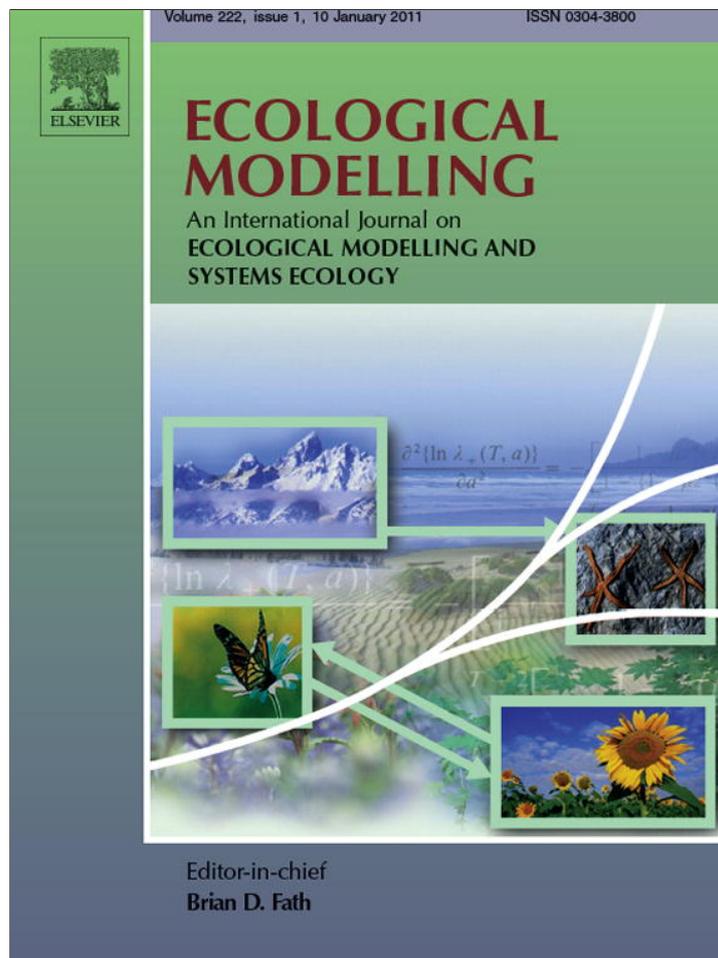


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

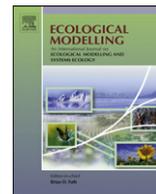
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Assessing biomass gains from marsh restoration in Delaware Bay using Ecopath with Ecosim

M.G. Frisk^{a,*}, T.J. Miller^b, R.J. Latour^c, S.J.D. Martell^d

^a School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794, USA

^b Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, MD 20688, USA

^c Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, VA, 23062 USA

^d Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, BC, Canada

ARTICLE INFO

Article history:

Received 13 November 2009

Received in revised form 10 July 2010

Accepted 19 August 2010

Available online 8 October 2010

Key words:

Ecopath with Ecosim (EwE)

Delaware Bay

Marsh

Restoration

ABSTRACT

The Delaware Bay ecosystem has been the focus of extensive habitat restoration efforts to offset fin-fish losses due to mortality associated with power plant water intake. As a result, a 45 km² or a 3% increase in total marsh area was achieved by 1996–1997 through the restoration efforts of the Public Service Enterprise Group (PSEG). To quantify the impact of restoration efforts on system productivity, an Ecopath with Ecosim model was constructed that represented all major components of the ecosystem. The model consisted of 47 functional groups including: 27 fish species, 5 invertebrate groups, 4 multi-species benthic groups, 6 multi-species fish groups, 3 plankton groups, 1 shorebird group and 1 marine mammal group. Biomass, abundance, catch, and demographic data were obtained from the literature or from individual stock assessments conducted for principal ecosystem components. A base Ecosim model was fitted to time series of key species in the Bay representing the period 1966–2003. To access the gains from marsh restoration, model simulations reflecting no restoration were conducted to estimate the productivity that would have been lost if restoration efforts had not occurred. The results indicated that restoration increased total ecosystem biomass by 47.7 t km⁻² year⁻¹. Simulations indicated increased biomasses across a wide range of species including important forage and commercially important species. The marsh restoration also significantly impacted ecosystem structure increasing the ratio of production-to-respiration, increasing system path length and decreasing the ratio of production-to-biomass.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Estuaries are ecologically and economically important features of the coastal landscape. They represent focal regions of production supported by the flow of river-borne nutrients into estuarine waters and the exchange of production with the coastal ocean. The reliability of estuarine production has meant that they serve as important nursery areas for many invertebrates and fishes. They also serve as important feeding grounds and migratory rest areas for birds and waterfowl. However, coupled with their close proximity to sources of human activity, these features, also make estuaries susceptible to anthropogenically driven changes, such as the alteration of shorelines (Seitz et al., 2006), eutrophication (Nixon, 1995; Smith et al., 2003; Kemp et al., 2005), depletion of bottom-water oxygen (Kemp et al., 2005; Diaz and Rosenberg, 2008; Breitburg et al., 2009), introduction of non-native species (Ruiz et al., 1997)

and over-exploitation of natural resources (Rothschild et al., 1994; Jackson et al., 2001).

The alteration and loss of shoreline estuarine habitats has been a prevalent issue in many estuaries (Rice, 2006; Seitz et al., 2006; McHorney and Neill, 2007; Bilkovic and Roggero, 2008). Specifically, habitats can be permanently lost as a result of shoreline development and hardening. Agricultural practices which alter riparian borders can destabilize shorelines and alter patterns of run-off and nutrient loading. Recognition of the impacts of habitat loss has generated interest in the restoration of estuarine habitats (Kennish, 2000). The spatial scale of restoration efforts has varied widely: at the smallest restoration scales are community-based shoreline clean-up programs, at intermediate scales are efforts to recreate specific habitats (Hinckle and Mitsch, 2005; Shin, 2007), and at larger scales are efforts to remediate entire estuaries (e.g., Baltic Sea – Kohn, 1998 and Chesapeake Bay – Kemp et al., 2005). However, the effectiveness of many of these programs remains unclear. Here, we report on an approach to quantify the benefits of shoreline restoration projects in the Delaware Bay that have been conducted to remediate against the loss of finfish produc-

* Corresponding author. Tel.: +1 632 631 3750.

E-mail address: mfrisk@notes.cc.sunysb.edu (M.G. Frisk).

tion associated with the intake of water to cool a large power plant.

The Delaware Bay is one of a series of important estuarine systems on the Atlantic seaboard of North America. The bay serves as the boundary between the states of Delaware and New Jersey (Fig. 1) and is approximately 2000 km². Like the majority of mid-Atlantic estuaries, the Delaware Bay supports a diverse flora and fauna (Dove and Nyman, 1995). Extensive fringing marshes of cordgrass (*Spartina* sp.) in brackish regions and riparian zones of freshwater tributaries provide important habitats for a variety of invertebrate and vertebrate species. Secondary production of benthic invertebrates in Delaware Bay ($P = 46,572 \text{ mg AFDW m}^{-2} \text{ year}^{-1}$; Maurer et al., 1992) is similar to that reported in other estuaries and is higher than that in the neighboring coastal regions. Numerous shorebirds (including the red knot, *Calidris canutus*, ruddy turnstone, *Arenaria interpres*, least sandpiper, *Calidris minutilla*, semipalmated sandpiper, *Calidris pusilla*, and sanderling, *Calidris alba*) use the bay as a refuge and for acquisition of energetic resources to support their annual migrations to wintering and nesting grounds (Tsipoura and Burger, 1999). The bay serves as a vital spawning ground for many species of fishes including weakfish, *Cynoscion regalis*, and striped bass, *Morone saxatilis*. In addition, the bay provides nursery grounds for many additional species including bluefish, *Pomatomus saltatrix*, and Atlantic menhaden (hereafter menhaden), *Brevoortia tyrannus*.

Power plants have used the waters of the Delaware Bay for cooling since 1977. The intake of huge volumes of water, and the associated impingement of fishes on filter screens, causes mortality to fish populations utilizing the bay. Since 1994, the Public Service Electric and Gas of New Jersey (PSE&G), now the Public Service Enterprise Group (PSEG), has been involved in preservation and restoration of marsh habitat in Delaware Bay as a means to off-

set the mortality caused by cooling water intake (Balletto et al., 2005; Hinckle and Mitsch, 2005). These restoration efforts alone have resulted in creation of 45.5 km² of wetland habitat, and thus, a 3% increase in the area of marsh habitat in the Delaware Bay ecosystem. The effects of this restoration effort have been assessed in a series of field studies conducted at the restoration sites. Kimball and Able (2007) reported that the nektonic assemblage on restored and undisturbed marshes were similar. Nemerson and Able (2005) found that juvenile fishes of the sciaenid family responded positively to the newly created wetland. Jivoff and Able (2003) reported that the new marshes may provide enhanced growth for blue crab, *Callinectes sapidus*. Focusing on the overall community, Able et al. (2008) reported that use of newly restored marsh was rapid, and relied on ease of access to a newly created habitat rather than on the specific floral and geomorphological characteristics of the habitat. However, these studies focus on diets, growth, production and patterns of use of individual species, or groups of species in the habitats themselves. What is missing is an assessment of the impact of restoration efforts on production in the broader ecosystem.

To evaluate the ecosystem level effects of the marsh restoration efforts, we developed a model to quantify the standing stocks and energy flows between the principal components of the Delaware Bay ecosystem. One possible approach would be to conduct a network analysis of the Delaware Bay (e.g., Baird and Ulanowicz, 1989). However, this approach assumes steady state conditions and may not be appropriate for a recently restored system. Instead, we developed a dynamic model of the bay's ecosystem which allowed us to estimate the temporal dynamics of production. For this application, we used Ecopath with Ecosim (EwE; Pauly et al., 2000), which has been frequently used to assess the structure and function of marine and estuarine ecosystems (Christensen et al., 2009), but to date, has not been used to evaluate the impacts of restoration efforts. EwE includes two main components: (1) a mass-balanced representation of the ecosystem network (Ecopath), and (2) a dynamic simulation model for evaluating fluctuations in biomass over time in response to changes in fishing policies, productivity and trophic interactions (Ecosim). Ecopath provides a static estimate of the state of the ecosystem during some initial reference period. Thus, Ecopath serves as a starting point for Ecosim and many of the Ecopath parameters are used to derive parameters that govern the dynamic ecosystem changes as a result of natural or anthropogenic factors.

Here we summarize this modeling effort by describing the underlying data and results of an EwE model of Delaware Bay, developed specifically to quantify the impact of marsh restoration on ecosystem production. For the purpose of this analysis, we define the model domain as that region of the Delaware Bay from the Chesapeake & Delaware Canal (C&D Canal) southward to the mouth of the Bay. However, ecological systems do not have abrupt borders, so these boundaries are an approximation. Where possible, we have aggregated biological and time series information for each model group within this region. Below, we provide a brief introduction to EwE and describe approaches to estimating individual parameters of the network and of the dynamic components of the model. Then, we describe the simulations conducted to assess the contribution of the restored habitat to changes in ecosystem dynamics. Any increase in production resulting from habitat alteration in Delaware Bay should be reflected in biomass indices for species in the ecosystem. As the restoration efforts have been completed, an ecosystem model of Delaware Bay should reflect biomass changes in the ecosystem for all associated trophic levels in the bay's food web induced by the increase in marsh habitat. Counter-intuitively, modification of the base Ecosim model structure is not needed to include marsh restoration effects. Rather, to capture changes in total system biomass that resulted from marsh restoration effects, the Ecosim model was run assuming a 3% decrease in marsh habitat

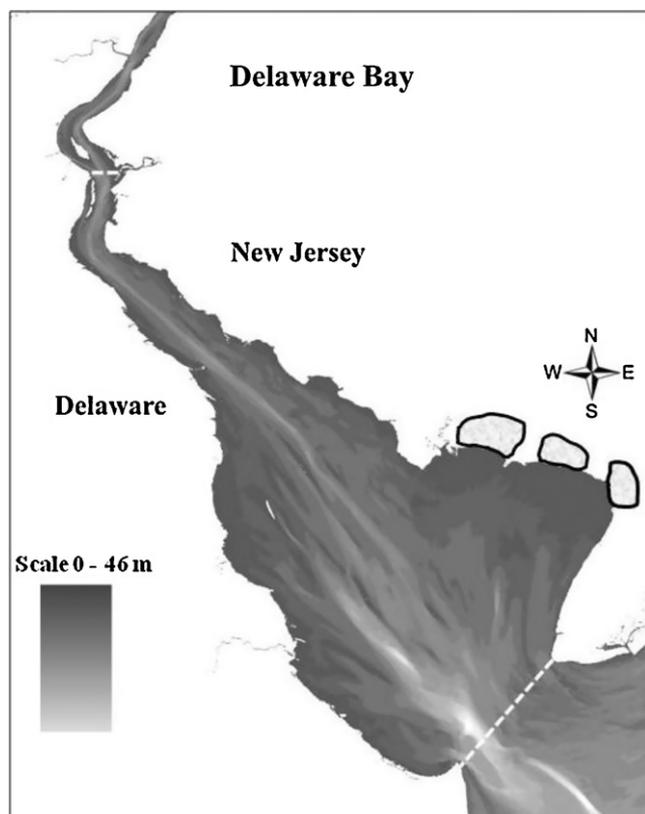


Fig. 1. Map of the Delaware Bay where shaded circles indicate restoration areas, scale represents depth in meters and dashed lines represent approximate model boundaries.

productivity from 1996 to 2003 (i.e., “non-restoration simulation”). This provides a measure of the production that would not have been realized if restoration efforts had not taken place. Results of additional simulations reflecting uncertainty in the total area restored are also presented.

2. Methods

The general structure and approach of EwE has been described in detail by Christensen and Pauly (1992), Walters et al. (1997), and Pauly et al. (2000), and is only summarized here. The first step in the modeling process is to develop a mass-balanced Ecopath network of trophically linked biomass pools. The biomass pools generally consist of either a single species or a group of species representing an ecological guild. Biomass pools are created for all major components of the ecosystem, including detritus and those at lower trophic levels such as plankton and invertebrates. When necessary each biomass pool can be split into life-history stanzas to represent different ecologically important life-history stages and ontogenetic dietary shifts (for example: larvae, juvenile and adults of any given species are likely to consume very different resources within an ecosystem). The central equation governing the standing stock and flows into and out of each pool can be written as:

$$B_i \left(\frac{P}{B} \right)_i EE_i = BA_i + E_i + Y_i + \sum_{j=1}^n B_j \left(\frac{Q}{B} \right)_j DC_{ji}, \quad (1)$$

where subscripts refer to different trophic groups, with i being the focal group and j referring to its predators. In Eq. (1), B is biomass, $(P:B)$ is the production-to-biomass ratio, which is equivalent to the total mortality rate in most instances (Allen, 1973), EE is the ecotrophic efficiency, or the fraction of the total mortality that is utilized within the modeled system, BA is the biomass accumulation rate, E is the net migration rate (emigration–immigration), Y is the fisheries catch; $(Q:B)$ is the consumption-to-biomass ratio, and DC is the average fraction (typically by weight) of prey in the diet.

Initial parameter estimates of standing stocks and flows often result in an unbalanced network. Thus, an important step is balancing the network such that there is no spontaneous creation of matter. This is ensured when all EE_i values are ≤ 1 . To balance our model, a systematic process of adjusting various input values was carried out to ensure all EE_i values were ≤ 1 . Input values that are suspected to have the greatest uncertainty were adjusted first.

The next step involved developing a time-dynamic simulation model, Ecosim, that re-expresses the static mass-balanced equations inherent to Ecopath as a system of coupled differential equations (Walters et al., 1997, 2000). In the modeling framework, Ecopath represents the initial states for Ecosim and is also used to derive parameters that determine overall growth efficiencies and predator–prey functional responses based on additional user-specified parameters in Ecosim. This system of equations is used to represent the spatially aggregated dynamics of entire ecosystems, and is combined with delay-difference age/size-structured equations for model groups that have complex life histories and selective harvesting of older animals (multi-stanza groups). Ecosim uses coupled differential equations to link a series of linear equations representing production for each group with the following equation (Walters et al., 1997, 2000; Christensen and Walters, 2004):

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^n c_{ji} - \sum_{j=1}^n c_{ij} + I_i - (M_i + F_i + e_i)B_i \quad (2)$$

where subscripts are as before and g is growth efficiency, c_{ji} is the consumption of biomass pool i , c_{ij} is the consumption by biomass pool i , I is the rate of immigration, M is the instantaneous natural mortality, F is the instantaneous fishing mortality, e is the rate of

emigration. Together, Eq. (2) and the underlying delay-difference equations representing age/size-structure, represent the dynamics of an ecosystem (Walters and Martell, 2004).

The link between predator and prey is a key element in Ecosim and is expressed in the consumption or “flow” rates among linked biomass pools. Consumption of prey i by predator j is based on foraging arena theory (Walters and Juanes, 1993), and this is represented in Ecosim as:

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}B_iB_j}{(2v_{ij} + a_{ij}B_j)}, \quad (3)$$

where a is the rate of effective search for prey i and v is the behavioral exchange rate between vulnerable and invulnerable prey pools. Conditional estimates of a_{ij} are obtained by solving Eq. (3) using input values of B_i , B_j , and Q_{Bij} from Ecopath. The estimates of a_{ij} are conditional on the user-specified value of v_{ij} , and this parameter essentially determines the shape of the predator–prey functional response; high values of v_{ij} ($v_{ij} > 30$) imply a top-down control or mass-action consumption rates, where as lower values of v_{ij} ($1.0 < v_{ij} < 15$) imply a donor control or type-II functional response.

2.1. Data and parameter estimation

We described the Delaware Bay ecosystem as comprising 47 biomass pools including 27 fish species, 5 invertebrate groups, 4 multi-species benthic groups, 6 multi-species groups, 3 plankton groups, 1 shorebird group and 1 marine mammal group. The marsh habitat was represented by meiofauna, macrofauna and biomass pools of marsh fishes (Fig. 2). Full details of the estimation procedures for individual parameters for each biomass pool are provided in Frisk et al. (2006) and are only summarized here.

The network model was developed for expected biomasses for the reference year 1966. For each biomass pool, estimates of standing stocks were either taken directly from the literature, or developed from analysis of raw data. For the principal fish and shellfish species, annual production was estimated from reconstructions of historical biomass and recruitment (stock assessments) and estimated losses from anthropogenic sources. Ecosim can be fitted to a time series of catches and species abundances alone. However, without estimates of exploitation rates, Ecosim has little information to calibrate species or group mortality. In order to correctly calibrate an Ecosim model, single-species assessments were needed to estimate a time series of fishing mortality as well as abundances for at least the ecosystem’s key species. We developed stock assessments for Atlantic croaker (*Micropogonias undulatus*, hereafter croaker), menhaden and bluefish to estimate times series of exploitation rates (see Frisk et al., 2006 for assessments). In addition, previously published assessments provided times series of exploitation rates for blue crab and striped bass (ASMFC, 2004; Kahn and Helser, 2005). We note that an unrealistic “knife-edged” increase in striped bass biomass was observed from the Delaware Department of Natural and Environmental Control (DNREC) surveys during the 1990s when compared to the continuous increase (of similar magnitude) derived from the coast-wide stock assessment (ASMFC, 2004). The coast-wide assessment was used in place of the DNREC survey for striped bass (ASMFC, 2004).

The dynamics of the Delaware Bay ecosystem were then modeled for the period 1966–2003. Biomass and catches were measured as wet weight. Time series of species biomass trends were developed from the DNREC Delaware Bay 30 ft trawl survey for the full time period. Catch time series for exploited species came from the National Oceanic Atmospheric Administration’s Fisheries Statistics Division. The Ecosim model was fitted to all time series simultaneously during initial model runs. Subsequently, some time

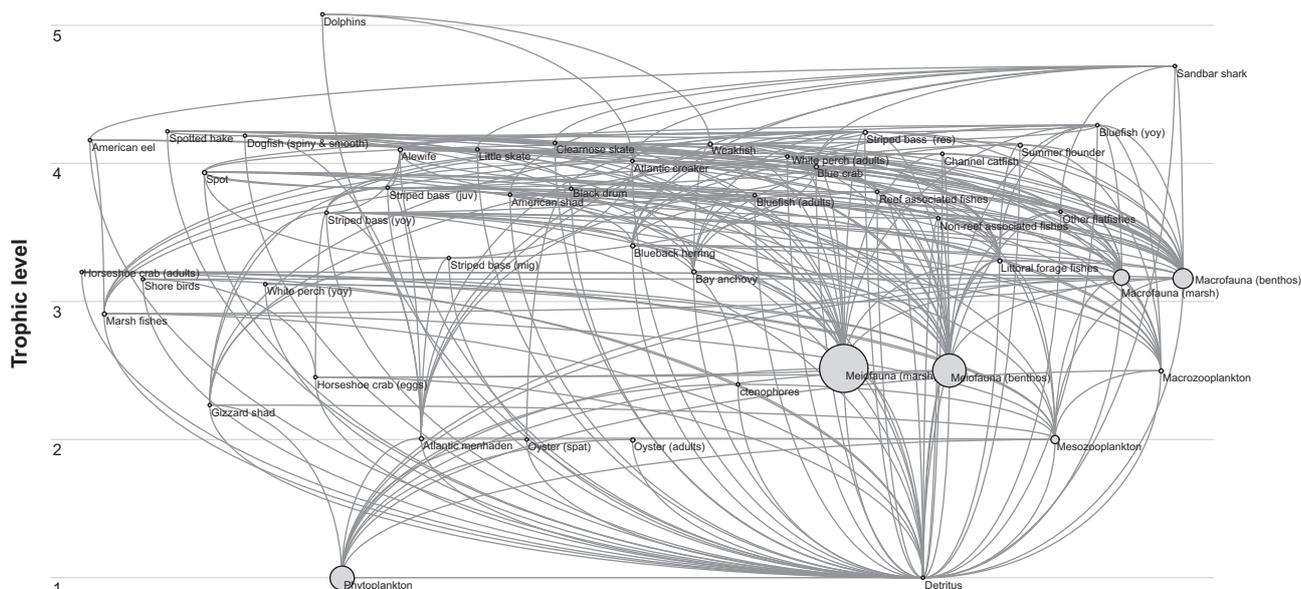


Fig. 2. Flow diagram created in EwE depicting all biomass pools (circles) and the strength of biomass flows (lines size). In the diagram *mig* stands for migratory, *res* for resident, *yoy* for young of year and *juv* for juvenile.

series were removed from the fitting algorithm if there were concerns that the data were not representative, if sampling methods did not adequately represent the species abundance trends, and/or if data were uninformative. The fitted model allowed 40 of the 233 total ν values to be adjusted to minimize the model log sum of squares while the remaining values were assumed to be $\nu=2$, a middle value between top-down and bottom-up control.

We note that blue crab landings for 1966–1978 were assumed to be 0.50 t km^{-2} , the average of 1979–1982, to fill a gap in the landings time series. Further, the model calculated catches rather than statistically fitting to observations for American eel, black drum, dogfish, horseshoe crab, spot, oysters, weakfish, and white perch. Instead, we opted to subtract the catches over time for these model groups because time series information on historical fishing mortality rates were not available, nor was there sufficient information to conduct a single-species stock assessment in order to estimate the historical fishing mortalities. Thus, these groups are conditioned on historical catches to ensure sufficient biomass would have to be present in the system to explain the historical catch series. This provides a lower bound on the product of the initial biomass inputs for individual groups and the production-to-biomass ratio.

2.2. Habitat restoration and system production

Because restoration has occurred, we compared the base simulation to marsh reduction (non-restoration) simulation in which the area of salt marsh was reduced by 3–9%. To achieve this, forcing functions that appropriately alter biomass can be applied to marsh related groups including meiofauna and macrofauna. We equated a 3–9% increase in biomass to a 3–9% decrease in the ($P:B$) ratio assuming constant production rates (i.e., $Z = P:B$). Thus, to mimic the ecosystem state had the restoration not occurred, an annual forcing function was assumed with the intervention occurring between 1996 and 2003. Both base and non-restoration models included constant marsh meiofauna and macrofauna biomass values from 1966 to 2003; except during 1996 to 2003 in the non-restoration simulation. This was done to keep models structurally similar and preliminary runs allowing marsh meiofauna and macro-

fauna to vary resulted in effectively constant predicted biomass values.

2.3. Ecosystem metrics

Indices reflecting basic system productivity and structure, network analysis and biodiversity were estimated for Delaware Bay. Basic productivity and structure were assessed by estimating primary productivity (P_p), total production (P), respiration (R), the ratio of $P_p:R$ and production to biomass ($P:B$) ratio. The ratio of $P_p:R$ provides a measure of system development. The ratio of $P:B$ provides a measure of ecosystem maturity with larger values being indicative of a developing system and lower values indicating a mature system (Odum, 1969; Christensen, 1995). Network analysis was used to estimate the developmental stage, energy flow and trophic behavior of the ecosystem by estimating total throughput (T), capacity (C), mean path length (PL), and Finn's cycling index (FCI) (Finn, 1976, 1980; Ulanowicz, 1986; Christensen, 1995; Shannon et al., 2009). Total system throughput measures the size of the ecosystem represented as "flows" (Ulanowicz, 1986). Throughput may represent a better measure of ecosystem size than biomass as it accounts for individual species' parameters such as production, respiration and consumption (Ulanowicz, 1986). Capacity measures the scope for further ecosystem development (Kay et al., 1989) and is expected to increase as a system matures and provides an upper limit to ascendancy (Ulanowicz, 1986; Christensen 1995; Cruz-Escalona et al., 2007). The ratio of ascendancy and capacity was estimated to provide a measure of the ecosystem's organization (Ulanowicz, 1986). Mean path length provides the average number of "groups that an inflow or outflow passes through" (Finn, 1980; user guide). Finn's cycling index (FCI) provides a measure of the proportion of total throughput that is recycled (Finn, 1976) and indicates system maturity (Christensen, 1995). Kempton's $Q(Q)$ index measures the biomass of species with trophic levels greater than 3, where an increase in the index indicates an increase in upper level biomass diversity (Kempton and Taylor, 1976; Shannon et al., 2009).

These ecosystem metrics were calculated for the base model averaged for all years and compared to the "non-restoration" simulation for the years 1996–2003. Significant differences between

the base model and the “non-restoration” simulation were assessed using a paired, two-sample means *t*-test.

3. Results

3.1. Ecopath

A balanced Ecopath model of Delaware Bay was achieved through an iterative process by changing input values until the model was mass balanced. The iterative approach in balancing an Ecopath model is, to some extent, subjective, and we acknowledge other users may produce different results. Wherever possible we used the data pedigree within Ecopath as a guide in model balancing by first changing highly uncertain parameters, followed by parameters with tighter confidence levels to reduce potential subjectivity (Table 1). Dietary patterns are presented by the magnitude of the flows in Fig. 2, and are detailed fully in Frisk et al. (2006).

3.2. Ecosim

The Ecosim model was fitted to observed biomass trends for croaker, menhaden, bluefish, clearnose skate, dogfish, horseshoe crab, spiny dogfish, striped bass and weakfish. Additionally, the model was fitted to catch time series for croaker, menhaden, blue crab, bluefish, striped bass and summer flounder. Overall the base model fitted biomasses and catches with a log sum of squares = 215.5. The model captured observed values and trends closely for menhaden and spiny dogfish and to a lesser extent for croaker, bluefish, horseshoe crab, and striped bass while the initial observed and predicted biomass levels were not matched for clearnose skate and in recent years were not matched for weakfish (Fig. 3). The fitted base model failed to capture the recent increase in weakfish. The base model captured the dynamics of the fisheries with predicted and observed catches showing similar trends and in most cases absolute values for all species; the exceptions being some spikes in reported landings and initial landings for menhaden, summer flounder, and blue crab, together with an under estimation of landings in croaker and in recent years for bluefish (Fig. 4).

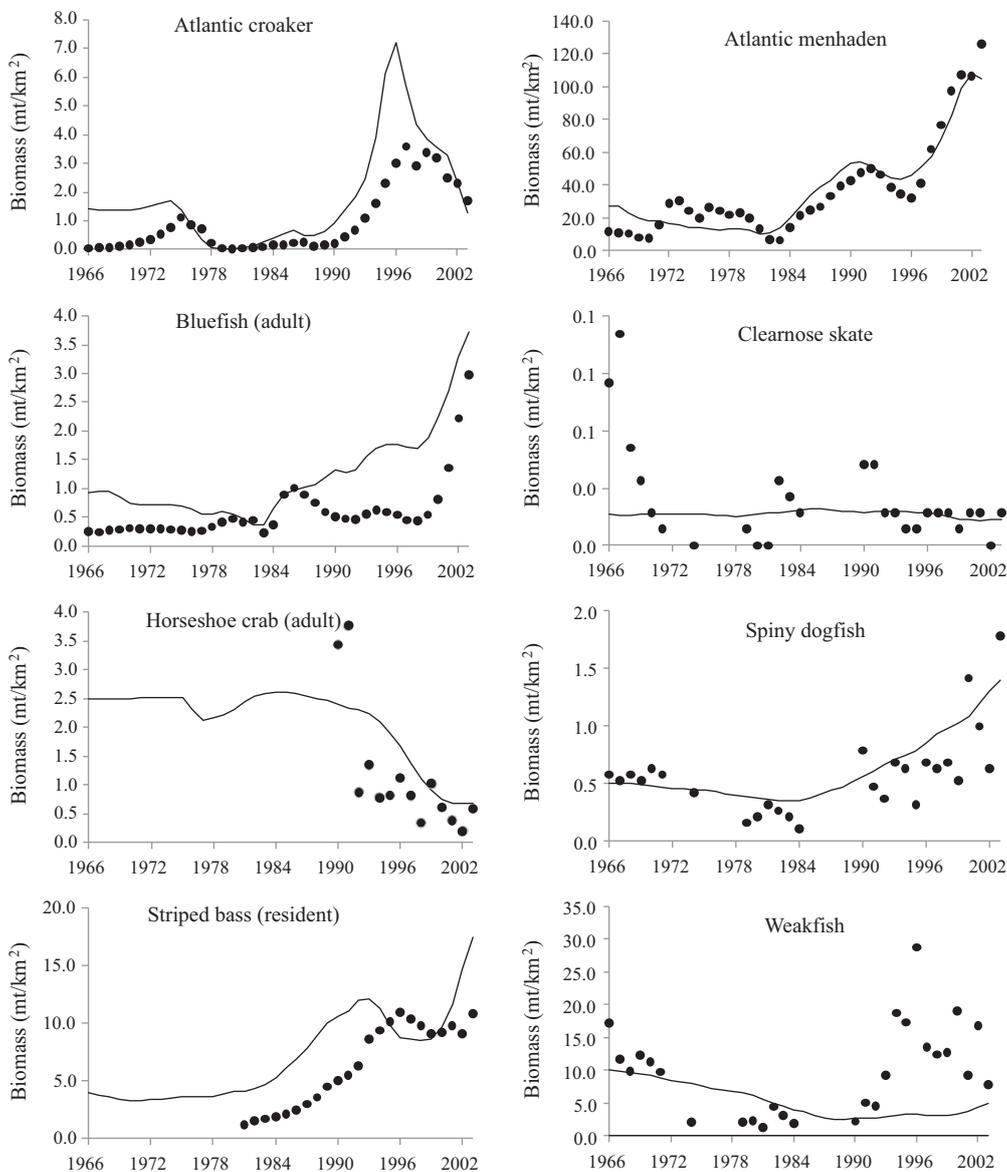


Fig. 3. Observed (dots) and predicted (solid lines) biomass for the Ecosim model for croaker, menhaden, bluefish (adults), clearnose skate, horseshoe crab (adult), spiny dogfish, striped bass (adults) and weakfish.

Table 1

Data pedigree and model inputs for the balanced Ecopath model where B is biomass, P:B is the ratio of production-to-biomass, Q:B is the ratio of consumption to biomass, diet column is for pedigree only, EE is ecotrophic efficiency and Catch is measured in $t\ km^{-2}$. Color scale represents the level of confidence in data inputs.

Species	B	P/B	Q/B	Diet	EE	Catch
Alewife	4.000	1.100	8.400			
American eel		0.100	2.900		0.500	0.055
American shad		1.050	3.100		0.800	
Atlantic croaker	1.400	1.700	3.300			0.000
Atlantic menhaden	26.000	1.100	28.000			5.000
Bay anchovy		2.400	9.700		0.990	
Black drum	1.500	0.100	2.200			0.003
Blue crab		1.400	19.078		0.950	0.200
Blueback herring		0.700	6.100		0.990	
Bluefish (adults)	0.950	0.800	3.100			0.097
Bluefish (yoy)	0.067	4.700	15.403			
Channel catfish	0.012	0.270	1.600			
Clearnose skate		0.550	3.800		0.990	0.001
Ctenophores		8.800			0.250	
Dogfish (Spiny and smooth)	0.500	0.430	4.770			0.000
Dolphins	0.000	0.130	1.400			
Gizzard shad	3.400	0.800	14.500			
Horseshoe crab (adults)	2.000	0.600	3.000			
Horseshoe crab (eggs)	0.177	6.500	19.634			0.016
Little skate	0.290	0.370	4.400			
Littoral fishes	15.000	1.900	20.000			
Marsh fishes		1.200	3.650		0.950	
Non reef fishes	1.400	1.000	2.000			
Other flatfishes	2.800	0.700	10.000			
Oyster (adult)	9.600	0.200	2.020			0.248
Oyster (spat)	2.224	6.000	8.819			
Reef fishes	3.500	0.800	2.800			
Sandbar shark	0.107	0.230	1.400			
Shore birds	0.080	0.511	150.000			
Spot	5.000	1.000	6.200			0.009
Spotted hake	1.800	0.600	5.100			
Striped bass (juv)	0.000	0.461			1.000	
Striped bass (mig)	3.313	0.500	2.086			0.030
Striped bass (res)	6.000	0.510	3.643			0.060
Striped bass (yoy)	0.544	6.500	29.631			
Summer flounder		0.600	2.600		0.100	0.550
Weakfish	10.000	0.300	3.000			0.210
White perch (adults)	1.000	0.400	3.700			0.031
White perch (yoy)	0.456	3.000	12.716			
Meiofauna (marsh)	6000.000	7.100				
Meiofauna (benthic)	600.000	1.900				
Macrofauna (marsh)	900.000	3.000				
Macrofauna (benthic)	2400.000	6.800				
Mesoplankton	200.000	25.000				
Macroplankton		8.000			0.900	
Phytoplankton		60.000			0.950	
Detritus	1.000	-92.000			0.000	

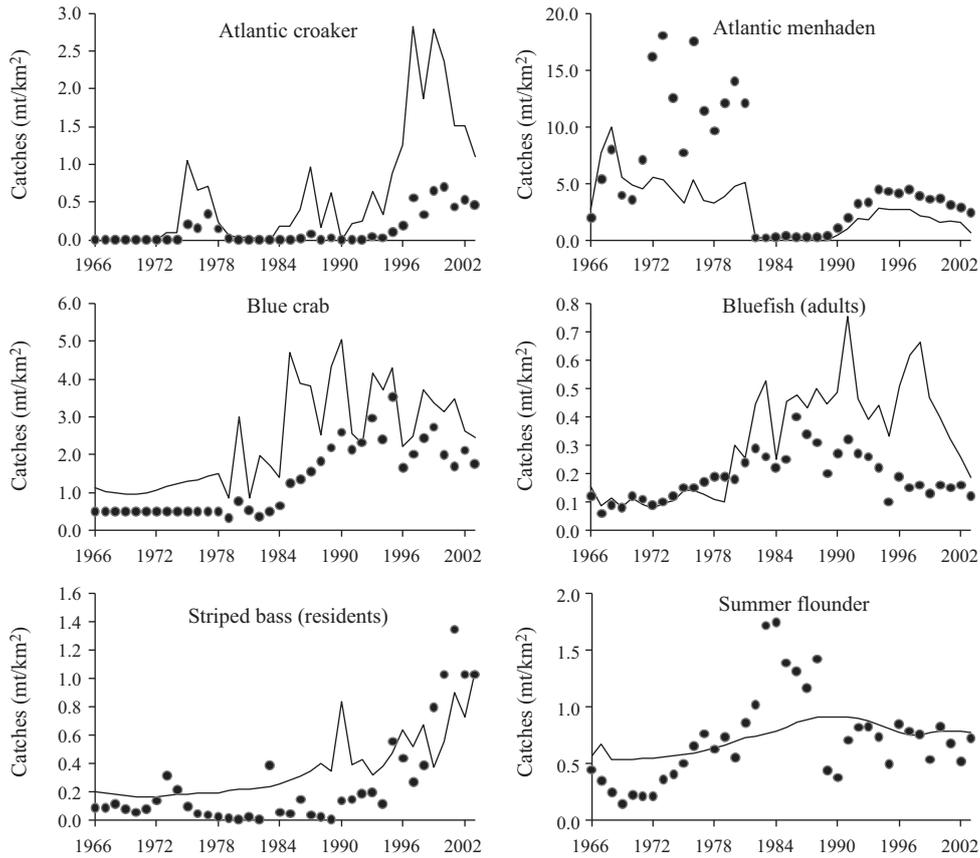


Fig. 4. Observed (dots) and predicted (solid lines) catches for the Ecosim model for croaker, menhaden, blue crab, bluefish (adults), striped bass (adults) and summer flounder.

3.3. Total system biomass trends

The base model showed that total standardized biomass for upper trophic level groups declined during the late 1960s and 1970s and increased during the 1980s and 1990s (Fig. 5). Lower trophic level biomass stayed relatively constant throughout the time series.

3.4. Marsh restoration results

Under the base model, the total system biomass summed from 1996 to 2003 was 39,259 t km⁻². Under the “no restoration” simulation the total system biomass from 1996 to 2003 was =38,877 t km⁻², a 1% reduction in total biomass. We reiterate that

we did not include biomass groups representing meiofauna (marsh) and macrofauna (marsh) in the above comparisons in order to measure the trophic impact of the marsh restoration and not just a “forced change” in marsh biomass groups. Model estimates indicated that without marsh restoration from 1996 to 2003 the total system biomass would have been 381.6 t km⁻² less than in the presence of the restoration. Annually, this corresponds to a total system biomass of 47.7 t km⁻² year⁻¹.

Results indicated that system production of biomass realized by marsh restoration efforts was not evenly distributed among all trophic groups (Fig. 6). Benthic meiofauna (155.2 t km⁻²), benthic macrofauna (93.9 t km⁻²), phytoplankton (76.2 t km⁻²) and mesozooplankton (25.7 t km⁻²) benefited most from the restoration in absolute terms. While the vast majority of biomass groups benefited from marsh restoration, a few biomass groups were impacted negatively by the marsh restoration. The model resulted in slight decreases in biomass of marsh fishes, blue crabs, littoral zone forage fishes, bluefish and American eel.

In addition to the 3% marsh reduction in the “non-restoration” scenario, we ran simulations for a 6% reduction and a 9% reduction to account for the uncertainty over the total amount of marsh area restored. For all of these scenarios, we compared the biomass of lower trophic level species vs. upper trophic level species (Fig. 7).

3.5. Ecosystem structure

Base model 1966–2003: The average system primary production was 78,433.0 t km⁻² year⁻¹, production averaged 146,376.6 t km⁻² year⁻¹ and respiration averaged 124,914.3 t km⁻² year⁻¹ (Table 2). The ratio of production-to-biomass was 12.7 and the ratio of production-to-respiration was 0.6 indicating a system that is developing. Throughput and capacity

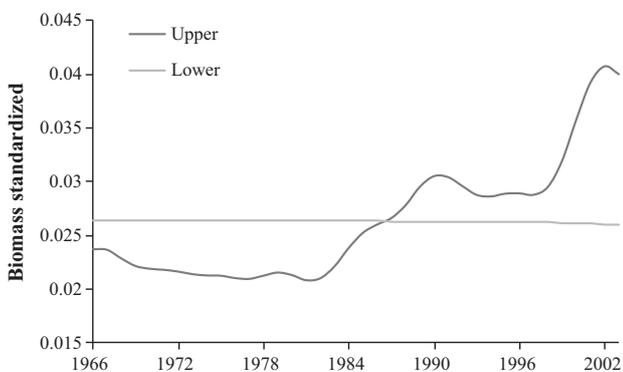


Fig. 5. Predicted total system biomass for the Ecosim model for upper trophic species including all biomass groups that are not meiofauna, macrofauna, phytoplankton or detritus and lower trophic groups including all meiofauna, macrofauna, phytoplankton and detritus biomass groups.

Table 2
Ecosystem structure was measured with the following indices (primary production (Pp), total production (P), respiration (R), the ratio of system production and total biomass (P:B), and the ratio of production and respiration (P:R)); network analysis (throughput (T), developmental capacity (C), ascendancy (A), average path length (PL), and Finn's cycling index (FCI)); and biodiversity (Kempton's Q (Q)) where the "base" model (includes marsh restoration) for the period 1966–2003, SD is standard deviation, "restoration" represents the "base" model for the period 1996–2003, "no restoration" is the reduced marsh productivity simulation for the period 1996–2003, "Diff." is the difference between the restoration and no restoration simulations, "Sig." is the significance of a *t*-test comparing the mean difference between restoration and no restoration simulations and % Δ is percent change.

	Base	SD	Restoration	SD	No restoration	SD	Diff.	Sig.	% Δ
<i>System indices</i>									
Primary production (Pp)	78433.03	362.91	77899.62	342.17	77863.74	349.40	35.89	0.08	0.05
Production (P)	146376.59	368.85	145837.81	353.09	148022.78	345.32	-2184.96	0.00	-1.50
Respiration (R)	124914.31	583.39	125707.92	632.85	129752.48	609.82	-4044.56	0.00	-3.22
Production/biomass ratio	12.68	0.01	12.67	0.01	12.70	0.01	-0.02	0.00	-0.19
Production/respiration (P:R)	0.63	0.01	0.62	0.01	0.60	0.01	0.02	0.00	3.16
<i>Network analysis indices</i>									
Throughput (T)	355310.31	975.47	356636.28	1065.69	366930.01	1047.33	-10293.73	0.00	-2.89
Developmental capacity (C)	1390027.17	6923.45	1398850.67	6893.39	1425511.28	6373.35	-26660.61	0.00	-1.91
Path length (PL)	3.07	0.01	3.06	0.01	3.04	0.01	0.02	0.00	0.51
Finn's cycling index (FCI)	27.94	0.03	27.99	0.02	28.05	0.03	-0.07	0.08	-0.23
<i>Biodiversity</i>									
Kempton's Q (Q)	6.40	0.47	5.97	0.29	6.03	0.35	-0.07	0.06	-1.10

results indicated that a 3% increase in marsh area resulted in a gain in total ecosystem biomass of $47.7 \text{ t km}^{-2} \text{ year}^{-1}$. Further, the results indicated that in addition to expected benefits that accrued to groups representing benthic invertebrates, several important forage and commercially important fish species also benefited from the restoration including large increases in menhaden, bay anchovy, and striped bass. Biomass gains were realized by the majority of species, but gains were not evenly distributed as species and groups such as macrozooplankton, blueback herring and menhaden increased over 3% and a few species decreased slightly. We view the increase in oyster biomass that resulted from the restoration as equally significant, given the well-documented role of this species as an ecosystem engineer (Newell et al., 2007; Rodney

and Paynter, 2006). Model results also indicated that ecosystem structure was also significantly impacted by the restoration with increases in the ratio of P:R and average path length (PL).

Previous field studies have documented the local benefits of marsh restoration efforts in the Delaware Bay. For example, field studies found that species abundance was greater or equal in restored sites for blue crabs (Jivoff and Able, 2003), weakfish, spot, croaker (Nemerson and Able, 2005), and striped bass (Tupper and Able, 2000). Our model results place these local studies in a broader context. Model results indicated that croaker, weakfish and spot all benefited from the restoration. In contrast, model results suggested a slight decline in blue crab abundance, likely a result of predator-prey interactions. We ran simulations to address the uncertainty in the total area of wetlands that had been restored (from the base level of 3% with additional simulations or 6% or 9%). In all simulations, the estimated biomass lost if restoration efforts had not taken place increased. Comparisons of the base model and the "non-restoration" simulation for the years 1996–2003 indicated restoration resulted in significant changes with P:R changing $3.16\% \Delta$, a $-3.22\% \Delta$ decrease in respiration, a $-2.9\% \Delta$ decrease in T and smaller changes in C, P, and PL. Ecological theory suggests that production is high in immature systems compared to biomass, and that biomass increases with development (Christensen, 1995). Thus, the high P:B ratio estimated for Delaware Bay indicates an immature or developing state. The Pp:R is expected to reach 1.0 for mature systems and lower values indicate high levels of remineralization and significant organic pollution (Odum, 1971; Christensen, 1995). The estimated Pp:R ratio of 0.63 is very low and out of the common range reported by Christensen (1995) of 0.8–3.2. Odum (1971) describes systems with low Pp:R as being characterized as heterotrophic and relying on imported organic matter. This result is not surprising considering Delaware Bay has a long history of nutrient enrichment and reduced nitrogen and carbon from sewage effluents (Sharp, 2010). Based on the P:B and Pp:R values Delaware Bay can be characterized as an immature system with significant organic inputs. The results of our simulations indicated that the restoration efforts decreased the P:B ratio, but only by $-0.19\% \Delta$, while the Pp:R ratio increased $3.16\% \Delta$.

The ratio of A:C for an ecosystem provides a measure of its organization. The Delaware Bay A:C estimate of 21% indicates the system is relatively disorganized. Simulations indicated that the marsh restoration did not result in meaningful changes to the ratio. The Delaware Bay ratio is low compared to the Chesapeake Bay, MD (29.7%, Monaco and Ulanowicz, 1997), Narragansett Bay, RI (31.6%, Monaco and Ulanowicz, 1997) and previous estimates

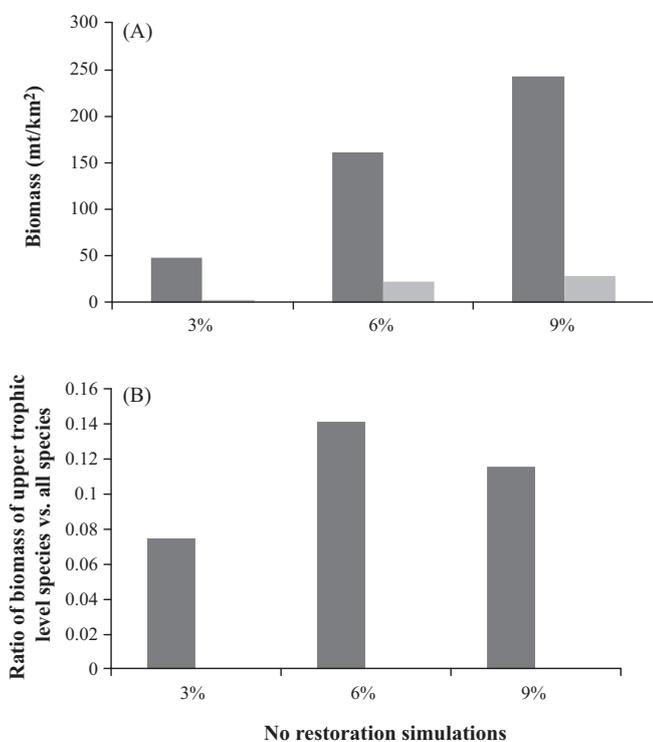


Fig. 7. The annual gains in biomass for upper (light grey) vs. lower trophic (dark grey) levels from restoration for marsh reduction simulations for a 3%, 6% and 9% reduction in marsh productivity (A) and the ratio of biomass of upper trophic level species vs. all species (B).

for the Delaware Bay (31.2, Monaco and Ulanowicz, 1997). Differences in previous estimates for Delaware Bay and other systems can result, in part, from different approaches to model development including model organization level and structure. However, given the present analysis Delaware Bay is not near its theoretical capacity for development and is in an immature or developing state.

Path length (PL) was significantly higher in the base model compared to the “non-restoration” simulation. As systems mature PL is expected to increase suggesting that restoration has maintained, or slightly increased, the diversity of flows between trophic groups. Kempton’s *Q* indicated that upper level trophic diversity was higher in the “non-restoration” simulation, although not substantially. This slight decrease in *Q* in the base simulation may have resulted from the uneven impacts of restoration on species leading to a shift in biomass within upper trophic species. For example, benthic macrofauna, summer flounder, striped bass adults and migratory striped bass benefited the most from marsh restoration, while other predators such as bluefish, blue crab and marsh macrofauna declined. The decrease of 1.09% in upper trophic level diversity associated with marsh restoration may not signify a shift in overall diversity, but a relative redistribution of species biomasses resulting from structural changes following restoration.

Finn’s cycling index measures the proportion of a system’s activity that is recycled (Finn, 1976; Rybarczyk and Elkaim, 2003). Odum (1971) argued that mature, highly organized systems, will have a high proportion of recycling and the index is commonly used as a measure of ecosystem development (Rybarczyk and Elkaim, 2003). The Delaware Bay estimate of 27.94% indicates the system recycles flows in a similar proportion to the Chesapeake Bay (24.1%, Monaco and Ulanowicz, 1997) but less than for Narragansett Bay, RI (48.2%, Monaco and Ulanowicz, 1997) and for previous estimates for the Delaware Bay (37.3%, Monaco and Ulanowicz, 1997). Here again the results indicate the system is not highly organized. Further, the “non-restoration simulation” did not result in meaningful changes to the proportion of total flows being recycled in the Bay.

Ecosystem models commonly have many unique but different parameter combinations that would explain the data equally well. Our main objective in fitting the Ecosim model to the observed time series (annual abundance and catch estimates, etc.) was to develop a parsimonious parameter set that, to the extent possible, reduced the uncertainty associated with our findings. Overall, our Ecosim model captured the dynamics of the system reasonably well, fitting the time series of biomass for 8 species and time series of catches for 6 species. The lack of fit in predicted biomass in recent years for several species can result from many factors including errors in catch and biomass (cpue) estimates or ecological factors not captured in current model structure (i.e., changes in movement patterns or diet preferences). Although optimal fits to catch data were not achieved in all cases, overall trends matched well and biomass estimates were well fit in most cases.

All models fail to capture the full dynamics of an ecosystem. Here we have defined boundaries, parameter estimates and used the software Ecopath with Ecosim to develop an ecosystem model of Delaware Bay. While this model represents an attempt to describe the dynamics of the Delaware Bay ecosystem it also highlights many of the areas needed for future modeling attempts. Modeling the food web dynamics of estuarine ecosystems is challenging since many species spend only part of their life-history within the defined “ecosystem boundaries.” Many of the species spend large portions of their life cycle outside the defined boundaries including menhaden, croaker, bluefish, striped bass, and weakfish. Our simulations addressed these migrations by either assuming a fraction of the mortality for each species was accrued outside the system or by defining a stanza that represents the period that the species was outside the ecosystem. In many cases definitions of the time

spent in and out of the system were imprecise, thereby adding uncertainty to the model structure and parameterization. Finally, uncertainty arises in the paucity of species biomass data estimated in the Delaware Bay ecosystem itself. Much of the data that went into the Ecopath parameter estimates came from research conducted in the Delaware Bay ecosystem; however, many parameter estimates were taken from research conducted in other ecosystems such as the Chesapeake Bay. Using data values from other systems and models adds uncertainty to parameter inputs for the Delaware Bay model.

A commonly held view is that restoration efforts increase species biodiversity and, as a result, ecosystem health. Odum (1971) argued that ecosystems develop by increasing complexity, internalizing flows and increasing in size and complexity. Further, he articulated the negative impacts organic pollution can have on the structure and flows of ecosystems reducing systems to an earlier successional stage. The associated concepts of system maturity and ecosystem stability have been the subject of decades of debate with some authors arguing that mature systems are more stable (i.e., Odum, 1971; many others); while other have suggested immature systems show higher stability (i.e., Pimm, 1984, many others). Recently, Worm et al. (2006) conducted a meta-analysis that did demonstrate advantages to biodiversity in fishery ecosystems. However, Ulanowicz (2003) points out that “worldwide efforts to preserve biodiversity have transpired largely in the absence of a theoretical justification” and offers the concept of ascendancy to relate diversity and stability. In the current effort, it was not our intent to enter this debate; but instead, to use existing ecosystem metrics developed for the Delaware Bay to measure the response of an ecosystem to restoration. We estimated several ecosystem metrics that can be compared between the base model and the no restoration simulations to measure the impacts of restoring the marsh habitat in Delaware Bay. Our results indicated that restoring marsh habitat likely resulted in increased system biomass and changed the structural composition of the Delaware Bay ecosystem potentially increasing its long-term health and stability.

Acknowledgments

We thank the scientists and management agencies that have collected data in the Delaware Bay ecosystem. We thank all the participants of the two workshops held to facilitate the development of the model. Adrian Jordaan and members of the Frisk lab helped edit the text and provided critical comments that greatly improved the manuscript. This work was funded by the Public Service Enterprise Group (PSEG) and we are grateful for their support and assistance in conducting this research.

References

- Able, K.W., Grothues, T.M., Hagan, S.M., Kimball, M.E., Nemerson, D.M., Taghon, G.L., 2008. Long-term response of fishes and other fauna to restoration of former salt hay farms: multiple measures of restoration success. *Reviews in Fish Biology and Fisheries* 18, 65–97.
- Allen, K.R., 1973. The influence of random fluctuations in the stock-recruitment relationships on the economic return from salmon fisheries. *Fish stocks and recruitment*. Rapp. Et Proces-Verbaux Reun. Cons. Int. Explor Mer 164, 350–359.
- ASMFC, 2004. Stock assessment report for Atlantic striped bass: catch-at-length-based VPS and tag release/recovery based survival estimation. SBTC Report #2004-4:93.
- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59, 329–364.
- Balletto, J.H., Heimbuch, M.V., Mahoney, H.J., 2005. Delaware Bay salt marsh restoration: Mitigation for a power plant cooling water system in New Jersey, USA. *Ecological Engineering* 25, 204–213.
- Bilkovic, D.M., Roggero, M.M., 2008. Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology-Progress Series* 358, 27–39.
- Breitbart, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annual Review of Marine Science* 1, 329–349.

- Christensen, V., Pauly, D., 1992. Ecopath-II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61, 169–185.
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172, 109–139.
- Christensen, V., 1995. Ecosystem maturity—towards quantification. *Ecological Modelling* 77 (1), 3–32.
- Christensen, V., Walters, C.J., Ahrens, R., Alder, J., Buszowski, J., Christensen, L.B., Cheung, W.W.L., Dunne, J., Froese, R., Karpouzi, V., Kaschner, K., Kearney, K., Lai, S., Lam, V., Palomares, M.L.D., Peters-Mason, A., Piroddi, C., Sarmiento, J.L., Steenbeek, J., Sumaila, R., Watson, R., Zeller, D., Pauly, D., 2009. Database-driven models of the world's Large Marine Ecosystems. *Ecological Modelling* 220, 1984–1996.
- Cruz-Escalona, V.H., Arreguin-Sanchez, F., Zetina-Rejon, M., 2007. Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. *Estuarine Coastal and Shelf Science* 72, 155–167.
- Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929.
- Dove, L.E., Nyman, R.M., 1995. Living Resources of the Delaware Bay. The Delaware Estuary Program.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56, 363–380.
- Finn, J.T., 1980. Flow-analysis of models of the Hubbard Brook ecosystem. *Ecology* 61, 562–571.
- Frisk, M.G., Miller, T.J., Latour, R.J., Martell, S.J.D., 2006. An Ecosystem Model of Delaware Bay. Prepared for PSEG, New Jersey.
- Hinckle, R.L., Mitsch, W.J., 2005. Salt marsh vegetation recovery at salt hay farm wetland restoration sites on Delaware Bay. *Ecological Engineering* 25, 240–251.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Jivoff, P.R., Able, K.W., 2003. Evaluating salt marsh restoration in Delaware Bay: the response of blue crabs. *Callinectes sapidus*, at former salt hay farms. *Estuaries* 26, 709–719.
- Kahn, D.M., Helser, T.E., 2005. Abundance, dynamics and mortality rates of the Delaware Bay stock of blue crabs, *Callinectes sapidus*. *Journal of Shellfish Research* 24, 269–284.
- Kay, J.J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), *Network Analysis in Marine Ecology: Methods and Applications*. Springer-Verlag, Heidelberg, pp. 15–61.
- Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwell, J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., Houde, E.D., Kimmel, D.G., Miller, W.D., Newell, R.I.E., Roman, M.R., Smith, E.M., Stevenson, J.C., 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology-Progress Series* 303, 1–29.
- Kempton, R.A., Taylor, L.R., 1976. Models and statistics for species diversity. *Nature* 262, 818–820.
- Kennish, M.J., 2000. *Estuary Restoration and Maintenance*. CRC Press, Boca Raton, FL, pp. 350.
- Kimball, M.E., Able, K.W., 2007. Tidal utilization of nekton in Delaware bay restored and reference intertidal salt marsh creeks. *Estuaries and Coasts* 30, 1075–1087.
- Kohn, J., 1998. An approach to Baltic Sea sustainability. *Ecological Economics* 27, 13–28.
- Maurer, D., Howe, S., Leathem, W., 1992. Secondary production of Macrobenthic invertebrates from Delaware Bay and Coastal Waters. *Internationale Revue Der Gesamten Hydrobiologie* 77, 187–201.
- McHorney, R., Neill, C., 2007. Alteration of water levels in a Massachusetts coastal plain pond subject to municipal ground-water withdrawals. *Wetlands* 27, 366–380.
- Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three US mid-Atlantic estuaries. *Marine Ecology-Progress Series* 161, 239–254.
- Nemerson, D.M., Able, K.W., 2005. Juvenile sciaenid fishes respond favorably to Delaware Bay marsh restoration. *Ecological Engineering* 25 (3), 260–274.
- Newell, R.I.E., Kemp, W.M., Hagy III, J.D., Cerco, C.F., Testa, J.M., Boynton, W.R., 2007. Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: comment on Pomeroy et al. (2006). *Marine Ecology-Progress Series* 341, 293–298.
- Bay marsh restoration. *Ecological Engineering*, 25:260–274.
- Nixon, S.W., 1995. Coastal marine eutrophication—a definition, social causes, and future concerns. *Ophelia* 41, 199–219.
- Odum, E.P., 1969. Strategy of ecosystem development. *Science* 164, 262–8.
- Odum, E.P., 1971. *Fundamentals of Ecology*, 3rd ed. Saunders, Philadelphia, pp. 54.
- Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *Ices Journal of Marine Science* 57, 697–706.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Rice, C.A., 2006. Effects of shoreline modification on a northern Puget Sound beach: microclimate and embryo mortality in surf smelt (*Hypomesus pretiosus*). *Estuaries and Coasts* 29, 63–71.
- Rodney, W.S., Paynter, K.T., 2006. Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* 335, 39–51.
- Rothschild, B.J., Ault, J.S., Gouletquer, P., Heral, M., 1994. Decline of the Chesapeake Bay oyster population—a century of habitat destruction and overfishing. *Marine Ecology-Progress Series* 111, 29–39.
- Ruiz, G.M., Carlton, J.T., Grozholz, E., Hines, A.H., 1997. Global invasion of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. *American Zoology* 47, 621–632.
- Rybarczyk, H., Elkaim, B., 2003. An analysis of the trophic network of a macrotidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). *Estuarine Coastal and Shelf Science* 58, 775–791.
- Seitz, R.D., Lipcius, R.N., Olmstead, N.H., Seebo, M.S., Lambert, D.M., 2006. Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology-Progress Series* 326, 11–27.
- Shannon, L.J., Coll, M., Neira, S., 2009. Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. *Ecological Indicators* 9 (6), 1078–1095.
- Sharp, J.H., 2010. Estuarine oxygen dynamics: what can we learn about hypoxia from long-time records in the Delaware Estuary? *Limnology and Oceanography* 55, 535–548.
- Shin, R.K., 2007. *A costly standoff: The Hart and Miller Islands Controversy*. Maryland Legal History Publications, University of Maryland School of Law, p. 42.
- Smith, S.V., Swaney, D.P., Talaue-McManus, L., Bartley, J.D., Sandhei, P.T., McLaughlin, C.J., Dupra, V.C., Crossland, C.J., Buddemeier, R.W., Maxwell, B.A., Wulff, F., 2003. Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. *Bioscience* 53, 235–245.
- Tsipoura, N., Burger, J., 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* 101, 635–644.
- Tupper, M., Able, K.W., 2000. Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. *Marine Biology* 137, 1049–1058.
- Ulanowicz, R.E., 1986. *Growth and Development: Ecosystems Phenomenology*. Springer-Verlag, New York.
- Ulanowicz, R.E., 2003. Some steps toward a central theory of ecosystem dynamics. *Computational Biology and Chemistry* 27 (6), 523–530.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7, 139–172.
- Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3, 70–83.
- Walters, C.J., Juanes, F., 1993. Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50, 2058–2070.
- Walters, C.J., Martell, S.J.D., 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, NJ, pp. 399.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314 (5800), 787–790.