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

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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.

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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., Gallager 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 (Soniat, 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; Soniat 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., Dekshenieks 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°C 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 (Soniat 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 (lag value − value 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 ($Rs = expected value − observe value$). 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 ($−1.5 < Rs < 1.5$). 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 ($\frac{value−average value}{average value}$) 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 R² 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 R² of 0.11, confirming the limited influence of salinity in explaining variation in the food dataset. The regression equation used for subsequent analyses was:

\[
\text{Food} = 4.899 + (1.007 \times \text{Temperature Anomaly}) \\
+ (0.051 \times \text{abs(Temperature Anomaly)}) \\
- (0.849 \times \text{Site-specific Temperature Anomaly}) \\
- (0.227 \times \text{Year-specific Temperature Anomaly}) \\
+ (0.156 \times \text{Temperature Lagged 1 Month}).
\] (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 $Rs > 1.5$, $Rs < -1.5$, and $-1.5 < Rs < 1.5$.

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).
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
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.
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
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 \textit{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

\textit{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 \textit{et al.}, 2009). Inter-annual variation is manifested in the higher bay-wide food values in the spring and early summer.
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
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 \( \frac{\text{value} - \text{average value}}{\text{average value}} \).

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; Kittiwanich 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 \( \frac{\text{value} - \text{average value}}{\text{average value}} \).

Incorporating 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 \((\text{value} - \text{average value}) / \text{average value}\).

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 \[
\frac{(\text{value} - \text{average value})}{\text{average value}} \times 100.
\]

<table>
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<th>Tukey Grouping</th>
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</tr>
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<td>September 2010</td>
</tr>
<tr>
<td>F</td>
<td>−53.57</td>
<td>November 2010</td>
</tr>
<tr>
<td>F</td>
<td>−56.30</td>
<td>September 2009</td>
</tr>
</tbody>
</table>
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
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 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 \( \frac{\text{value} - \text{average value}}{\text{average value}} \).
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 preferred 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
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 \( \frac{\text{value} - \text{average value}}{\text{average value}} \).

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 Dekshenieks 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 (Dekshenieks 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 $(\text{value} - \text{average value}) \div \text{average value} \times 100$.

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

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 (Dekshenieks 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.

<table>
<thead>
<tr>
<th>Reef</th>
<th>Study Abundances</th>
<th>Estimated 1970–1984 Abundances</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Laminar Assumption</td>
<td>Vertical Mixing Assumption</td>
</tr>
<tr>
<td>Middle</td>
<td>0.23</td>
<td>0.06</td>
</tr>
<tr>
<td>Sea Breeze</td>
<td>0.65</td>
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</tr>
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<td>Cohansay</td>
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</tr>
<tr>
<td>Ship John</td>
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<td>0.12</td>
</tr>
<tr>
<td>Shell Rock</td>
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<td>0.07</td>
</tr>
<tr>
<td>Bennies</td>
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<td>0.02</td>
</tr>
</tbody>
</table>

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.

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