Using a fisheries ecosystem model with a water quality model to explore trophic and habitat impacts on a fisheries stock: A case study of the blue crab population in the Chesapeake Bay

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\textbf{A B S T R A C T}

Recent calls for the development of ecosystem-based fisheries management compel the development of resource management tools and linkages between existing fisheries management tools and other resource tools to enable assessment and management of multiple impacts on fisheries resources. In this paper, we describe the use of the Chesapeake Bay Fisheries Ecosystem Model (CBFEM), developed using the Ecopath with Ecosim (EwE) software, and the Chesapeake Bay Water Quality Model (WQM) to demonstrate how linkages between available modeling tools can be used to inform ecosystem-based natural resource management. The CBFEM was developed to provide strategic ecosystem information in support of fisheries management. The WQM was developed to assess impacts on water quality. The CBFEM was indirectly coupled with the WQM to assess the effects of water quality and submerged aquatic vegetation (SAV) on blue crabs. The output from two WQM scenarios (1985–1994), a baseline scenario representing actual nutrient inputs and another with reduced inputs based on a tributary management strategy, was incorporated into the CBFEM. The results suggested that blue crab biomass could be enhanced under management strategies (reduced nutrient input) when the effective search rate of blue crab young-of-the-year’s (YOY’s) predators or the vulnerability of blue crab YOY to its predators was adjusted by SAV. Such model linkages are important for incorporating physical and biological components of ecosystems in order to explore ecosystem-based fisheries management options.

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\section{Introduction}

\subsection{Ecosystem-based fisheries management}

Traditionally, fisheries management plans have been targeted to manage a single species. Multispecies management adds ecological interaction (e.g., competition and predation) and technical interaction (e.g., bycatch and discard). Ecosystem-based management may further include fish habitat requirements and water quality. For fisheries management, conventional single species approaches should be incorporated into the broader discipline of ecosystem-based fisheries sciences (\textit{Latour et al., 2003; Francis et al., 2007}). To support ecosystem-based fisheries management, tools that incorporate ecosystem dynamics are necessary. Complex ecosystem models for natural resource management (\textit{sensu Atlantis software—Fulton, 2004; Fulton et al., 2004; Brant et al., 2007}) are in their nascent stages, with few relatively simple ecosystem models being actively used for management plans (\textit{Townsend et al., 2008}). In addition to complex ecosystem models, available resource models can be linked directly or indirectly in effort to provide insight to ecosystem dynamics for resource management. In this paper, we describe a case study in the Chesapeake Bay using a fisheries ecosystem model and a water quality model.

In support of the Fisheries Ecosystem Plan for the Chesapeake Bay (\textit{Chesapeake Bay Fisheries Ecosystem Advisory Panel, 2006}), the NOAA Chesapeake Bay Office, in collaboration with the University of British Columbia Fisheries Centre, has been developing the Chesapeake Bay Fisheries Ecosystem Model (CBFEM) (\textit{Christensen et al., in press}). The CBFEM is based on Ecopath with Ecosim (EwE), a trophic dynamics mass-balance model. The EwE software is a...
modeling tool used to evaluate quantitative trophic interactions within an ecosystem in order to evaluate options for ecosystem-based management of fisheries (Christensen and Walters, 2004a). The CBFEM was created in response to a management need in the Chesapeake Bay region for a quantified estimate of trophic pathways in the Bay. This model is used to study how stocks affect each other within the food web and how the many Bay fisheries impact both target and non-target species. The species groups of particular interest are the multi-age/stanza groups (striped bass, bluefish, weakfish, white perch, Atlantic menhaden, blue crab, and oyster) and other commercially important species (Christensen et al., in press). Specific changes have been made to the parameters for all of these species on the basis of new assessment information that became available since the inception of the CBFEM model in 2001. The CBFEM is thus continuously being updated as new information becomes available.

In the current study, we explored how environmental/habitat factors could impact trophic interactions in the CBFEM. The output (including algae and submerged aquatic vegetation (SAV) biomass) from the Chesapeake Bay Program’s Water Quality Model (WQM) was used in CBFEM to assess the effects of nutrient reduction on fishery species. The WQM computes algal biomass, nutrient cycling, and dissolved oxygen, as well as several key living resources such as SAV and benthos (Cerco et al., 2004; Cerco and Noel, 2004). The model has 13 thousand grids, and computed loads and transport are input. This model has been employed as a tool to guide management since the formation of the water quality targets in the Bay (e.g., Cerco et al., 2004). Using the CBFEM and WQM, we looked at the potential effects of increased SAV biomass (as the result of a nutrient management strategy) on blue crab young-of-the-year (Y0Y) and adults considering the trophic interaction with their prey and predators in the Bay.

1.2. The Chesapeake Bay and the blue crab fishery

The Chesapeake Bay is the largest estuary in North America, providing habitat for thousands of species of plants and animals and supporting a $4 billion/year recreational boating and fishing industry (Chesapeake Bay Program, 2004). Many tributaries drain into the Bay from a 64 000 miles² watershed that stretches across New York, Pennsylvania, Maryland, Delaware, Virginia, West Virginia, and the District of Columbia. The mixture of freshwater from the tributaries and seawater from the coastal ocean creates and maintains diverse brackish habitats within the Chesapeake Bay. These habitats are degraded by excessive nutrients from storm-water runoff, agricultural runoff, sewage treatment plant overflow, failing septic systems, and atmospheric deposition of pollutants (e.g., Kemp et al., 2005). High nutrient levels promote algal blooms, which have caused a zone of low dissolved oxygen commonly referred to as the ‘dead zone’ in deep water. Algal blooms on the water surface also block sunlight from reaching the SAV and other benthic life, limiting their growth and survival. In Chesapeake Bay, seagrasses in saline regions and freshwater angiosperms colonizing lower salinity portions constitute a diverse (about 20 species, see Dennison et al., 1993) community of submerged aquatic vegetation, collectively known as SAV. Without SAV and other benthic habitat such as oyster reefs, much of the habitat structure of the Bay has been lost (Chesapeake Bay Program, 2004). Such habitat is important for benthic species in the Bay including blue crabs and oysters.

The blue crab is an icon for the Chesapeake Bay region. It is an important component of the estuarine ecosystem (Baird and Ulanowicz, 1989), probably playing a dominant role in structuring benthic communities. In addition to its ecological importance, it supports important commercial and recreational fisheries in the Chesapeake Bay and throughout its range. Since 1950, annual landings of blue crab along the Gulf and Atlantic coasts of the United States have been 75 811 metric tons on average, with an average annual value of $57 million (Miller et al., 2005). In the 1950s, the Chesapeake Bay region represented almost 80% of the national landings, but by 2003, the Bay represented only about 30% of U.S. landings. Despite this relative decline, the Chesapeake Bay remains the largest single source of blue crab harvest in the United States (Miller et al., 2005). Thus, the Chesapeake Bay blue crab stock is an important part of the socioeconomic structure of the region and the nation.

A recent stock assessment and assessment update show that blue crab stocks in the Chesapeake Bay are in decline and at historically low levels (Miller et al., 2005). Analyses in the recent stock assessment report (Miller et al., 2005) suggest that (1) the early-season fishery is comprised of adults that overwintered in the Bay and (2) the late-season crab fishery is largely driven by new recruits to the stock. In addition, the report shows that harvest can largely be forecast based on a dredge survey conducted in the winter, prior to the beginning of the spring crabbing season. However, better forecasting can be achieved with improved understanding of factors that influence recruitment. The current stock assessment is based on a catch-multiple-survey model and focuses on traditional fisheries biological reference points as means to understand and manage the fisheries activities that influence the stock.

Current stock assessment methodologies allow for limited incorporation of additional ecological factors that may influence fisheries stocks. For blue crabs in the Chesapeake Bay, stocks may also be influenced by such factors as: (1) SAV habitat that may influence recruitment (Stockhausen and Lipcius, 2003), (2) predation (especially cannibalism), and (3) climate and ocean circulation patterns that influence recruitment (Roman and Boicourt, 1999). The combination of existing water quality/habitat models, hydrodynamic models, and trophic models can allow for evaluation of the impact of these factors on blue crab stocks. In this paper we use a fisheries ecosystem model with a water quality model to explore the habitat and trophic influences using blue crab as a target species.

2. Methods

2.1. CBFEM: an Ecopath and Ecosim model

The Ecopath module of the Chesapeake Bay Fisheries Ecosystem Model uses biomass estimations of 45 trophic groups representing the fisheries species of the Bay and their prey and predators to create a mass-balanced snapshot of the organisms and trophic linkages in the Bay as it may have looked like in 1950 (Christensen et al., in press). The 45 biomass pools represent either a single species or species group that comprises an ecological guild. The species groups of particular interest are the multi-age/stanza groups (striped bass, bluefish, weakfish, white perch, Atlantic menhaden, blue crab, and oyster) and other commercially important species including American eel, Atlantic croaker, summer flounder, spot, alewife, American shad, black drum, catfish, and bivalves (Christensen et al., in press).

Ecopath model parameterization is based on satisfying two ‘master’ equations for each model group: one for production and the other for consumption. The first ‘master’ equation describes each group’s production for an arbitrary time period, i.e., the production is the sum of catch, predation, net migration, biomass accumulation, and other mortality. At minimum, Ecopath requires input of diet composition and catch and three of the following four parameters for each species or biomass pool in the model: biomass, production-to-biomass ratio, consumption-to-biomass ratio, and the eutrophic efficiency (mass-balance principles are then used to estimate the fourth parameter). The second ‘master’ equation is based on the principle of conservation of matter within a group and is designed to balance the
energy flows of a biomass pool, i.e., consumption equal to the sum of production, respiration, and unassimilated food. Balance of the energy equation is achieved by estimating respiration from the difference between the consumption, the production, and unassimilated food terms.

In the Ecosim model, the system of linear equations in Ecopath is re-expressed as a system of coupled differential equations. The Ecosim module of the CBDEM provides a 53-year (1950–2002) simulation, attempting to estimate the current status and dynamics of the Bay. This module can be used to simulate various management options for the Chesapeake Bay, by varying parameters over time to estimate potential ecosystem changes.

The system of equations in Ecosim simulates the trophic dynamics of an entire ecosystem and is combined with explicit age/size-structured delay-difference equations to represent populations that have complex life histories and selective harvesting of older animals. An important aspect of Ecosim is the expression of the consumption or ‘flow’ rates among linked species or biomass pools. Consumption of prey $i$ by predator $j$ ($Q_{ij}$) is modeled as:

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

where $B_i$ is the prey biomass; $B_j$ is the biomass of a consumer/predator; $a_{ij}$ is the rate of effective search for prey $i$ by predator $j$; $v_{ij}$ and $v_i$ are the behavioral exchange rates between vulnerable and invulnerable prey pools.

Eq. (1) is based on the concept that consumption is limited by ‘risk management’ behaviors of predators and prey at very small time scales. That is, predator–prey interactions are assumed to take place primarily in restricted ‘foraging arenas’ where prey only become vulnerable to predation through their own requirements for resource acquisition (Walters et al., 1997, 2000). Ecosim expanded the simple Lotka-Volterra (mass action) assumption $Q_{ij}(B_i, B_j) = a_{ij}B_iB_j$ by viewing each prey pool $B_i$ as having an available component to each predator $j$, $V_{ij}$ (Fig. 1; Walters et al., 1997).

The biomass $V_{ij}$ may exchange rapidly with unavailable biomass ($B_i - V_{ij}$). Assuming that the exchange process between $V_{ij}$ and ($B_i - V_{ij}$) operates on short time scales relative to changes in $B_i$ and $B_j$, then $V_{ij} = v_{ij}B_i/(v_{ij} + v_i + a_{ij}B_j)$ (see page 146 of Walters et al., 1997 for the derivation). Substituting $V_{ij}$ in $Q_{ij}(B_i, B_j) = a_{ij}V_{ij}$, then $Q_{ij}(B_i, B_j) = a_{ij}v_{ij}B_i/(v_{ij} + v_i + a_{ij}B_j)$.

In addition to direct trophic interaction, Ecosim also allows for the modification of vulnerability in a prey/predator pair through a third type of organism. This third group may not be trophically linked to the prey or predators. The vulnerability modification is achieved via a mediation function $M_{ij}$ (Eq. (2)), which can be a function of the biomass of the third group.

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}M_{ij}B_iB_j}{(v_{ij} + v_i + a_{ij}B_j)}$$

In addition, Ecosim allows physical or other environmental factors to influence trophic interactions via forcing functions $F_j$ (Eq. (3)). A forcing function is generally used to affect the effective search rate $a_{ij}$.

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}B_iB_j}{(v_{ij} + v_i + a_{ij}F_jB_j)}$$

In this study the search rate of blue crab YOY’s predators was affected by SAV through a forcing function. The forcing function’s value was 1 at baseline in 1950. Its values at other years were based on the ratio of that year’s SAV to the SAV in 1950. The assumption was that the predators of blue crab YOY would be less effective in searching when there was more SAV. For comparison, we also explored the impact of SAV on blue crab YOY’s vulnerability via mediation functions. The blue crab YOY’s vulnerability was assumed lower with more SAV. SAV mediation enhancement was explored using five mediation functions where vulnerability is 2–6 times the baseline vulnerability when SAV biomass is very low. The mediation functions are in a linear form, $M_t = a - (a - 1) \times (SAV_t/SAV_0)$, $M_t$ is the value for mediation function at time $t$, $a$ is an integer value from 2 to 6, SAV$_t$ is the SAV biomass at time $t$, and SAV$_0$ the SAV biomass at the beginning of 1950. $M_t$ is a (an integer chosen from 2 to 6) when SAV$_t$ is zero, and $M_t$ is 1 when SAV$_t$ is equal to SAV$_0$. The lowest values for $M_t$ are just little lower than 1 because maximum SAV$_t$ is only slightly larger than SAV$_0$ (see Fig. 3). The values 2–6 for $a$ in the equation for $M_t$ were chosen based on the resulting ranges of changes in biomass for blue crabs. When the first linear function ($a=2$) as a mediation function was compared with the sigmoid curves (built in EwE) with steeples of 2 and 3, we only noted slight differences in the model output.

### 2.2. Input parameters and time series data

Two types of data were compiled for use in EwE for each group: basic input data for 1950 and time series data for 1950–2002. In Ecopath, the diet compositions for all species must be entered, and these were based upon advice from local experts at several Chesapeake Bay Ecopath workshops in the CBDEM. Basic input parameters were extracted from peer-reviewed literature sources, tagging studies in the Chesapeake Bay, FishBase (http://www.fishbase.org), other models, and estimations made by Ecopath itself. These values were used to estimate a trophic ‘snapshot’ of what the Bay might have looked like in 1950.

Time series data depicting trends in relative and absolute biomass, time forcing data, fishing effort by gear type, fishing and total mortality rates, and catches were input for Ecosim. Currently, 92 time series are included in the CBDEM. In this paper, we only describe the data sources for blue crabs and SAV. The data sources for other species can be found in Christensen et al. (in press).

The basic input and diet composition for blue crabs (adult and YOY) are shown in Table 1. Other model input can be found at ftp://noaa.chesapeakebay.net/CB Fisheries Ecosystem Model. Time series for blue crab biomass was based on the combined index from four fishery-independent surveys compiled in the 2005 Blue Crab Stock Assessment Report (Miller et al., 2005). In addition, that report also provided the data for catch and fishing mortality. The effort data was from an earlier stock assessment report for blue crabs (Rugolo et al., 1998). SAV monitoring data were provided by the VIMS SAV Monitoring Program (http://web.vims.edu/bio/sav).
by Chesapeake Bay Program segment with indication of whether each segment was not surveyed, was partially surveyed, or was fully surveyed for each year from 1971 to 2002. Only those segments that were fully surveyed were included in the SAV index (cover) used in the CBREEM. For each year, SAV acreage for those segments that were fully surveyed was totaled and divided by the total surface area of the segments. This resulted in a single value for each year of the survey from 1971 to 2002, representing the ratio of SAV identified/SAV surveyed.

For each Ecosim run, a statistical measure of goodness of fit to the reference data (relative or absolute biomass time series) is given, i.e., fit SS. Fit SS is a weighted sum of squared deviations (SS) of log biomasses from log predicted biomasses (B), scaled in the case of relative abundance data (y) by the maximum likelihood estimate of the relative abundance scaling factor q in the equation $y = qB$ (Christensen et al., 2005).

### 2.3. Water quality protection and restoration

Improving water quality is the most critical element in the overall protection and restoration of the Chesapeake Bay and its tributaries (Gillmore et al., 2000). In 1987, it was committed to achieving a 40% reduction in controllable nutrient loads to the Bay (Ballies et al., 1987). In 1992, it was further committed to tributary-specific reduction strategies to achieve this reduction and agreed to stay at or below these nutrient loads once attained. The Chesapeake Bay Program’s water quality model (Cerco and Noel, 2004) has been employed as a tool to guide management with the water quality targets (e.g., Cerco et al., 2004). In this study, we examined SAV and chlorophyll-a (chl-a) changes under nutrient management strategies, based on the output from the water quality model. There were two types of model runs: a calibration run (with historical nutrient input) and a combined tributaries strategy run (40% reduction in nutrient input) for 1985–1994. To explore the impact of this nutrient management strategy on the fisheries ecosystem, SAV biomass from 1985 to 1994 in EwE was adjusted according to ratio of change in the SAV output from the water quality model. Currently there is not direct coupling between the WQM and CBREEM due to different temporal and spatial scales used. Here we used indirect (one-way) coupling, i.e., the output from WQM was used to adjust the input for CBREEM. The spatial output at daily interval from WQM was averaged to get Bay-wide monthly estimates for use in CBREEM. One of the limitations of such indirect coupling is that the spatial variation and finer-scale temporal variation in WQM would be lost in the input for EwE.

In CBREEM, we also used the output from the Chesapeake Bay Regional Estuarine Ecology Model (CBREEM, Ma et al., in press) to force primary production rates for phytoplankton and benthic microalgae. The WQM output was not used for this purpose because WQM usually provides output for years, not for five decades as covered in CBREEM. CBREEM is a simple hydrographic model with two layers (deep and shallow) which uses monthly time steps to simulate for 50+ years. CBREEM is suitable for generating long-term historic primary production estimates in response to notably nutrient input. Major inputs for CBREEM include wind, rainfall, gage inflow, and relative loading (Ma et al., in press). The time series of chlorophyll-a from the CBREEM output was significantly related to nutrient loading and the chlorophyll-a model output was used as a forcing function to force primary production rates. Adding this forcing function significantly improved the model fit (Christensen et al., in press).

### 3. Results and discussion

#### 3.1. Trophic links for blue crab in Ecopath

The mass-balance in Ecopath estimated that the trophic levels for blue crab YOY and adults are 2.80 and 3.09. The blue crab predators (with trophic levels >3.09) are sandbar sharks and reef-associated fish, and the prey groups (trophic level <3.09) include blue crab YOY, other in/epi fauna, other suspension feeders, hard clams, soft clams, oyster YOY, benthic algae, SAV, and detritus (Fig. 2; Table 1). The predators of YOY (trophic levels >2.8) are blue crab

### Table 1

<table>
<thead>
<tr>
<th>Groups</th>
<th>Biomass (t km⁻²)</th>
<th>P/B (year⁻¹)</th>
<th>Q/B (year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Basic input parameters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue crab YOY</td>
<td>1.6</td>
<td>5.0</td>
<td>12.1</td>
</tr>
<tr>
<td>Blue crab adult</td>
<td>4.0</td>
<td>1.0</td>
<td>4.0</td>
</tr>
<tr>
<td>SAV</td>
<td>8.8</td>
<td>5.1</td>
<td>160.0</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>27.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Predators of blue crabs and the contribution of blue crab to the predator’s diets</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Striped bass resident</td>
<td>0.3</td>
<td>Sandbar shark</td>
<td>5.0</td>
</tr>
<tr>
<td>Striped bass migrant</td>
<td>2.3</td>
<td>Reef-associated fish</td>
<td>10.0</td>
</tr>
<tr>
<td>Atlantic croaker</td>
<td>14.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>American eel</td>
<td>5.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reef-associated fish</td>
<td>10.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Littoral forage fish</td>
<td>4.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandbar shark</td>
<td>5.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Piscivorous birds</td>
<td>0.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue crab adult</td>
<td>25.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Prey of blue crabs and the fractions of the blue crab diet that they represent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oyster YOY</td>
<td>5.0</td>
<td>Oyster YOY</td>
<td>25.0</td>
</tr>
<tr>
<td>Soft clam</td>
<td>5.0</td>
<td>Soft clam</td>
<td>7.5</td>
</tr>
<tr>
<td>Hard clam</td>
<td>5.0</td>
<td>Hard clam</td>
<td>7.5</td>
</tr>
<tr>
<td>Other suspension feeders</td>
<td>15.0</td>
<td>Other suspension feeders</td>
<td>5.0</td>
</tr>
<tr>
<td>Other in/epi fauna</td>
<td>45.0</td>
<td>Other in/epi fauna</td>
<td>35.0</td>
</tr>
<tr>
<td>Benthic algae</td>
<td>7.5</td>
<td>Benthic algae</td>
<td>2.5</td>
</tr>
<tr>
<td>SAV</td>
<td>7.5</td>
<td>SAV</td>
<td>2.5</td>
</tr>
<tr>
<td>Detritus</td>
<td>10.0</td>
<td>Detritus</td>
<td>10.0</td>
</tr>
</tbody>
</table>

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Fig. 2. The trophic links for blue crab YOY (a) and adult (b). The red lines link to predators (above the target groups) and blue lines to prey groups (below target groups). While the vertical placements of linked species/groups reflect their trophic levels, the horizontal placements are arbitrary. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

3.2. Biomass of blue crab (adult and YOY) and SAV in Ecosim

The biomass of blue crab YOY is estimated to be around 1.5 t km$^{-2}$ with some fluctuations in the last several years (Fig. 3a). Blue crab adult has a decreasing trend in biomass after 1992 (Fig. 3b). The SAV biomass changes by an order of a magnitude over the study period, with a significant decrease beginning in the 1970s (Fig. 3c). The fit SS is 1815.7. The modeled biomass time series is driven by the trophic interaction (e.g., prey and predator interaction) and fishing in EwE. The fitted lines do not follow the data points very closely. To fit to data in this long-term ecosystem model is difficult because of (1) lack of data on fisheries ecosystem drivers in earlier years (e.g., little fishing mortality data is available for prior to 1990) and (2) high uncertainty in the earlier data used for developing fitting indices.

In CBFEM, the model fits well when long time series of driving data (for Ecosim input) exists. Potential drivers in EwE include fishing mortality, time forcing data, forced biomass, forced total mortality, and forced catch. If a biomass time series is forced, the fitted lines will exactly follow the biomass data points. In the time series input for blue crabs and SAV, there is only one driver: fishing mortality for blue crab adult for 1990–2002 based on the Bay-wide bottom dredge survey (Sharov et al., 2003; Miller et al., 2005). There is a significant correlation between model output for biomass and the reference biomass for 1990–2002. In spite of the apparent poor fit between the model output and the data point in Fig. 3, we believe that the CBFEM has captured the major trophic dynamics of the Chesapeake Bay fisheries ecosystem. The model fitted biomass lines follow the data points in trend for most species/groups in the model (Christensen et al., in press). The poor fit for blue crab adults before 1991 may be due to their invariance before 1991 when a shift occurred (Lipcius and Stockhausen, 2002).

For blue crab YOY, there was no apparent correlation between the fit line and the biomass data. In the model, the biomass for YOY is driven by the biomass of adult (based on simple population dynam-
Seagrass beds are important nursery areas for juvenile blue crabs in the Chesapeake Bay (Beck et al., 2001; Pardieck et al., 1999). Field studies in the lower Bay have shown higher densities of juvenile blue crabs in seagrass habitats compared to adjacent marsh and unvegetated area (e.g., Orth et al., 1996). Blue crab megalopae may select seagrass for settlement (van Montfrans et al., 2003), and post-larvae megalopae and early-instar juvenile blue crabs are found in up to two orders of magnitude greater abundance in SAV beds than in adjacent marsh creeks or unvegetated habitats (Orth and van Montfrans, 1987). Predation upon juvenile blue crabs is significantly lower in seagrass than unvegetated habitats until they reach a refuge size (Orth and van Montfrans, 1987, 2002; Pile et al., 1996). SAV beds also offer an abundance of prey items and may provide a substantial growth advantage (Perkins-Visser et al., 1996).

Based on these studies described above, we assumed that with more SAV biomass, the predators of blue crab YOY in the Bay as a whole would be less effective in searching or blue crab YOY would be less vulnerable to its predators. It was a simplification because the juveniles disperse to other shallow-water habitats (subtidal mud and sand flats) as they reach a size refuge from predation and use the ample prey occurring in unstructured shallow-water mud and sand flats with benthic infauna (Lipcius et al., 2007). Refuge value of SAV for blue crabs also increases with structural complexity of seagrasses (Heck and Crowder, 1991). Juvenile blue crabs are denser and exhibit greater survivability in smaller patches (10–100 m²) of SAV with high shoot density, likely because low shoot densities increase the ability of predators to search for and capture their prey (Hovet and Lipcius, 2002; Orth, 1992; Heck and Crowder, 1991; Orth and van Montfrans, 2002). In addition, spatial distribution of SAV at different locations of the rivers and the Bay would have impacts too (Stockhausen and Lipcius, 2003).

In the CBFEM, when a forcing function (as a function of SAV biomass) is used to adjust the effective search rate of blue crab YOY’s predators, the biomass for blue crab adult and YOY decrease especially after 1970 compared with the model output without a forcing function (Fig. 4). The fit SS value decreased to 1786.8 from the base fit SS (1815.7). The correlation between the model output and the biomass index for blue crab YOY also improved (r changed from 0.06 to 0.26). The forcing function’s values were inversely proportional to the ratio of SAV output (time series) to the SAV baseline in 1950. The YOY biomass decrease after 1970 was the result of reduced SAV biomass after that time (Fig. 3). The change in adult biomass was linked to change in YOY biomass (SAV was not used to affect the search rate of blue crab adult’s predators). However, the correlation between the model output and the biomass index did not improve for blue crab adults.

Vulnerability is a key parameter in Ecosim. The base vulnerabilities express the rate with which prey move between being vulnerable and not vulnerable prey biomass, where low vulnerabilities imply bottom-up and high vulnerabilities top-down trophic control in the ecosystem (Christensen and Walters, 2004a). Sometimes, the vulnerability of the prey to the predators can be mediated by a third type of organism in the ecosystem that may not have direct trophic interactions with the prey/predators. We explored the possible impacts of SAV, an example of this third type of organism, on the vulnerability of blue crab YOY. The assumption is that SAV provides protection for blue crab YOY and the YOY crabs are more available to their predators when there is less SAV. The mediation function values at low SAV abundance were assigned as

Fig. 3. The biomass time series for blue crab YOY (a), blue crab adult (b), and SAV (c). The lines are model output and the points are scaled biomass indices from time-series input for the Ecosim model. The scaled biomass indices are references for calculating the fit SS (sum of squared deviations), not drivers for the Ecosim model runs. The biomass for SAV is not forced in the input for Ecosim.

Fig. 4. Baseline biomass of blue crab YOY (a) and adult (b) (thin lines as in Fig. 3) and the blue crab biomass output with a forcing function (function of SAV biomass) on the effective search rate of blue crab YOY’s predators. SAV biomass was not forced in the input for Ecosim with the forcing function (forcing SAV biomass in the input would give same results).
values are 2, 3, 4, 5, or 6 when SAV biomass is the lowest.

The thin lines labeled with numbers are with mediation functions whose five different mediation functions. The thick lines are biomass time series without mediation. The thin lines labeled with numbers are with mediation functions whose values are 2, 3, 4, 5, or 6 when SAV biomass is the lowest.

Fig. 5. The biomass time series of blue crab YOY (a) and adult (b) as in Fig. 3 with five different mediation functions. The thick lines are biomass time series without mediation. The thin lines labeled with numbers are with mediation functions whose values are 2, 3, 4, 5, and 6. The fit SS without mediation was 1815.7. The fit SS were 1784.0, 1782.4, 1848.1, 2114.7, and 2812.8 for different mediation functions explored in this study. The first two mediation functions reduced the fit SS. The results from the first mediation function were closest to those with a forcing function (Fig. 5). In that mediation function, vulnerability is twice the baseline vulnerability when SAV biomass is very low.

In this paper, we incorporated habitat (SAV) as a forcing function and mediation functions for blue crab YOY. The similarities between the forcing function we simulated and the mediation function with minimum fit SS may suggest that the forcing function is reasonable. Field et al. (2006) used climate information as either a bottom-up (forcing functions) or a top-down (mediation of vulnerability) forcing mechanism for the Northern California Current System. Each of these explorations resulted in substantial improvements in model performance. For our study, adding a forcing function or mediation functions for blue crab YOY improved the fit for the whole ecosystem model (the fit SS was reduced). In addition, the correlation between fitted biomass and biomass index also improved for blue crab YOY. The still low correlation ($r=0.26$) suggests that we may need to consider other habitat factors such as hypoxia (Breitburg et al., 2009) and physical circulation in the Bay and along the coast.

3.4. Effects of enhanced SAV under a management strategy and tradeoff between enhanced SAV and reduced phytoplankton/benthic microalgae production

The water quality model showed that SAV biomass increased by ~30% to more than 150% in 1985–1994 under a management strategy (cutting nutrient input by 40%). Chl-a output on the other hand decreased up to 40%. The SAV biomass in EwE from 1985 to 1994 was changed according to the water quality model output under a management strategy, the enhancement will be smaller (Fig. 6). However, the overall results are still positive, especially for blue crab adult.

The reduced nutrient under a management strategy may not reduce the benthic microalgae production rate because they are probably more limited by light (e.g., MacIntyre et al., 1996). Reduced phytoplankton under the management strategy would improve light penetration, which would enhance the production of benthic microalgae. The method we used probably detects the more extreme impact of reduction in primary production.

3.5. Applications for resource management

EwE has been widely used to explore optimal fishing scenarios for fisheries management (e.g., Christensen and Walters, 2004b; Tsehaye and Nagelkerke, 2008). Few studies looked at the habitat and environmental/climate impacts (but see Field et al., 2006). In CBFEM (Christensen et al., in press), the chl-a output from CBREEM has been used as a forcing function to affect primary production. The CBREEM chl-a was mainly influenced by nutrient input into the Bay. In this contribution, we incorporated SAV as a forcing function and mediation functions for blue crab YOY. Assuming the forcing function and mediation function we simulated are realistic, the enhanced SAV under a management strategy would increase the biomass of blue crab in the face of the potential negative impact of reduced primary production from phytoplankton and benthic microalgae. With additional data and analysis, other water quality variables such as dissolved oxygen and water clarity can be modeled in similar ways for blue crab and other species in the Bay to allow exploration of habitat impacts on the Chesapeake Bay fisheries ecosystem.

The CBFEM is useful for developing a coarse but broad understanding of ecosystem dynamics that influence fisheries stocks of biomass using the first mediation function (with enhanced SAV) is similar to that using the forcing function (data not shown).

In all previous simulations, the forcing for primary production rates of phytoplankton and benthic microalgae was based on the CBREEM baseline output. If forcing for primary production rates for these two groups is modified according to the water quality model output under a management strategy, the enhancement will be smaller (Fig. 6). However, the overall results are still positive, especially for blue crab adult.

The reduced nutrient under a management strategy may not reduce the benthic microalgae production rate because they are probably more limited by light (e.g., MacIntyre et al., 1996). Reduced phytoplankton under the management strategy would improve light penetration, which would enhance the production of benthic microalgae. The method we used probably detects the more extreme impact of reduction in primary production.
interest. This approach alone may not provide direct tactical management advice, but is useful for strategic thinking and planning about environmental resources (Townsend et al., 2008). In addition, single species stock assessment models, statistical analysis of other factors influencing stocks, and mechanistic models are also needed to provide necessary information into a strategic ecosystem management framework. We argue for a multiple model approach (from single species to ecosystem) to include population dynamics, predator–prey interaction, habitat, and water quality for resource management.

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