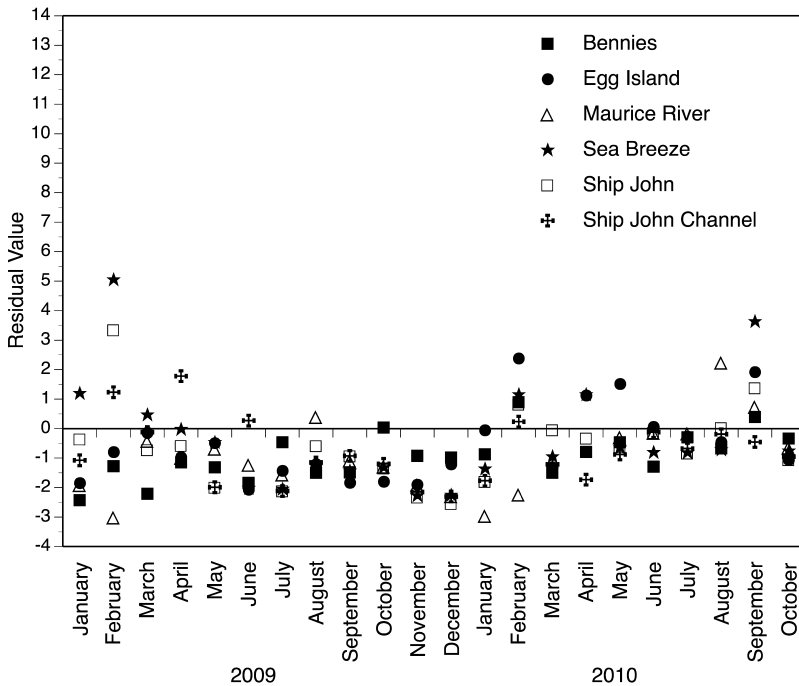


Figure 8. Pattern of residuals calculated from the observed value and the expected value derived from the best 5-variable regression equation ($R_s = \text{expected value} - \text{observed value}$) for sites on the oyster beds of New Jersey and downestuary that clustered together (Fig. 2).

time period in both years. Three sites failed to cluster with the remainder. One of these, Nantuxent Point, often fell well above the bay-wide mean, but sporadically during the year (Fig. 17). An analogous pattern was observed at the other two sites, Arnolds and the site off the Smyrna River.

An ANOVA reported a significant site effect ($P < 0.0001$). An *a posteriori* Tukey's test aligned the stations in a similar order as the cluster analysis (Figs. 13–17, Table 3). The consistently higher food resources at the Nantuxent Point site and much of the Delaware side of the bay is manifestly obvious from this analysis.

4. Discussion

a. Temporal and spatial trends in food

Delaware Bay shows a typical spring bloom, centered in March and April, with declining food supply thereafter into the early fall. In 2009, a late fall bloom may have occurred on the Delaware side of the bay, but no equivalent occurrence was observed in 2010 at most sites (see also Pennock, 1985; Pennock and Sharp, 1994; Sharp *et al.*, 2009). Inter-annual variation is manifested in the higher bay-wide food values in the spring and early summer

Table 1. Results of a Tukey's *a posteriori* test on regression model residuals by sampling location.

	Tukey Grouping		Mean	Site
	A		2.0362	Nantuxent Point
	A			
B	A		1.173	Lower Side of Delaware
B	A			
B	A	C	0.6084	Ridge
B	A	C		
B	A	C	0.4425	Arnolds
B	A	C		
B	A	C	0.264	Over the Bar
B		C		
B		C	0.1939	Hope Creek
B		C		
B		C	-0.0294	Smyrna River
B		C		
B		C	-0.2595	Elbow of Crossledge
B		C		
B		C	-0.298	Sea Breeze
B		C		
B		C	-0.3876	Liston Point
B		C		
B		C	-0.5388	Egg Island
		C		
		C	-0.6707	Ship John
		C		
		C	-0.8014	Ship John Channel
		C		
		C	-0.9301	Bennies
		C		
		C	-0.9762	Maurice River

of 2009 compared to 2010 and a detectable fall bloom in October of 2010 over the New Jersey oyster beds that did not materialize in 2009. Regardless, in both years, food supply declined throughout the late spring and summer to nadirs in the August to October time frame.

The within-bay distribution of food also varied temporally, but this variability was a second order overlay on the seasonal changes that influenced the bay as a whole. The differential development of the fall bloom on the Delaware and New Jersey sides of the bay, more pronounced on the Delaware side in 2009 and on the New Jersey side in 2010, is a good example (Figs. 4–5). The geographic and temporal structure of food was more predictable in summer to late fall, and considerably less predictable in the spring.

The within-bay spatial distribution of food did have a strong and predictably uneven differential between the Delaware and New Jersey sites, however. Food values averaged

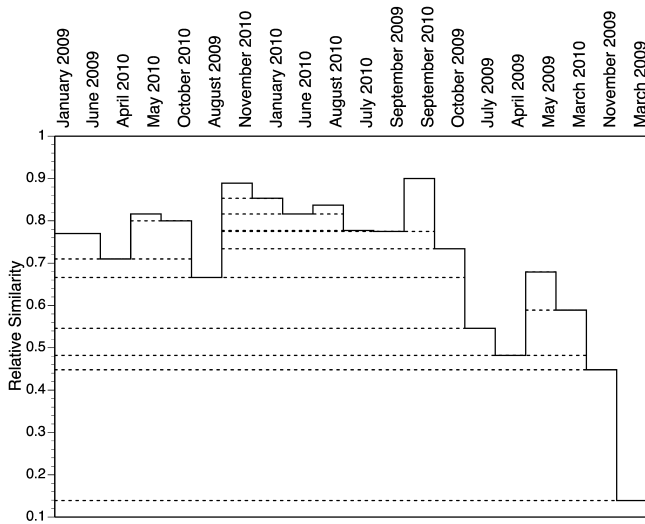


Figure 9. Cluster analysis based on the fractional deviation of each site's food value for each sampling relative to the average for all 20 samplings for that site over the study period calculated as $\left(\frac{\text{value}-\text{average value}}{\text{average value}}\right)$.

lower essentially in all months at all New Jersey oyster bed sites downestuary of Arnolds, the exception being Nantuxent Point, and also at most ship channel sites. This differential was particularly strong during the summer and fall when most Delaware oyster bed sites averaged higher food values than the bay-wide mean of 15 sites, while the New Jersey beds averaged lower. The distribution of sites based on the proportional deviation of the food value relative to the bay-wide 15-site mean did not follow an upestuary-downestuary trend that might be anticipated if the origin of this phenomenon was to be found within the salinity gradient. Rather, the differential was cross-bay and was distinctive throughout the estuarine salinity gradient.

b. Food datasets in ecological modeling of bivalve resources

Planning for estuarine management under conditions beyond those observed, such as different climatologies, higher sea levels, or differential channel reconfigurations (e.g., Kennedy, 1990, 1994; Scavia *et al.*, 2002; Walsh, 2004), includes evaluation of the impact on biological resources. Oysters, being a keystone bay species (Gutiérrez *et al.*, 2003), are an obvious source of interest. They provide essential habitat, filtering capacity, secondary production, and a variety of other services for many temperate estuaries (e.g., Harwell *et al.*, 2010; Newell, 2004; Stunz *et al.*, 2010). The population dynamics of these animals is strongly influenced by environmental conditions, especially temperature and salinity (Jordan, 1995; Powell *et al.*, 1996; Kimmel and Newell, 2007), but also by biological

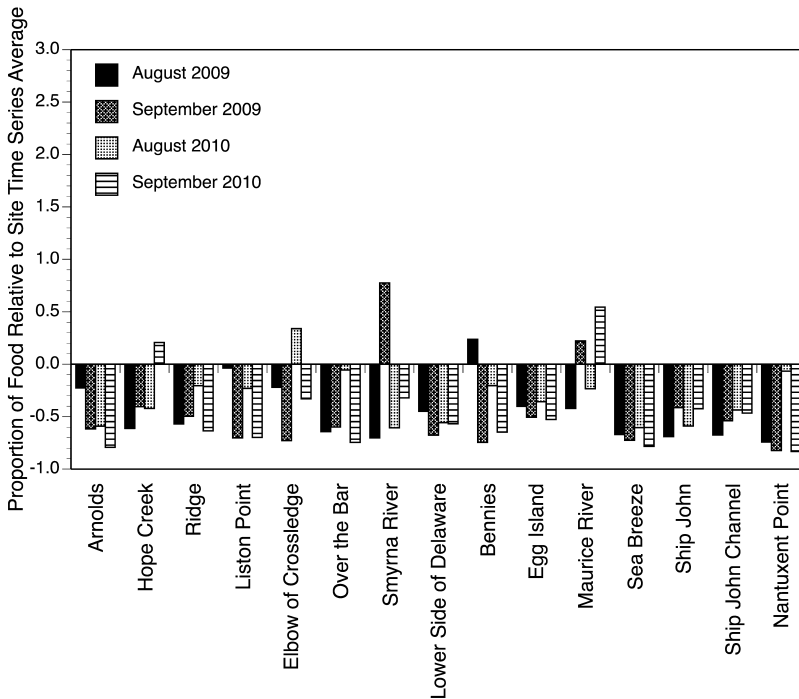


Figure 10. The differential in site values for a given sampling time relative to the 20-month mean for each site. Months depicted are representative of those that fell into a large cluster of months as shown in Figure 9. Plotted values are the fractional deviation of each site's food value for each sampling relative to the average for all 20 samplings for that site calculated as $\left(\frac{\text{value} - \text{average value}}{\text{average value}}\right)$.

conditions, and very likely especially food supply (e.g., Berg and Newell, 1986; Powell *et al.*, 1996; Rheault and Rice, 1996; Norkho *et al.*, 2005).

Three alternatives exist in developing food supply time series for evaluating future environmental conditions, whether naturally caused or the products of anthropogenic manipulation of the estuary. One can assume invariance and use an observed food time series of the type analyzed here. This alternative is a frequent choice (e.g., Hofmann *et al.*, 2001; Powell *et al.*, 1997, 2003; Fulford *et al.* 2007), but provides for a degree of uncertainty as to the range of inferences that can be made from simulation results, as the food supply is not allowed to vary with the environmental regime. One can develop a complex ecosystem model. Such implementations are rare (e.g., Meyers *et al.*, 2000; Ortiz and Wolff, 2002; Kittiwanch *et al.*, 2007) and closure terms for such complex models remain a challenge (e.g., Hannon, 1991; Steele, 1976; Steele and Henderson, 1992). An intermediate option is to derive needed time series from hydrodynamic models. This option is routinely chosen for environmental parameters such as temperature and salinity. The question addressed here is the degree to which food supply time series can be obtained in the analogous way without

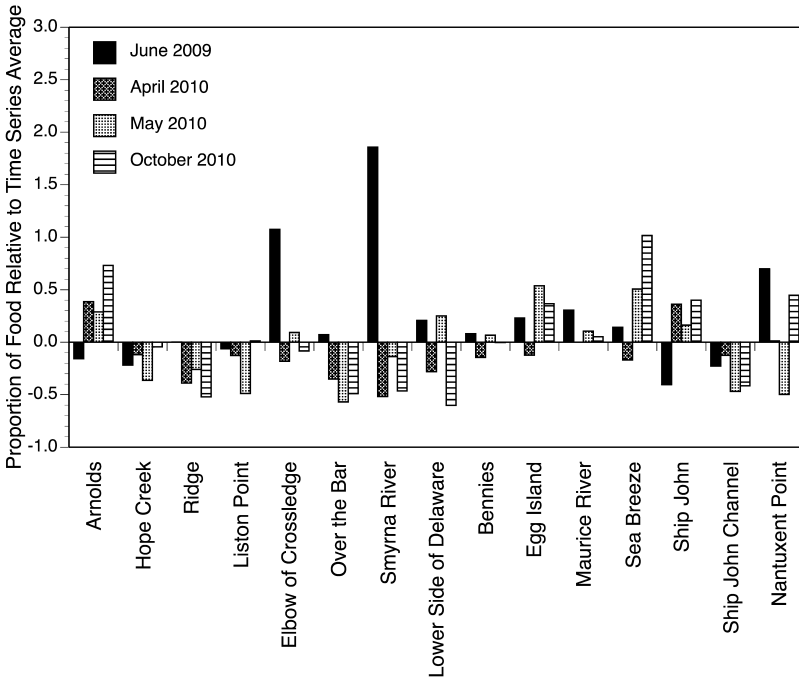


Figure 11. The differential in site values for a given sampling time relative to the 20-month mean for each site. Months depicted are representative of those that fell into a large cluster of months as shown in Figure 9. Plotted values are the fractional deviation of each site’s food value for each sampling relative to the average for all 20 samplings for that site calculated as $(\frac{value - average\ value}{average\ value})$.

including a food web submodel in the implementation (MacIsaac *et al.*, 1999; Chapelle *et al.*, 2000; Batchelder *et al.* 2002).

Fifteen locations were sampled across much of the salinity gradient in Delaware Bay, including the central ship channel, but also a range of sites lateral to the ship channel covering representative regions of the muddy bottom and oyster reef habitats of the bay on the Delaware and New Jersey sides. A multiple regression, focused on information available from the hydrodynamics model, proved only mildly predictive of food supply over this geographic range and over two full sampling years. Temperature and variables built upon the temporal and spatial variation in temperature afforded the only explanatory signals. However, the minimal success achieved was not due to randomly occurring poorly-predicted food values in time and space. Rather, the pattern of deviations between observed and expected values from residual analyses identified three sets of sites. For one set, the predictive capability of the multiple regression was relatively good. For a second set, the regression routinely predicted food values higher than observed. For one site, the diametric opposite occurred. These sites were not randomly distributed around the bay. Rather, the one group of sites adequately predicted represented the ship channel sites, sites west of

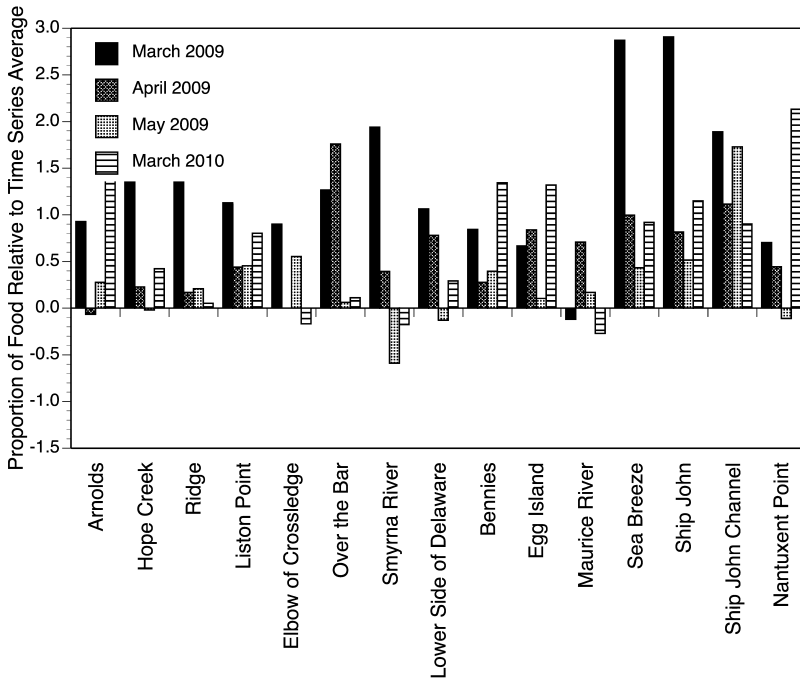


Figure 12. The differential in site values for a given sampling time relative to the 20-month mean for each site. Months depicted are examples of those that fell outside of the two large clusters of months as shown in Figure 9. Plotted values are the fractional deviation of each site’s food value for each sampling relative to the average for all 20 samplings for that site calculated as $(\frac{value - average\ value}{average\ value})$.

the channel (all Delaware sites) and the most upestuary New Jersey sites. The group for which food supply was consistently overestimated by the regression model were all but the most upestuary New Jersey oyster beds plus one site downestuary from them in a region of leased grounds where oysters also are abundant (Powell *et al.*, 1997) and one site along the ship channel immediately adjacent to one of the major New Jersey oyster reefs. Finally, the regression equation frequently underestimated food supply at one site, Nantuxent Point, a nearshore site just downestuary of Egg Island Point (Fig. 1). The cross-bay counterpart, Lower Side of Delaware, is interesting in being the next least similar site, though falling within the larger Delaware group, and also the only other site with an average residual value above 1.0 (Table 1).

The cross-bay bias in the distribution of these site groups explains the surprising lack of significance of any salinity-related variable. Primary production is light-limited in Delaware Bay (e.g., Pennock, 1985; Pennock and Sharp, 1994), a product of an upper estuary turbidity maximum. As a consequence, one might expect salinity, a potential surrogate for and contributor to the downestuary environmental gradient, to correlate in some measure with food supply. Why it does not is revealed by the distribution of the two largest clusters of

Table 2. Results of a Tukey's *a posteriori* test on the percentage deviation of each site's food value for each sampling relative to the average for all 20 samplings for that site calculated as $(\frac{\text{value}-\text{average value}}{\text{average value}} \times 100.)$.

Tukey Grouping		Percentage Change	Month
	A	135.49	March 2009
	A		
B	A	73.53	March 2010
B			
B	C	65.44	April 2009
B	C		
B	C D	35.27	November 2009
B	C D		
B	C D	33.60	May 2009
B	C D		
B	E C D	24.97	January 2009
B	E C D		
F	B E C D	11.38	July 2009
F	E C D		
F	G E C D	7.69	June 2009
F	G E C D		
F	G E C D H	3.63	October 2010
F	G E D H		
F	G E D H	-7.72	May 2010
F	G E D H		
F	G E D H	-10.18	April 2010
F	G E D H		
F	G E D H	-27.30	June 2010
F	G E H		
F	G E H	-30.23	July 2010
F	G E H		
F	G E H	-31.51	August 2010
F	G E H		
F	G E H	-33.70	October 2009
F	G E H		
F	G E H	-36.67	January 2010
F	G H		
F	G H	-43.14	August 2009
F	G H		
F	G H	-48.64	September 2010
	G H		
	G H	-53.57	November 2010
	H		
	H	-56.30	September 2009

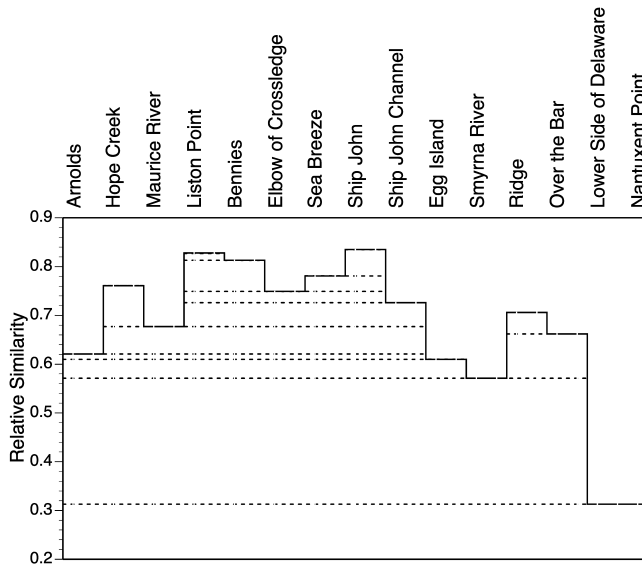


Figure 13. Cluster analysis based on the fractional deviation of each site’s food value for each sampling relative to the average for all 15 samplings for that site in that month calculated as $\left(\frac{\text{value}-\text{average value}}{\text{average value}}\right)$.

sites (Fig. 2). These two site groups are oriented upbay-downbay, not cross-bay. Thus, each cluster covers a substantial fraction of the entire salinity gradient, on the Delaware side in one case and on the New Jersey side in the other. As a consequence, a low regression coefficient is achieved, because simple environmental variables based on temperature and salinity explain only a portion of the spatial and temporal variance in food supply. The effect is to minimize the usefulness of environmental variables derived from observation or predicted from a hydrodynamic model to predict food supply distributions in coupled hydrodynamic-biological models. The cross-bay differential cannot be extracted from such datasets.

c. A possible influence of oysters

The low regression coefficient, 0.28, shows that one or more major variables are not included in the model. Among the environmental variables, turbidity might be an option. However, turbidity is high over much of Delaware Bay (Sharp *et al.*, 2009) and the sites near the turbidity maximum and downestuary of it all fall into the large cluster of sites including all on the Delaware side of the bay (Fig. 2), the food values of which are relatively well predicted by the regression model. Few environmental variables differentiate laterally across the bay, and such variables are required to explain much of the unexplained variance. No environmental variable does so in such dramatic fashion as would be required. However, the oyster reefs of Delaware Bay are dominantly sited on the New Jersey side. In fact, all

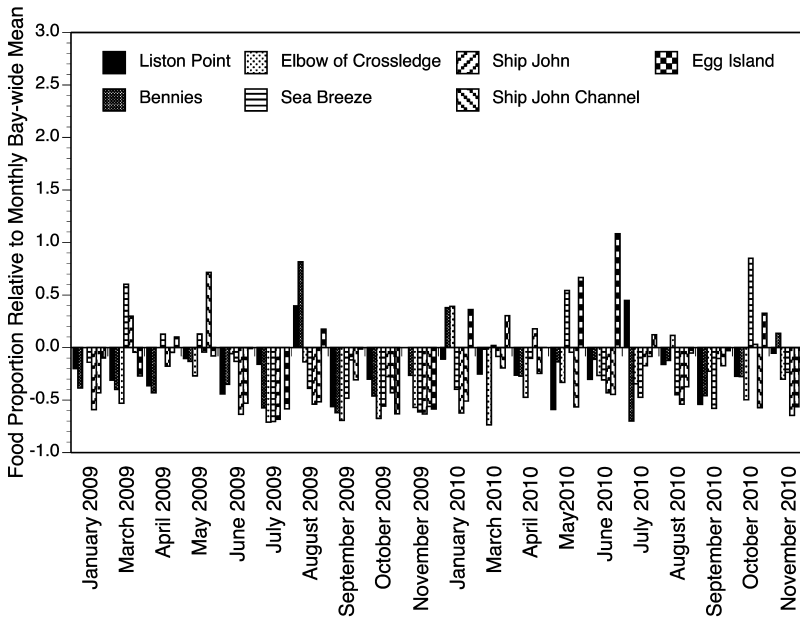


Figure 14. The differential in site values for a given sampling time relative to the monthly 15-site mean for each site. Sites depicted are those that fell into a large cluster of sites as shown in Figure 13. Plotted values are the fractional deviation of each site's food value for each sampling relative to the average for all 15 samplings for that site in each month calculated as $\left(\frac{\text{value} - \text{average value}}{\text{average value}}\right)$.

but one of the sites characterized by food values frequently overestimated by the regression are New Jersey oyster reef sites. The two exceptions include a site downbay on the leased grounds (see Kraeuter *et al.*, 2003) where oysters are also present in substantial numbers and a site on the New Jersey side of the ship channel immediately adjacent to a major reef. Were oysters to be effective at cropping down food organisms in Delaware Bay, the anticipated spatial effect on the distribution of food would be to produce lower observed values over the New Jersey beds. That is exactly what is observed.

That bivalves, including oysters, can exert top-down control (Cloern, 1982; Loo and Rosenberg, 1989) on primary production and phytoplankton standing stock is well documented (e.g., Ruesink *et al.*, 2003; Gobler *et al.*, 2005). A principal controlling factor is the flux of food near-bottom across the population (e.g., Wilson-Ormond *et al.*, 1997; Grizzle and Lutz, 1989). The ability of oysters to exert a top-down influence on phytoplankton food in Delaware Bay can be investigated using the flux model of Wilson-Ormond *et al.* (1997), based on the filtration rate model of Powell *et al.* (1992) and the distribution and size-frequency of the oyster populations in 2010 (HSRL, 2011). The model assumes an upestuary-downestuary flux of food across a known region harboring a known population of oysters with a known size frequency. The model is a 'single pass' upstream-downstream model and so permits an estimate of the impact of the oyster population over one tidal

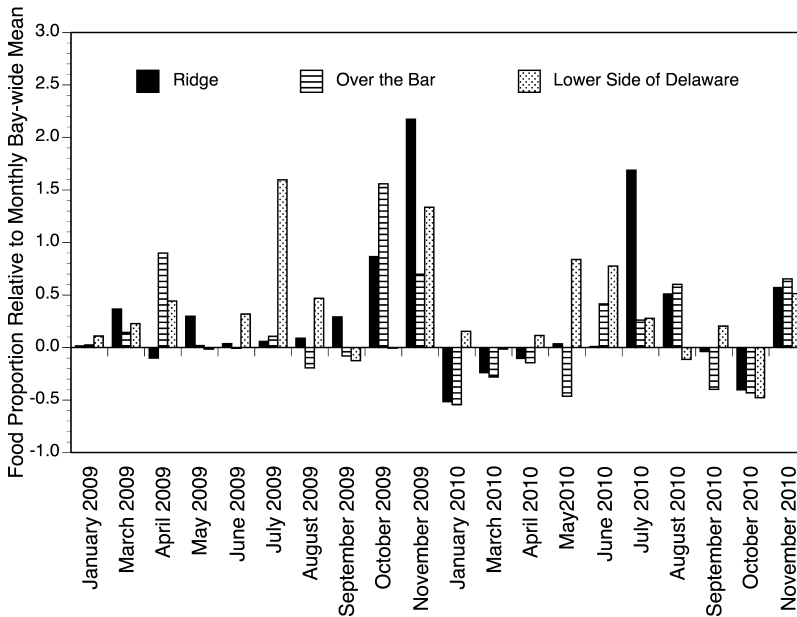


Figure 15. The differential in site values for a given sampling time relative to the monthly 15-site mean for each site. Sites depicted are those that fell into a small cluster of sites as shown in Figure 13. Plotted values are the fractional deviation of each site's food value for each sampling relative to the average for all 15 samplings for that site in each month calculated as $(\frac{\text{value} - \text{average value}}{\text{average value}})$.

excursion on the near-bottom food supply. The most significant uncertainty resides in the degree to which the flow across the reef is laminar. Consequently, we calculate a filtration effect based on a vertical mixing rate of 0.1% of the alongestuary tidal flow and a gracious (and thus conservative) effect height of 10 cm (see Ackerman (1999) for an example of a lesser effect height) and compare that to the laminar (no vertical mixing) alternative. Larger vertical mixing rates would severely limit any local reduction in food supply (e.g., Plutchak *et al.*, 2010), although regional scale effects might still be observed.

For the oyster population in Delaware Bay in 2010, for the beds sampled for this study, filtration rate is sufficient to remove about 1–44% of the available food flowing across the bed in the 10 cm of the water column immediately above the bottom depending on the reef and assumption of vertical mixing (Table 4). While not conclusive, this simple model evaluation suggests that oysters can influence food values on the New Jersey side of the bay at present biomass. Thus, the proffered explanation for the cross-bay gradient in food values as an outcome of oyster feeding is feasible.

d. Bay oddities

Nantuxent Point, and to some extent its counterpart on the Delaware side (Lower Side of Delaware), offer an interesting exception to the cross-bay trends that dominate the

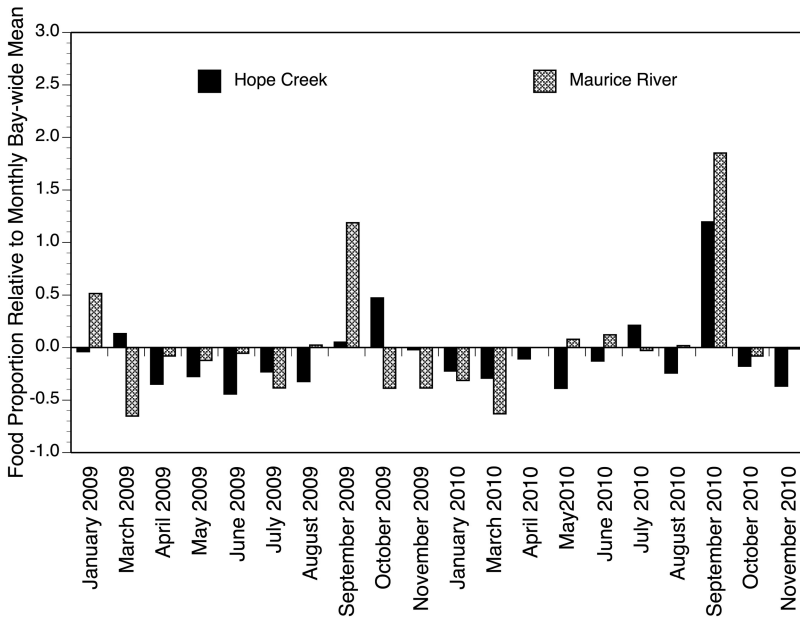


Figure 16. The differential in site values for a given sampling time relative to the monthly 15-site mean for each site. Sites depicted those that fell into a small cluster of sites as shown in Figure 13. Plotted values are the fractional deviation of each site's food value for each sampling relative to the average for all 15 samplings for that site in each month calculated as $\left(\frac{\text{value} - \text{average value}}{\text{average value}}\right)$.

distribution of food downestuary of Arnolds. These two sites often had very high food values in comparison to other sites. Both are found downestuary of the point at which the bay widens dramatically, more so on the New Jersey side (Fig. 1). The coincidence of similar behavior on both sides of the bay is intriguing, but causation is unclear.

The tendency for the two upestuary New Jersey sites, Arnolds and Hope Creek, to cluster with the Delaware sites or to be outlier sites is also noteworthy. Food supply tended to be higher in this region relative to the remaining New Jersey sites, but comparable to sites on the Delaware side. Simulations of transport of passively-advected particles in the period 2006–2009 using the Delaware Bay circulation model (Wang *et al.*, this issue) show sites on the Delaware side of the bay to be relatively well connected with the two upestuary sites, Arnolds and Hope Creek. In contrast, passive particles released on or near the New Jersey oyster reefs have longer residence times near their points of release and very little connectivity with upbay sites, particularly Arnolds and Hope Creek. Food supply in the water column should be transported, approximately, as a passive component of the water column. Consequently, these model-derived patterns of passive connectivity within the bay are mutually consistent with the observed clustering of the sites within the bay (e.g., the Delaware side sites with Arnolds and Hope Creek) and the deficit of food on the New Jersey

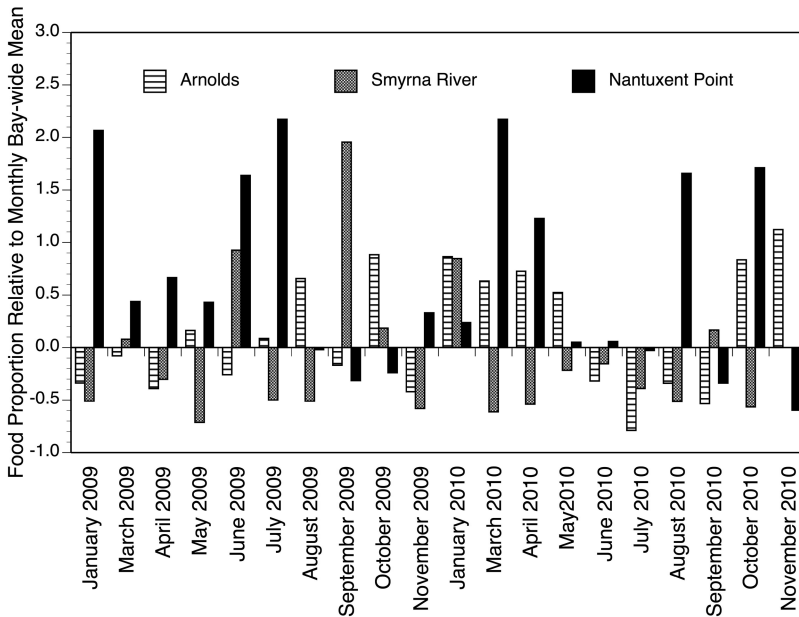


Figure 17. The differential in site values for a given sampling time relative to the monthly 15-site mean for each site. Sites depicted are those that did not fall into any primary cluster of sites as shown in Figure 13. Plotted values are the fractional deviation of each site's food value for each sampling relative to the average for all 15 samplings for that site in each month calculated as $\left(\frac{\text{value} - \text{average value}}{\text{average value}}\right)$.

side predicted by the regression model, as longer residence times provide an opportunity for greater top-down effects on food supply. Interestingly, estimates of larval connectivity using the Delaware Bay circulation model and the Dekshenierks *et al.* (1993, 1996) larval model show similar trends (Narváez *et al.*, this issue; Munroe *et al.*, this issue). Downestuary of Arnolds, the ship channel is an effective barrier to cross-bay transport (see also Jacobsen *et al.*, 1990; Garvine *et al.*, 1992) and may be considered to render an important limitation to secondary productivity on the New Jersey side.

e. Match-mismatch and oyster larvae

The match-mismatch hypothesis originated as an explanation for good and poor year classes of fish (Cushing, 1990). The gist of the hypothesis is that larvae are sensitive to food supply and that coincidental timing of high food and spawning is a principal reason for high recruitment events. Oyster larvae are high food-requiring organisms, as maximal growth rate shortens larval life span and promotes increased survival to and through metamorphosis (Dekshenierks *et al.*, 1993; Bochenek *et al.*, 2001). In some cases, food supply tends to be highest in the summer coincident with the oyster's spawning season (e.g., Galveston Bay,

Table 3. Results of a Tukey's *a posteriori* test on the percentage deviation of each site's food value for each sampling relative to the average for all 15 samplings for that month calculated as $(\frac{\text{value} - \text{average value}}{\text{average value}} \times 100)$.

	Tukey Grouping	Percentage Deviation	Site
	A	69.40	Nantuxent Point
	A		
B	A	32.65	Lower Side of Delaware
B	A		
B	A	28.35	Ridge
B			
B	C	13.95	Arnolds
B	C		
B	C	13.34	Over the Bar
B	C		
B	C	5.83	Maurice River
B	C		
B	C	3.70	Egg Island
B	C		
B	C	-7.39	Hope Creek
B	C		
B	C	-11.42	Smyrna River
B	C		
B	C	-16.15	Sea Breeze
B	C		
B	C	-21.84	Bennies
B	C		
B	C	-22.26	Liston Point
	C		
	C	-28.95	Ship John
	C		
	C	-29.70	Ship John Channel
	C		
	C	-34.32	Elbow of Crossledge

Texas – Soniat and Ray, 1985; some Maryland bays – Glibert *et al.*, 2007). In Delaware Bay, as in other estuaries (e.g., Fulford *et al.*, 2007), the perverse opposite routinely occurs. Our data indicate that food may be variable interannually during the mid-summer, but is almost always low in late summer to early fall. Highest food supplies occur in the early spring, prior to water warming sufficiently to generate increased filtration rates and gametogenesis (see also Parker, 2005).

Oysters spawn in late June though early September (Ford and Figueras, 1988; Dittman *et al.*, 2001) during a time of declining food supply. Later spawns would appear to occur invariably during times of greatly diminished food supply. Thus, the relative rate of diminishment of the spring bloom relative to the timing of the spawn would appear to be a critical

factor in determining the outcome of the spawning event. The study took place during two years of relatively good recruitment (HSRL, 2011), after a decade of below-average recruitment. Unfortunately, no food data are available for this earlier period. However, late summer food supplies measured in this study (Figs. 3–5) are sufficiently low to reduce larval growth rate (Deksheniaks *et al.*, 1993) and, consequently, larval success should decline incrementally as spawning time progresses into the year.

f. Carrying capacity

Powell *et al.* (2009a) described a sequence of regime shifts in the oyster stock of Delaware Bay. From 1970 until 1985, oyster abundance was about five times the level observed prior to that time or since. Powell *et al.* (2009b) evaluated the time series of oyster abundance from the stratified random survey begun in 1953 (Powell *et al.*, 2008), from which they developed a surplus production model that permitted two estimates of carrying capacity. One of these applied to the stock during times of minimal mortality from oyster diseases (MSX and dermo: causative agents *Haplosporidium nelsoni* and *Perkinsus marinus*, respectively). The other applied to the stock during times when mortality from oyster diseases dominated other sources of adult mortality. During the 1970–1984 period, stock abundance remained near the higher carrying capacity. During our study, stock abundance was near, but slightly below the lower carrying capacity (HSRL, 2011), consistent with the intensity of dermo disease during the 2000s (Powell *et al.*, 2011). The differential between the 1970s and 2000s abundances is primarily dictated by the abundance of oysters on the downestuary half of the oyster beds where disease mortality is highest. In the central part of the reef tract (Shell Rock to Middle; Fig. 1), abundances during our study were only approximately a factor of three lower than in the 1970s, whereas downestuary, the differential exceeded a factor of 10 (HSRL, 2011).

Oyster abundance during this study was sufficient to affect food supply over the New Jersey beds, if inferences made from this study and the Wilson-Ormond model are correct. However, food supply does not control abundance; rather, abundance is controlled by adult mortality rate and indirectly by broodstock availability (Powell *et al.*, 2008), although the origin of the relationship between recruitment and broodstock remains unclear (Powell *et al.*, 2009b; this issue). However, in the 1970s, spawning stock abundance fell along the compensatory portion of the broodstock-recruitment curve (Powell *et al.*, 2009a); that is, recruitment was less influenced by variations in broodstock abundance. Thus, the influence of the stock on food supply might have been much higher than observed today. Unfortunately, observations of food supply over the oyster beds are not available for the 1970s. However, a crude comparison can be made by comparing the Wilson-Ormond estimates for present-day to expectation under 1970s abundances (Table 4). This comparison suggests a 1.5 to 2 times increase in the impact of the stock on the upper half of the beds (Shell Rock to Arnolds, Fig. 1) and a factor of 3 or more on the downestuary half of the oyster beds. The fact that food supply over the New Jersey oyster beds is depressed today by up to 50% relative to the bay-wide

Table 4. Estimated fraction of food removed during upstream-downstream transport of food across reefs in the central portion of the New Jersey reef tract, including three of the reefs sampled in this study, using the model of Wilson-Ormond *et al.* (1997) assuming that oysters can directly affect the bottom 10 cm of the water column. Vertical mixing is assumed in the right column and laminar flow in the middle column. Reef location is shown in Figure 1. Top panel shows estimates for the time period of the study (HSRL, 2011). Bottom panel shows estimates for the 1970–1984 period based on an estimated 3X increase in abundance for the top five beds and an estimated 10X increase in abundance for Bennies.

Reef	Study Abundances	
	Laminar Assumption	Vertical Mixing Assumption
Middle	0.23	0.06
Sea Breeze	0.65	0.20
Cohansey	0.40	0.10
Ship John	0.44	0.12
Shell Rock	0.27	0.07
Bennies	0.10	0.02
Estimated 1970–1984 Abundances		
Reef	Laminar Assumption	Vertical Mixing Assumption
Middle	0.41	0.11
Sea Breeze	0.36	0.11
Cohansey	0.63	0.18
Ship John	0.67	0.22
Shell Rock	0.48	0.13
Bennies	0.34	0.09

mean suggests that the cross-bay gradient in food supply was much more significant in the 1970s and that food limitation played an important role in determining abundance on the New Jersey beds at that time, in establishing the compensatory relationship between broodstock and recruitment, and, hence, in defining carrying capacity under conditions of minimal mortality from disease.

5. Conclusions

Modification of the estuarine environment whether anthropogenic or through climate change is an increasingly serious issue for management of estuarine resources (e.g., Ulanowicz *et al.*, 1980; Hofmann and Powell, 1998; Klinck *et al.*, 2002; Powell *et al.*, 2003). Sophisticated hydrodynamic and population dynamic models are often invoked to evaluate the potential influence of climate change, channelization, etc. The ability of an estuary to generate food and the timing of this process is an important component of the estuarine environment. The question arises as to the importance of increasing model complexity to adequately simulate food supply and secondary production of the benthos. In Delaware

Bay, simple surrogates in lieu of a fully-implemented production model to estimate food supply failed to provide adequate simulated food resources for a significant portion of the bay. The reason for this failure was the cross-bay gradient in food that did not respect the salinity gradient. This cross-bay gradient in food is coincident with a cross-bay gradient in filtration capacity dominated by the bay's oyster resources. Whether oysters are directly responsible for the lower food values observed on the New Jersey side of the bay cannot be proven from our data; however, the hypothesis that oysters at present-day population densities exert some top-down influence on the primary producers is fully supported by our data. Any evaluation of the influence of climate change or anthropomorphic impact through modeling would appear to require the inclusion of both a primary production model and an oyster population dynamics model. This degree of sophistication is far from routine today in studies of this kind.

The analysis also supports the inference of Powell *et al.* (2009b) that a 1970s period of high abundance likely reached carrying capacity for the New Jersey side of Delaware Bay, with significant impact on phytoplankton standing stock an expected consequence. The potential for regime shifts to influence population carrying capacity is a subject of intense investigation (Collie *et al.*, 2004; Knowlton, 2004; Rothschild *et al.*, 2005). In estuaries, where bivalve resources may be effective modulators of phytoplankton standing stock, environmental shifts, by modifying either filtration capacity or the rate of primary production, may introduce large changes in bivalve population dynamics inordinately exceeding what might be inferred from the environmental data. Monitoring of bay food supply is suggested by this study to be an essential component of bay resource management, as this variable cannot be readily reconstructed from other data resources as it participates in an important feedback loop with the benthos that cannot be easily divined.

Acknowledgments. Funding was provided by the U. S. Army Corps of Engineers under their Section 22 funding authority, contract #W912BU-11-C-0004, through the Seaboard Fisheries Institute, in collaboration with the Sponsor, the South Jersey Port Corporation, a public agency of the State of New Jersey. We appreciate this support.

REFERENCES

- Ackerman, J. D. 1999. Effect of velocity on the filter feeding of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for trophic dynamics. *Can. J. Fish. Aquat. Sci.*, 56, 1551–1561.
- Andrews, J. D. 1988. Epizootiology of the disease caused by the oyster pathogen *Perkinsus marinus* and its effects on the oyster industry. *Am. Fish. Soc. Spec. Publ.*, 18, 47–63.
- Baldwin, B. S. and R. I. E. Newell. 1995. Feeding rate response of oyster larvae (*Crassostrea virginica*) to seston quantity and composition. *J. Exp. Mar. Biol. Ecol.*, 189, 77–91.
- Batchelder, H. P., C. A. Edwards and T. M. Powell. 2002. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. *Prog. Oceanogr.*, 53, 307–333.

- Berg, J. A. and R. I. E. Newell. 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar. Coast. Shelf Sci.*, 23, 375–386.
- Bochenek, E. A., J. M. Klinck, E. N. Powell and E. E. Hofmann. 2001. A biochemically based model of the growth and development of *Crassostrea gigas* larvae. *J. Shellfish Res.*, 20, 243–265.
- Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Dept. Commerce NTIS PB-269-604, EPA-60013-77-033.
- Bos, O. G., I. E. Hendriks, M. Strasser, P. Dolmer and P. Kamermans. 2006. Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. *J. Sea Res.*, 55, 191–206.
- Burreson, E. M. and L. M. Ragone Calvo. 1996. Epizootiology of *Perkinsus marinus* disease of oysters in Chesapeake Bay, with emphasis on data since 1985. *J. Shellfish Res.*, 15, 17–34.
- Carmichael, R. H., A. C. Shriver and I. Valiela. 2004. Changes in shell and soft tissue growth, tissue composition, and survival of quahogs, *Mercenaria mercenaria*, and soft shell clams, *Mya arenaria*, in response to eutrophic-driven changes in food supply and habitat. *J. Exp. Mar. Biol. Ecol.*, 313, 75–104.
- Carriker, M. R. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. U.S. Fish Wildl. Serv. Spec. Sci. Rpt. Fish., 148, 1–150.
- Chapelle, A., A. Ménesguen, J.-M. Deslous-Paoli, P. Souchu, N. Mazouni, A. Vaquer and B. Millet. 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of oysters [sic] farming and inputs from the watershed. *Ecol. Model.*, 127, 161–181.
- Cloern, J. E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.*, 9, 191–202.
- Cognie, B., L. Barillé and Y. Rincé. 2001. Selective feeding of the oyster *Crassostrea gigas* fed on a natural microphytobenthos assemblage. *Estuaries*, 24, 126–131.
- Collie, J. S., K. Richardson and J. H. Steele. 2004. Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.*, 60, 281–302.
- Crenshaw Jr., J. W., P. B. Heffernan and R. L. Walker. 1996. Effect of grow out density on heritability of growth rate in the northern quahog, *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.*, 15, 341–344.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.*, 26, 249–293.
- Deksheniaks, M. M., E. E. Hofmann, J. M. Klinck and E. N. Powell. 2000. Quantifying the effects of environmental change on an oyster population: a modeling study. *Estuaries*, 23, 593–610.
- 1996. Modeling the vertical distribution of oyster larvae in response to environmental conditions. *Mar. Ecol. Prog. Ser.*, 136, 97–110.
- Deksheniaks, M. M., E. E. Hofmann and E. N. Powell. 1993. Environmental effects on the growth and development of Eastern oyster, *Crassostrea virginica* (Gmelin, 1791), larvae: a modeling study. *J. Shellfish Res.*, 12, 241–254.
- Dittman, D. E., S. E. Ford and D. K. Padilla. 2001. Effects of *Perkinsus marinus* on reproduction and condition of the Eastern oyster, *Crassostrea virginica*, depend on timing. *J. Shellfish Res.*, 20, 1025–1034.
- Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers and F. Smith. 1956. A calorimetric method for the determination of sugars and related substances. *Anal. Chem.*, 28, 350–356.
- Engle, J. B. 1953. Effect of Delaware River flow on oysters in the natural seed beds of Delaware Bay. *Natl. Shellfish. Assoc. Conv. Add.*, 1–26.
- Fach, B. A., B. Meyer, D. Wolf-Gladrow and U. Bathmann. 2008. Biochemically based modeling study of Antarctic krill *Euphausia superba* growth and development. *Mar. Ecol. Prog. Ser.*, 360, 147–161.

- Fernández-Reiriz, M. J., U. Labarta, M. Albetosa and A. Pérez-Camacho. 2006. Lipid composition of *Ruditapes philippinarum* spat: effect of ration and diet quality. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.*, 144, 229–237.
- Folch, J., M. Lees and G. Stanley. 1957. A simple method for the isolation and purification of total lipides from animal tissues. *J. Biol. Chem.*, 226, 497–509.
- Ford, S. E. and A. J. Figueras. 1988. Effects of sublethal infection by the parasite *Haplosporidium nelsoni* (MSX) on gametogenesis, spawning, and sex ratios of oysters in Delaware Bay, USA. *Dis. Aquat. Org.*, 4, 121–133.
- Ford, S., E. Powell, J. Klinck and E. Hofmann. 1999. Modeling the MSX parasite in Eastern oyster *Crassostrea virginica* populations. I. Model development, implementation, and verification. *J. Shellfish Res.*, 18, 475–500.
- Frechette, M. and E. Bourget. 1985. Food-limited growth of *Mytilus edulis* L. in relation to the benthic boundary layer. *Can. J. Fish. Aquat. Sci.*, 42, 1166–1170.
- Freitas, V., J. F. M. F. Cardoso, S. Santos, J. Campos, J. Drent, S. Saraiva, J. IJ. Witte, S. A. L. M. Kooijman and H. W. van der Veer. 2009. Reconstruction of food conditions for Northeast Atlantic bivalve species based on dynamic energy budgets. *J. Sea Res.*, 62, 75–82.
- Freund, R. J. and R. C. Littell. 2006. SAS[®] system for regression. SAS Institute, Inc., Cary, NC, 236 pp.
- Fulford, R. S., D. L. Breitburg, R. I. E. Newell, W. M. Kemp and M. Luckenbach. 2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. *Mar. Ecol. Prog. Ser.*, 336, 43–61.
- Gallager, S. M. and R. Mann. 1986. Growth and survival of larvae of *Mercenaria mercenaria* (L) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. *Aquaculture*, 56, 105–121.
- Gargnery, A., C. Bacher and D. Buestel. 2001. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranean, France) with a population dynamics model. *Can. J. Fish. Aquat. Sci.*, 58, 1012–1020.
- Garvine., R. W., R. K. McCarthy and K-C. Wong. 1992. The axial salinity distribution in the Delaware Estuary and its weak response to river discharge. *Estuar. Coast. Shelf Sci.*, 35, 157–165.
- Glibert, P. M., C. E. Wazniak, M. R. Hall and B. Sturgis. 2007. Seasonal and interannual trends in nitrogen and brown tide in Maryland's coastal bays. *Ecol. Appl.*, 17(Suppl.), S79–S87.
- Gobler, C. J., D. J. Lonsdale and G. L. Boyer. 2005. A review of the causes, effects, and potential management of harmful algal blooms caused by *Aureococcus anophagefferens* (Hargraves and Sieburth). *Estuaries*, 28, 726–749.
- Grizzle, R. E. and R. A. Lutz. 1989. A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. *Mar. Biol. (Berl.)*, 102, 95–105.
- Gutiérrez, J. L., C. G. Jones, D. L. Strayer and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, 101, 79–90.
- Hadley, N. H. and J. J. Manzi. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. *Aquaculture*, 36, 369–378.
- Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. di Lorenzo, K., Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J. Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J. C. Warner and J. Wilkin. 2008. Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the Regional Ocean Modeling System. *J. Comp. Phys.*, 227, 3595–3624.
- Hannon, B. 1991. Empirical cycle stabilization of an oyster reef ecosystem. *J. Theor. Biol.*, 149, 507–519.

- Harwell, H. D., P. R. Kingsley-Smith, M. L. Kellogg, S. M. Allen, S. K. Allen Jr., D. W. Meritt, K. T. Paynter Jr. and M. W. Luckenbach. 2010. A comparison of *Crassostrea virginica* and *C. ariakensis* in Chesapeake Bay: does oyster species affect habitat function. *J. Shellfish Res.*, 29, 253–269.
- Haven, D. S. and R. Morales-Alamo. 1970. Filtration of particles from suspension by the American oyster *Crassostrea virginica*. *Biol. Bull. (Woods Hole)*, 139, 248–264.
- Hendriks, I. E., L. A. van Duren and P. M. J. Herman. 2003. Effect of dietary polyunsaturated fatty acids on reproductive output and larval growth of bivalves. *J. Exp. Mar. Biol. Ecol.*, 296, 199–213.
- Hily, C. 1991. Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? *Mar. Ecol. Prog. Ser.*, 69, 179–188.
- Hofmann, E., S. Ford, E. Powell and J. Klinck. 2001. Modeling studies of the effect of climatic variability on MSX disease in eastern oyster (*Crassostrea virginica*) populations. *Hydrobiologia*, 460, 195–212.
- Hofmann, E. E., J. M. Klinck, J. N. Kraeuter, E. N. Powell, R. E. Grizzle, S. C. Buckner and V. M. Bricelj. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. *J. Shellfish Res.*, 25, 417–444.
- Hofmann, E. E., E. N. Powell, E. A. Bochenek and J. M. Klinck. 2004. A modeling study of the influence of environment and food supply on survival of *Crassostrea gigas* larvae. *ICES J. Mar. Sci.*, 61, 596–616.
- Hofmann, E. E. and T. M. Powell. 1998. Environmental variability effects on marine fisheries: four case histories. *Ecol. Appl.*, 8 (Suppl.), 523–532.
- Honkoop, P. J. C. and B. L. Bayne. 2002. Stocking density and growth of the Pacific oyster (*Crassostrea gigas*) and the Sydney rock oyster (*Saccostrea glomerata*) in Port Stephens, Australia. *Aquaculture*, 213, 171–186.
- HSRL. 2011. Report of the 2011 Stock Assessment Workshop (13th SAW) for the New Jersey Delaware Bay oyster beds. 156 pp.
- Huang, S.-C., D. A. Kreeger and R. I. E. Newell. 2003a. Seston available as a food resource for the ribbed mussel (*Geukensia demissa*) in a North American, mid-Atlantic saltmarsh. *Estuar. Coast. Shelf Sci.*, 56, 561–571.
- 2003b. Tidal and seasonal variation in the quantity and composition of seston in a North American, mid-Atlantic saltmarsh. *Estuar. Coast. Shelf Sci.*, 56, 547–560.
- Hyun, K.-H., I.-C. Pang, J. M. Klinck, K.-S. Choi, J.-B. Lee, E. N. Powell, E. E. Hofmann and E. A. Bochenek. 2001. The effect of food composition on Pacific oyster *Crassostrea gigas* (Thunberg) growth in Korea: a modeling study. *Aquaculture*, 199, 41–62.
- Jacobsen, T. R., J. D. Milutinovic and J. R. Miller. 1990. Observational and model studies of physical processes affecting benthic larval recruitment in Delaware Bay. *J. Geophys. Res. C Oceans Atmosph.*, 95, 20331–20345.
- Jordan, S. 1995. Population and disease dynamics of Maryland oyster bars: a multivariate classification analysis. *J. Shellfish Res.*, 14, 459–468.
- Kennedy, V. S. 1990. Anticipated effects of climate change on estuarine and coastal fisheries. *Fisheries*, 15, 16–24.
- 1994. Climate warming and estuarine and marine coastal ecosystems, in *Global Climate Change*, C. V. Mathai and G. Stensland, eds., Proc. Air and Waste Management Assoc., International Specialty Conf., Phoenix, AZ., 538–547.
- Kimmel, D. G. and R. I. E. Newell. 2007. The influence of climate variation on eastern oyster (*Crassostrea virginica*) juvenile abundance in Chesapeake Bay. *Limnol. Oceanogr.*, 52, 959–965.

- Kittiwanih, J., T. Yamamoto, O. Kawagushi and T. Hashimoto. 2007. Analyses of phosphorus and nitrogen cyclings in the estuarine ecosystem of Hiroshima Bay by a pelagic and benthic coupled model. *Estuar. Coast. Shelf Sci.*, 75, 189–204.
- Klinck, J. M., E. E. Hofmann, E. N. Powell and M. M. Deksheniaks. 2002. Impact of channelization on oyster production: a hydrodynamic-oyster model for Galveston Bay, Texas. *Environ. Model. Assess.*, 7, 273–289.
- Knowlton, N. 2004. Multiple “stable” states and the conservation of marine ecosystems. *Prog. Oceanogr.*, 60, 387–396.
- Krauter, J. N., S. Ford and W. Canzonier. 2003. Increased biomass yield from Delaware Bay oysters (*Crassostrea virginica*) by alteration of planting season. *J. Shellfish Res.*, 22, 39–49.
- Kreeger, D. A. 1993. Seasonal patterns in the utilization of dietary protein by the mussel, *Mytilus trossulus*. *Mar. Ecol. Prog. Ser.*, 95, 215–232.
- Kreeger, D. A., C. E. Goulden, S. S. Kilham, S. G. Lynn, S. Datta and S. J. Interlandi. 1997. Seasonal changes in the biochemistry of lake seston. *Freshw. Biol.*, 38, 539–554.
- Kreeger, D. A. and R. I. E. Newell. 2000. Trophic complexity between primary producers and invertebrate consumers in salt marshes, in *Concepts and Controversies in Tidal Marsh Ecology*, M. P. Weinstein and D. A. Kreeger, eds., Kluwer Press, NY, 187–220.
- Langdon, C. J. and R. I. E. Newell. 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. *Mar. Ecol. Prog. Ser.*, 58, 299–310.
- Loo, L-O. and R. Rosenberg. 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *J. Exp. Mar. Biol. Ecol.*, 130, 253–276.
- Lowry, O. H., N. J. Rosebrough, A. L. Farr and R. J. Randall. 1951. Protein measurement with the folin phenol reagent. *J. Biol. Chem.*, 193, 265–275.
- McCausland, M. A., M. R. Brown, S. M. Barrett, J. A. Diemar and M. P. Haesmai. 1999. Evolution of live microalgae and microalgal pastes as supplementary food for juvenile Pacific oysters (*Crassostrea gigas*). *Aquaculture*, 174, 323–342.
- MacIsaac, H. J., O. E. Johannsson, J. Ye, W. G. Sprules, J. H. Leach, J. A. McCorquodale and I. A. Grigorovich. 1999. Filtering impacts of an introduced bivalve (*Dreissena polymorpha*) in a shallow lake: application of a hydrodynamic model. *Ecosystems*, 2, 338–350.
- Meyers, M. B., D. M. Di Toro and S. A. Lowe. 2000. Coupling suspension feeders to the Chesapeake Bay eutrophication model. *Water Qual. Ecosystem Model.*, 1, 123–140.
- Munroe, D. M., J. M. Klinck, E. E. Hofmann and E. N. Powell. 2012. The role of larval dispersal in metapopulation gene flow: local population dynamics matter. *J. Mar. Res.*, 70, 441–467.
- Narváez, D. A., J. M. Klinck, E. N. Powell, E. E. Hofmann, J. Wilkin and D. B. Haidvogel. 2012. Modeling the dispersal of eastern oyster (*Crassostrea virginica*) larvae in Delaware Bay. *J. Mar. Res.*, 70, 381–409.
- Nevejan, N., I. Saez, G. Gajardo and P. Sorgeloos. 2003. Energy vs. essential fatty acids: what do scallop larvae (*Argopecten purpuratus*) need most? *Comp. Biochem. Physiol. B Biochem Mol. Biol.*, 134, 599–613.
- Newell, R. I. E. 2004. Ecosystem influence of natural and cultivated populations of suspension feeding bivalve molluscs: a review. *J. Shellfish Res.*, 23, 51–61.
- Norkho, J., C. A. Pilditch, S. F. Thrush and R. M. G. Wells. 2005. Effects of food availability and hypoxia on bivalves: the value of using multiple parameters to measure bivalve condition in environmental studies. *Mar. Ecol. Prog. Ser.*, 298, 205–218.
- Officer, C. B., T. J. Smayda and R. Mann. 1982. Benthic filterfeeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.*, 9, 203–210.

- Ortiz, M. and M. Wolff. 2002. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. *Ecol. Model.*, *148*, 277–291.
- Parker, A. E. 2005. Differential supply of autochthonous organic carbon and nitrogen to the microbial loop in the Delaware Estuary. *Estuaries*, *28*, 856–867.
- Pennock, J. R. 1985. Chlorophyll distributions in the Delaware estuary: regulation by light-limitation. *Estuar. Coast. Shelf Sci.*, *21*, 711–725.
- Pennock, J. R. and J. H. Sharp. 1994. Temporal alternation between light- and nutrient-limitation of phytoplankton production in a coastal plain estuary. *Mar. Ecol. Prog. Ser.*, *111*, 275–288.
- Pernet, F., R. Tremblay and E. Bourget. 2003. Biochemical indicator of sea scallop (*Placopecten magellanicus*) quality based on lipid class composition. Part II: larval growth, competency and settlement. *J. Shellfish Res.*, *22*, 377–388.
- Peterson, C. H. and R. Black. 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnol. Oceanogr.*, *32*, 145–166.
- Plutchak, A., K. Major, J. Cebrian, C. D. Foster, M-E. C. Miller, A. Anton, K. L. Sheehan, K. L. Heck Jr. and S. P. Powers. 2010. Impacts of oyster reef restoration on primary productivity and nutrient dynamics in tidal creeks of the north central Gulf of Mexico. *Estuaries Coasts*, *33*, 1385–1364.
- Powell, E. N., K. A. Ashton-Alcox, J. N. Kraeuter, S. E. Ford and D. Bushek. 2008. Long-term trends in oyster population dynamics in Delaware Bay: regime shifts and response to disease. *J. Shellfish Res.*, *27*, 729–755.
- Powell, E. N., E. A. Bochenek, J. M. Klinck and E. E. Hofmann. 2002. Influence of food quality and quantity on the growth and development of *Crassostrea gigas* larvae: a modeling approach. *Aquaculture*, *210*, 89–117.
- 2004. Influence of short-term variations in food on survival of *Crassostrea gigas* larvae: a modeling study. *J. Mar. Res.*, *62*, 117–152.
- Powell, E. N., E. E. Hofmann, J. M. Klinck and S. M. Ray. 1992. Modeling oyster populations I. A commentary on filtration rate. Is faster always better? *J. Shellfish Res.*, *11*, 387–398.
- Powell, E. N., J. M. Klinck, K. A. Ashton-Alcox and J. N. Kraeuter. 2009a. Multiple stable reference points in oyster populations: biological relationships for the eastern oyster (*Crassostrea virginica*) in Delaware Bay. *Fish. Bull.*, *107*, 109–132.
- 2009b. Multiple stable reference points in oyster populations: implications for reference point-based management. *Fish. Bull.*, *107*, 133–147.
- Powell, E. N., J. M. Klinck, X. Guo, S. E. Ford and D. Bushek. 2011. The potential for oysters, *Crassostrea virginica*, to develop resistance to Dermo disease in the field: evaluation using a gene-based population dynamics model. *J. Shellfish Res.*, *30*, 685–712.
- Powell, E. N., J. M. Klinck and E. E. Hofmann. 1996. Modeling diseased oyster populations. II. Triggering mechanisms for *Perkinsus marinus* epizootics. *J. Shellfish Res.*, *15*, 141–165.
- Powell, E. N., J. M. Klinck, E. E. Hofmann and S. Ford. 1997. Varying the timing of oyster transplant: implications for management from simulation studies. *Fish. Oceanogr.*, *6*, 213–237.
- Powell, E. N., J. M. Klinck, E. E. Hofmann and M. A. McManus. 2003. Influence of water allocation and freshwater inflow on oyster production: a hydrodynamic-oyster population model for Galveston Bay, Texas, USA. *Environ. Manage.*, *31*, 100–121.
- Powell, E. N., J. M. Klinck, E. E. Hofmann, E. A. Wilson-Ormond and M. S. Ellis. 1995. Modeling oyster populations. V. Declining phytoplankton stocks and the population dynamics of American oyster (*Crassostrea virginica*) populations. *Fish. Res.*, *24*, 199–222.
- Ren, J. S. and A. H. Ross. 2001. A dynamic energy budget model of the Pacific oyster *Crassostrea gigas*. *Ecol. Model.*, *142*, 105–120.

- Rheault, R. B. and M. A. Rice. 1996. Food-limited growth and condition index in the Eastern oyster, *Crassostrea virginica* (Gmelin 1791), and the bay scallop, *Argopecten irradians irradians* (Lamarck 1819). *J. Shellfish Res.*, 15, 271–283.
- Rothschild, B. J., C. Chen and R. G. Lough. 2005. Managing fish stocks under climate uncertainty. *ICES J. Mar. Sci.*, 62, 1531–1541.
- Ruesink, J. L., G. C. Roegner, B. R. Dumbauld, J. A. Newton and D. A. Armstrong. 2003. Contributions of coastal and watershed energy resources to secondary production in a northeastern Pacific estuary. *Estuaries*, 26, 1079–1093.
- Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, V. Burkett, D. R. Cayan, M. Fogarty, M. A. Harwell, R. W. Howarth, C. Mason, D. J. Reed, T. C. Royer, A. H. Sallenger and J. G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries*, 25, 149–164.
- Sharp, J. H., K. Yoshiyama, A. E. Parker, M. C. Schwartz, S. E. Curless, A. Y. Beauregard, J. E. Ossolinski and A. R. Davis. 2009. A biogeochemical view of estuarine eutrophication: seasonal and spatial trends and correlations in the Delaware Estuary. *Estuaries Coasts*, 32, 1023–1043.
- Shchepetkin, A. F. and J. C. McWilliams. 2005. The Regional Ocean Modeling System: a split-explicit, free-surface, topography following coordinates ocean model. *Ocean Model.*, 9, 347–404.
- Smaal, A. C., J. H. G. Verhagen, J. Coosen and H. A. Haas. 1986. Interaction between seston quantity and quality and benthic suspension feeders in the Oosterschelde, The Netherlands. *Ophelia*, 26, 385–399.
- Soniat, T. M. 1985. Changes in levels of infection of oysters by *Perkinsus marinus*, with special reference to the interaction of temperature and salinity upon parasitism. *N. E. Gulf Sci.*, 7, 171–174.
- Soniat, T. M., E. N. Powell, E. E. Hofmann and J. M. Klinck. 1998. Understanding the success and failure of oyster populations: the importance of sampled variables and sample timing. *J. Shellfish Res.*, 17, 1149–1165.
- Soniat, T. M. and S. M. Ray. 1985. Relationships between possible available food and the composition, condition, and reproductive state of oysters from Galveston Bay, Texas. *Contrib. Mar. Sci.*, 28, 109–121.
- Southworth, M. and R. Mann. 1998. Oyster reef broodstock enhancement in the Great Wicomico River, Virginia. *J. Shellfish Res.*, 17, 1101–1114.
- Steele, J. H. 1976. The role of predation in ecosystem models. *Mar. Biol. (Berl.)*, 35, 9–11.
- Steele, J. H. and E. W. Henderson. 1992. The role of predation in plankton models. *J. Plankton Res.*, 14, 157–17.
- Stickle, W. B. 1985. Effects of environmental factor gradients on scope for growth in several species of carnivorous marine invertebrates, in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms.*, J. S. Gray and M. E. Christiansen, eds., John Wiley and Sons, 601–616.
- Strathmann, R. R., L. Fenaux, A. T. Sewell and M. F. Strathmann. 1993. Abundance of food affects relative size of larval and postlarval structures of a mollusan veliger. *Biol. Bull. (Woods Hole)*, 185, 232–239.
- Stunz, G. W., T. J. Minello and L. R. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Mar. Ecol. Prog. Ser.*, 406, 147–159.
- Thompson, P. A., M. Guo and P. J. Harrison. 1996. Nutritional value of diets that vary in fatty acid composition for larval Pacific oysters (*Crassostrea gigas*). *Aquaculture*, 143, 379–391.
- Thompson, P. A. and P. J. Harrison. 1992. Effects of monospecific algal diets of varying biochemical composition on the growth and survival of Pacific oyster (*Crassostrea gigas*) larvae. *Mar. Biol. (Berl.)*, 113, 6445–654.
- Ulanowicz, R. E., W. C. Caplins and E. A. Dunnington. 1980. The forecasting of oyster harvest in central Chesapeake Bay. *Estuar. Coast. Mar. Sci.*, 11, 101–106.

- Versar. 2002. Oyster and water quality monitoring study for the main channel deepening project, Delaware Bay, New Jersey and Delaware. Final Report, U. S. Army Corps of Engineers contract #DCAW61-95-0-0011. Versar, Inc., Columbia, Maryland.
- Walsh, D. R. 2004. Anthropogenic influences on the morphology of the tidal Delaware River and Estuary: 1877–1987, M.S. Thesis, University of Delaware, 90 pp.
- Wang, Z., D. Haidvogel, D. Bushek, S. Ford, E. Hofmann, E. Powell and J. Wilkin. 2012. Circulation and water properties and their relationship to the oyster disease, MSX, in Delaware Bay. *J. Mar. Res.*, 70, 279–308.
- Ward, J. E., J. S. Levinton, S. E. Shumway and T. Cucci. 1998. Particle sorting in bivalves: *in vivo* determination of the pallial organs of selection. *Mar. Biol. (Berl.)*, 131, 283–292.
- Wikfors, G. H., J. W. Twarog Jr. and R. Ukeles. 1984. Influence of chemical composition of algal food sources on growth of juvenile oysters, *Crassostrea virginica*. *Biol. Bull. (Woods Hole)*, 167, 251–263.
- Wilson-Ormond, E. A., E. N. Powell and S. M. Ray. 1997. Short-term and small-scale variation in food availability to natural oyster populations: food, flow and flux. *Mar. Ecol.*, 18, 1–34.

Received: 10 October, 2011; revised: 21 June, 2012.