

A Spatially-Explicit Approach for Estimating Carrying Capacity: An Application for the Atlantic Menhaden (*Brevoortia tyrannus*) in Chesapeake Bay

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ABSTRACT: A spatially-explicit methodology was developed for estimating system carrying capacities of fish stocks, and used to estimate the seasonal and spatial patterns of carrying capacity of Chesapeake Bay for Atlantic menhaden (*Brevoortia tyrannus*). We used a spatially-explicit three-dimensional (3-D) model that divided the heterogeneous habitat of Chesapeake Bay into over 4,000 cubes. Each cube represented a volume of water that was characterized by a specific set of environmental variables (phytoplankton biomass, temperature, and dissolved oxygen) driven by the 3-D water quality model. Foraging and bioenergetics models transformed the environmental variables into measures of potential growth rates of menhaden. Potential carrying capacity of menhaden was estimated as a function of phytoplankton production, menhaden consumption rate, and potential growth rate, combining phytoplankton production, thermal habitat, and menhaden physiology into one ecological value that is a measure of habitat quality from the perspective of the fish. Seasonal analysis of the Chesapeake Bay carrying capacity for Atlantic menhaden suggested two bottleneck periods: one in early June and a second during the fall. The fall bottleneck in carrying capacity was at about 10 billion age-0 fish. Annual recruitment of age-0 menhaden for the entire Atlantic coast of the U.S. ranged from 1.2–18.6 billion fish between 1955 and 1986. It appears that carrying capacity of Chesapeake Bay does not limit the coastwide production of young menhaden. Any conditions such as nutrient reduction strategies, further eutrophication, or global climatic warming, that may influence the carrying capacity during the fall or early June periods, may ultimately alter coastwide abundance of menhaden through changes in Chesapeake Bay carrying capacity.

Introduction

Carrying capacity is the maximum number of individuals that a given environment can support. Traditionally, carrying capacity is estimated as a single value for a given environment, such as the carrying capacity of habitat *y* for species *x*, or the carrying capacity of Chesapeake Bay for the Atlantic menhaden (*Brevoortia tyrannus*). Carrying capacity can be derived from quantitative studies of energy flow (i.e., production) in the whole ecosystem, and requires information on abundances of the living and nonliving ecosystem components,

diets of the feeding species, and rates at which ingested materials are used and transferred among various entities in the food web (Baird and Ulanowicz 1989; Peters and Schaaf 1991; Christensen and Pauly 1998). Most such studies assume processes occur over a homogeneous environment both spatially and temporally (e.g., Baird and Ulanowicz 1989). Recent studies in spatial ecology (Brandt et al. 1992; Brandt 1993; Brandt and Kirsch 1993; Luo and Brandt 1993; Mason and Patrick 1993) indicate that spatial heterogeneity in the environment can have significant effects on overall estimates of carrying capacity because most ecological processes occur within a short time period and at small spatial scales; a school of planktivorous fish will likely not interact with a patch of zooplankton 10 km away in a short time period (e.g., one day).

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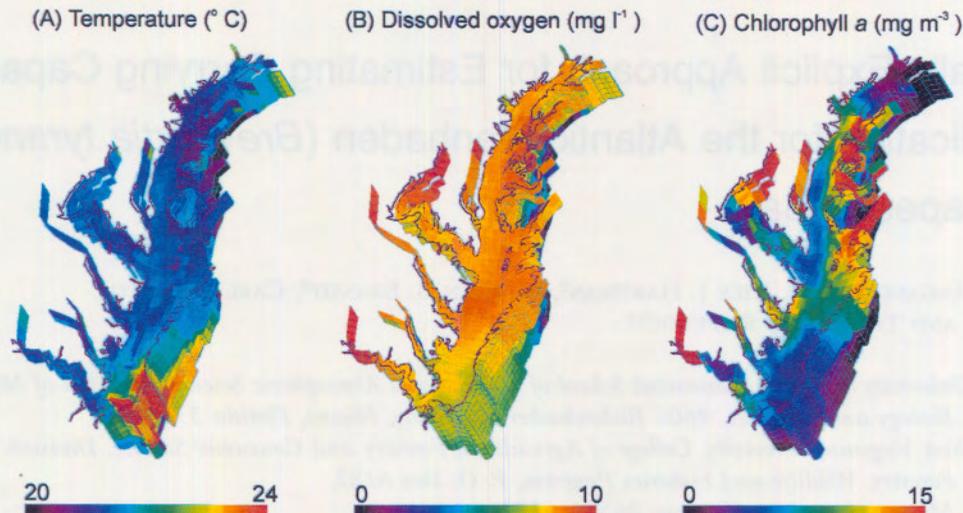


Fig. 1. Water temperature (A), dissolved oxygen (B), and chlorophyll *a* (C) from a three-dimensional water quality model of Chesapeake Bay on July 1, 1986. The color scale for temperatures ranges from 20°C to 24°C, dissolved oxygen ranges from 0 to 10 mg l⁻¹, and chlorophyll *a* ranges from 0 to 15 mg m⁻³.

The main objective of this study is to develop a spatially-explicit approach to link a bioenergetics model with a water quality model to explore the ideas of spatial and temporal dynamics of carrying capacity. In this paper, we used the Atlantic menhaden in Chesapeake Bay as a test case. We linked an Atlantic menhaden bioenergetics model with a three-dimensional (3-D) water quality model of Chesapeake Bay, and used the linked models for evaluating spatial and temporal patterns of carrying capacity, growth rate potential, and habitat quality of Chesapeake Bay for age-0 Atlantic menhaden.

The Atlantic menhaden is an abundant and commercially important fish in Chesapeake Bay and nearshore habitats of the eastern United States (U.S. National Marine Fisheries Service 1978; Lewis and Peters 1984). Menhaden account for nearly half the total east coast commercial fishery harvest (Peters and Schaaf 1991). Menhaden are also an important component of the diet of many commercially and recreationally important species such as bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), and weakfish (*Cynoscion regalis*) (Hartman and Brandt 1995). Atlantic menhaden is mostly a filter-feeding phytoplanktivore; it converts primary production (phytoplankton and plant detritus) directly into fish production (Peter and Schaaf 1991; Rippeto 1993).

Chesapeake Bay is the major nursery ground of the Atlantic menhaden (Hildebrand and Schroeder 1928). The menhaden spawns in coastal ocean water during late fall and winter (Warlen 1994). The larvae enter Chesapeake Bay in winter and

spring, and use Chesapeake Bay as an important nursery ground in summer and fall. The carrying capacity of Chesapeake Bay for young menhaden is critical to the population levels of menhaden along the Atlantic coast.

Materials and Methods

To estimate the seasonal carrying capacity of Chesapeake Bay for age-0 Atlantic menhaden we used a combination of models and field data. The models included a water quality model, menhaden foraging model, and menhaden bioenergetics model. The water quality model provided information on the spatial patterns in water temperatures, dissolved oxygen (important to the bioenergetics models), and chlorophyll *a* (chl *a*) concentrations (which determined the phytoplankton biomass). Phytoplankton biomass was then used with field data (on weight trajectories and mouth gape) for menhaden to evaluate critical phytoplankton densities needed to support menhaden and to estimate the daily spatial carrying capacity for menhaden in the bay. Each of these models and field data are discussed in further detail below. Abbreviations and symbols used in this paper are listed in Appendix 1.

3-D WATER QUALITY MODEL

The spatial framework of the 3-D water quality model (WQM) of Chesapeake Bay (Cerco and Cole 1993) was used to develop the spatially-explicit model of Atlantic menhaden growth. The model has over 4,000 cells (Fig. 1). The surface of Chesapeake Bay was divided into a grid of 729 cells

(roughly 5×10 km each). Cells underlying the surface cells were each 2 m in depth. The number of cells underlying each surface cell varied according to the local water depth (2 to 15 cells). A 3-yr simulation (1984–1986) of the WQM produced a 2-hourly output of 12 water quality variables in each cell. We used the average daily water quality output of 1986 as inputs to the spatially-explicit bioenergetics model described below. The year 1986 was considered as an average hydrologic year for Chesapeake Bay (Cercio and Cole 1993).

Three variables (water temperature, dissolved oxygen, and chl *a*, Fig. 1) from the WQM outputs were used as inputs to the spatially-explicit model of menhaden growth. Chlorophyll *a* (mg m^{-3}) was converted to carbon (mg m^{-3}) and phytoplankton biomass (mg m^{-3}) according to the following ratios: carbon:chl *a* = 65 (Cercio and Cole 1994) and carbon:wet biomass = 0.1 (Peters and Downing 1984). Therefore,

$$\text{phy}_{ij} = (\text{chl}_{a,ij} 65 / 0.1) / 1000 \quad (1)$$

where phy_{ij} is wet phytoplankton biomass density (g m^{-3}), $\text{chl}_{a,ij}$ is chl *a* concentration (mg m^{-3}) for spatial cell *i* and day *j*; i.e., 1 mg m^{-3} chl *a* was converted into 0.65 g m^{-3} wet phytoplankton biomass.

MENHADEN FORAGING MODEL

Atlantic menhaden of 50 mm total length (TL) or larger are mostly filter feeders on phytoplankton (Friedland et al. 1984; Rippetoe 1993). The consumption rate of a filter feeding menhaden was estimated as a product of phytoplankton biomass, area filtered by menhaden, filtering efficiency, and swimming speed:

$$\text{con}_{ij} = \text{phy}_{ij} \times \text{gap}(L) \times u(T_{ij}, L) \times \text{eff}(L) \quad (2)$$

where, con_{ij} is the consumption rate (g s^{-1}) for spatial cell *i* and day *j*, $\text{gap}(L)$ is mouth open area (m^2) as a function of total length (*L*), $\text{eff}(L)$ is the dimensionless phytoplankton retention efficiency as a function of total length, and $u(T, L)$ is swimming speed (m s^{-1}) of the menhaden as a function of water temperature (T_{ij}) and total length. The weight specific con_{ij} was derived by dividing consumption rate (con_{ij}) by fish weight (*wt*), i.e., $\text{con}_{ij} = \text{con}_{ij} / \text{wt}$.

To determine the mouth open area as a function of total length, Atlantic menhaden of different sizes were sampled from Chesapeake Bay and brought back to the laboratory. The height and width of the mouth, and the total length of menhaden were measured with a caliper to the nearest 0.1 mm. The shape of the mouth is a close approximation of an ellipse. We used the height and width to estimate the mouth opening area as an ellipse, and we mod-

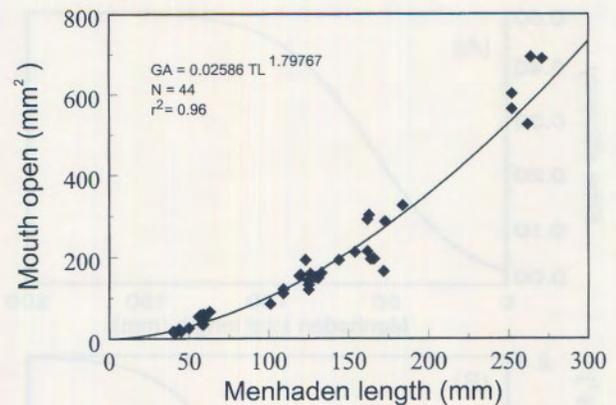


Fig. 2. Atlantic menhaden mouth open area (mm^2) as an exponential function of total body length (mm).

eled the mouth opening area as an exponential function of total body length (Fig. 2).

Larval and pre-juvenile menhaden feed almost entirely on zooplankton by individual acts of capture because their gill rakers are not completely developed to retain phytoplankton (June and Carlson 1971; Durbin and Durbin 1975). As the menhaden grow, the gill rakers are gradually developed to filter the phytoplankton. The maximum efficiency for filtering phytoplankton was reported at about 50% (Durbin and Durbin 1975; Friedland et al. 1984), but there are not sufficient data for us to build a functional response of filtering efficiency on fish size. In this paper, we used the simplest function which could describe the general shape of the function. We know that the function is bounded between a minimum and maximum value. We also know the rate of increase in response per unit independent variable (*x* axis) is very low in the region of the minimum and maximum of the response, but higher in the intermediate region. This is a typical sigmoid response curve (Finney 1947). The filtration retention efficiency, $\text{eff}(L)$, was modeled as a function of fish length by fitting a sigmoid curve through 20% at 50 mm and 50% at 200 mm (Fig. 3a):

$$\text{eff}(L) = 0.5 / (1 + e^{-(0.0527811 \times L + 2.96973)}) \quad (3)$$

Water temperature affects fish behavior and swimming speed (Bergman 1987). For Atlantic menhaden the maximum foraging speed was reported at about 2.5 body-length s^{-1} (Durbin and Durbin 1975). Similar to filtering efficiency, we modeled the swimming speed of menhaden as a function of body length and water temperature by fitting a sigmoid curve through 1 body-length s^{-1} at 15°C and 2.5 body-length s^{-1} at 30°C, and multiplying body-length (*L*, in mm) and 10^{-3} to obtain swimming speed ($u(T_{ij}, L)$) in m s^{-1} (Fig. 3b):

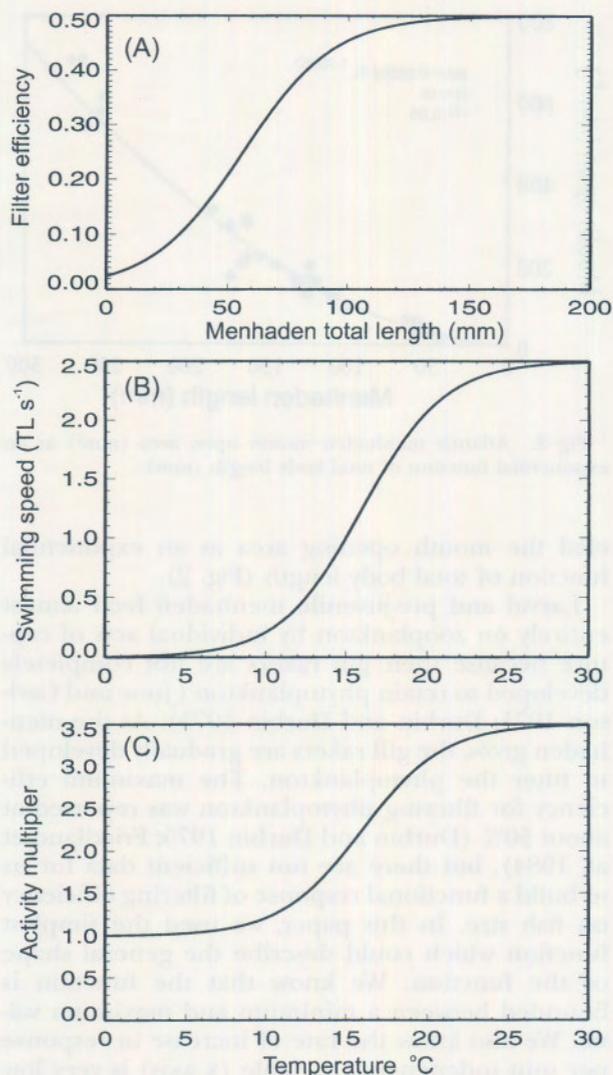


Fig. 3. Sigmoid functional response curves. (A) Filter efficiency as a function of menhaden total length (mm); (B) swimming speed (TL s^{-1}) as a function of water temperature ($^{\circ}\text{C}$); (C) activity multiplier as a function of water temperature ($^{\circ}\text{C}$).

$$u(T_{ij}, L) = (2.5 / (1 + e^{(-0.798T_{ij} + 6.378)})) L \times 10^{-4} \quad (4)$$

BIOENERGETICS MODEL

We adopted the basic Wisconsin bioenergetics modeling framework (described by Kitchell et al. 1977; Stewart et al. 1981; Bartell et al. 1986; Brandt and Hartman 1993) to develop the species specific bioenergetics model of Atlantic menhaden. The bioenergetics model balances the flow of energy through an individual fish among the pathways of consumption, growth, and energy loss (respiration, specific dynamic action, egestion, and excretion). The parameters of the bioenergetics model were derived by Rippetoe (1993) and are presented in

Table 1. Simulations of age-0 menhaden were started on June 1 at 50 mm TL (1 g wet weight), based upon field measures of size and mass from Chesapeake Bay (Bonzek et al. 1992; Rippetoe 1993). Temperature and fish physiology determine the maximum potential consumption of phytoplankton by menhaden, but phytoplankton density determines the amount of food that a fish can retain by filtering the water through its gill rakers. The temperature-dependence of maximum consumption was defined by the Thornton-Lessem algorithm (Thornton and Lessem 1978) which includes two sigmoid curves; one fits the increasing portion of the water temperature dependence curve; the other fits the decreasing portion. Respiration rate was modeled as an allometric function of body weight, water temperature, fish activity level, and specific dynamic action. The temperature-dependence of respiration is defined by a non-linear function as in Kitchell et al. (1977). Specific dynamic action (SDA) coefficient is defined as the metabolic cost of digestion, absorption, and deposition of consumed energy. Since the menhaden is an herbivore, we used the highest SDA, 17.2%, as listed by Hewett and Johnson (1987). Since fish swimming speed is a function of water temperature (described above), the activity multiplier was also modeled as a function of water temperature by fitting a sigmoid curve through 2.0 at 15°C and 3.5 at 30°C (Fig. 3c):

$$\text{ACT}_{ij} = 1 + 2.5 / (1 + e^{(-0.798T_{ij} + 6.378)}) \quad (5)$$

where ACT_{ij} represents the activity multiplier of metabolism for a given cell of a given water temperature (T_{ij}). The resulting range of activity levels (2.0–3.5) is similar to that used in modeling herring (Rudstam 1988).

SPATIALLY-EXPLICIT MODEL OF GROWTH RATE POTENTIAL

We used a 3-D Chesapeake Bay geographic information system program to link fish bioenergetics models to the Chesapeake Bay WQM (Cercio and Cole 1993), and to demonstrate how the spatial patterning of the environment affects species-specific consumption and growth rates and potential habitat. In spatially-explicit modeling, the aquatic habitat is modeled as an explicit feature of the environment by subdividing the pelagic habitat into small homogeneous units that define a cube for a geographical coordinate system and water depth. Each cubic cell represents a volume of water that is characterized by a specific set of attributes including prey (algae) density, water temperature, and dissolved oxygen that have been measured in the field or have been simulated (e.g., Chesapeake Bay WQM).

TABLE 1. Atlantic menhaden bioenergetics model parameters as derived by Rippeto (1993) for model conventions corresponding with the Wisconsin Bioenergetics Model (Hansen et al. 1997).

Symbol	Description	Value/Function	Unit
Ca	Intercept for maximum consumption	1.294	(g g ⁻¹ d ⁻¹)
Cb	Exponent for maximum consumption	-0.312	dimensionless
f _c (T)	Temperature dependence of maximum consumption	f _c (T) = f(K ₁ , K ₂ , K ₃ , K ₄ , T ₁ , T ₂ , T ₃ , T ₄), Thornton and Lessem (1978)	dimensionless
K ₁	Proportion of C _{max} at T ₁	0.525	dimensionless
K ₂	Proportion of C _{max} at T ₂	0.980	dimensionless
K ₃	Proportion of C _{max} at T ₃	0.980	dimensionless
K ₄	Proportion of C _{max} at T ₄	0.810	dimensionless
T ₁	Temperature for K ₁ in f _c (T)	18.2	°C
T ₂	Temperature for K ₂ in f _c (T)	28.0	°C
T ₃	Temperature for K ₃ in f _c (T)	29.0	°C
T ₄	Temperature for K ₄ in f _c (T)	30.1	°C
Ra	Intercept for maximum standard respiration	0.003301	(g O ₂ g ⁻¹ d ⁻¹)
Rb	Exponent for maximum standard respiration	-0.2246	dimensionless
RQ	Slope for temperature dependence of standard respiration	2.07	dimensionless
RTO	Optimum temperature for standard respiration	33.0	°C
RTM	Maximum temperature for standard respiration	36.0	°C
SDA	Specific dynamic action coefficient	0.172	dimensionless
ACT	Temperature dependence of Activity parameter	ACT = 1 + (2.5/(1 + e ^(-0.798T+6.378)))	dimensionless
F _a	Proportion of consumed food egested	0.14	dimensionless
U _a	Proportion of assimilated food excreted	0.10	dimensionless

Our conceptual framework of the 3-D fish growth and production model is similar to 2-D, spatially-explicit models (Brandt et al. 1992; Brandt and Kirsch 1993; Luo and Brandt 1993; Mason and Patrick 1993). Fish production is determined by the functional relationship of the supply of prey resources to the amount of prey that the fish requires for growth (predator demand).

In the spatial growth rate potential model, process-oriented simulation models of the same model structure were run in each cell according to the habitat conditions (physical and biological) of each cell and the specific size and species of fish being modeled. The foraging submodel (described above) estimated consumption rate by converting prey densities into prey availability for the predator. The growth submodel estimated the growth rate potential (G_{ij} , g g⁻¹ d⁻¹) of the predator from consumption rate and was based on the physiology of the predator and prevailing habitat conditions in the cell. Growth rate potential is defined as the expected growth rate of an individual fish calculated for a given set of physical and biological conditions regardless of the presence of fish in the area (Brandt et al. 1992). The simulation produced a 3-D representation of growth rate potential for each day of the model year (June 1–December 31). The growth rate potential integrates the physiological response and the needs of the predator and can be interpreted in the context of habitat quality.

We used volumetric analysis of growth rate potentials over the entire bay to define the propor-

tion of the bay volume that can support various levels of growth for a particular size of fish. Field data on the weights of age-0 menhaden during December were used to determine levels of growth rate required to achieve final weights. These growth rates were then used to determine a minimum level of habitat quality (growth rate potential) needed to support menhaden in the estimates of carrying capacity. For example, if fish needed a minimum growth rate potential of 0.01 g g⁻¹ d⁻¹ to achieve final weights, then only cells that supported this level of growth rate potential or above were included in the estimates of carrying capacity for that day.

SPATIALLY-EXPLICIT CARRYING CAPACITY ESTIMATION FOR MENHADEN

We estimated the carrying capacity of Chesapeake Bay for the Atlantic menhaden as a spatially-explicit and temporally-explicit feature of the environment based on the spatially-explicit model of growth rate potential. The spatially-explicit carrying capacity (CC_{ij} , g m⁻³) was estimated for each cell ($i = 1 \dots 4,073$) and for each day ($j = 1 \dots 365$):

$$CC_{ij} = (fp \times pb_j \times phy_{ij}/cons_{ij})f(G_{ij}) \times f(DO_{ij}) \quad (6)$$

where, fp is the fraction of phytoplankton production (10%, assuming zooplankton and benthic filter-feeders consume a major portion of phytoplankton production) that can be consumed by the menhaden, pb_j is daily phytoplankton produc-

(A) Growth rate potential ($\text{g g}^{-1} \text{d}^{-1}$)

-0.02 0.04

(B) Carrying capacity ($\# \text{ fish m}^{-3}$)

0 1.65

Fig. 4. Three-dimensional distributions of growth rate potential (A) and carrying capacity (B) of Chesapeake Bay for the Atlantic menhaden on July 1, 1986. The color scale for growth rates ranges from -0.02 to $0.04 \text{ g g}^{-1} \text{ d}^{-1}$ and for carrying capacities ranges from 0 to 1.65 fish m^{-3} .

tion to biomass ratio (Nixon 1981) on day j , phy_{ij} is wet phytoplankton biomass density (g m^{-3}), cons_{ij} is weight specific consumption ($\text{g g}^{-1} \text{ d}^{-1}$), $f(G_{ij})$ is a growth rate-dependent scale function, and $f(\text{DO}_{ij})$ is a dissolved oxygen dependent scale function for cell i and on day j . The rationale for the selection of f_p as 10% is that we do not have the data for the exact fraction, but the available literatures suggest that all other grazers in the system take only about 50–80% of phytoplankton production (Barid and Ulanowicz 1989), so we decided to use the conservative 10%. The $f(G_{ij})$ and $f(\text{DO}_{ij})$ were modeled as hypothetical functions based on the general concept of fish physiological processes in response to stress (Bartell 1990):

$$f(G_{ij}) = 1/(1 + e^{(-1358.46G_{ij}+4.5951)}) \quad (7)$$

$$f(\text{DO}_{ij}) = 1/(1 + e^{(-2.1972\text{DO}_{ij}+6.5916)}) \quad (8)$$

Generally, these equations limit inclusion of cells in carrying capacity calculations, where DO ($< 2.0 \text{ mg l}^{-1}$) or poor growth ($\text{GRP} < 0$) might restrict use by menhaden. Calculation of numeric daily carrying capacity (number of fish per cell, or summed for the whole bay) is derived by dividing the biomass carrying capacity by average fish weight on that date.

Results

GROWTH RATE POTENTIAL

Atlantic menhaden growth rate potential varied over space and time. Growth rate potential is generally high in the middle part of Chesapeake Bay and in the tributaries due to high phytoplankton production resulting from high nutrient loadings (Fig. 4a). It is low at the mouth of the bay and deeper water due to low phytoplankton production related to low nutrient loadings of oceanic water and low light intensity in deeper water. Growth rate potential ranged from -0.02 to $0.08 \text{ g g}^{-1} \text{ d}^{-1}$ over the entire bay in early summer, and more than 90% of the volume of the bay supported positive growth rate potential (June 1 in Fig. 5). On July 1 (Fig. 5), maximum growth rate potential was about $0.04 \text{ g g}^{-1} \text{ d}^{-1}$, and 50% of the bay had negative growth rate potential (i.e., menhaden would lose weight if they remained in these areas). On October 1 (Fig. 5), growth rate potential ranged from -0.01 to $0.04 \text{ g g}^{-1} \text{ d}^{-1}$, and over 80% of the bay water would support positive menhaden growth.

If we assume that menhaden would only stay in cells with growth rate greater than a given value, the percentage of those cells available in the bay defines the quantity of menhaden habitat. At

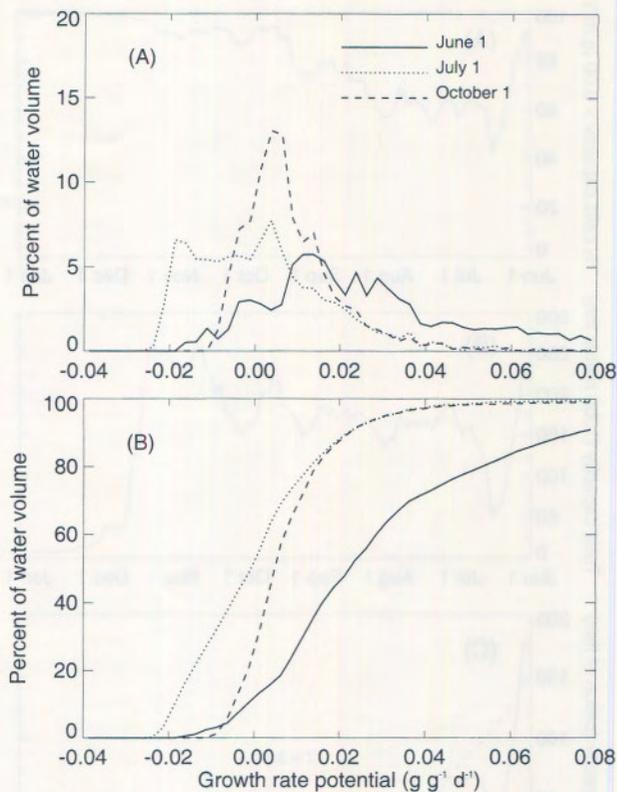


Fig 5. Frequency (A) and cumulative distribution (B) of the growth rate potential ($\text{g g}^{-1} \text{d}^{-1}$) of Chesapeake Bay for Atlantic menhaden on June 1 (solid line), July 1 (dotted line), and October 1 (dashed line).

growth rates greater than $0.0 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6a, solid line), the amount of menhaden habitat in Chesapeake Bay ranged from 30% to 90% of the bay on a daily basis during summer and fall, and the average growth rate of these cells ranged from 0.01 to $0.02 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6b, solid line). A 1-g (50 mm) menhaden growing under these conditions would reach 15 g (about 110 mm) by the end of the year (Fig. 6c, solid line). At growth rates greater than $0.005 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6a, dotted line), the percentage of habitat ranged from 20% to 80% of the bay, and the average growth rate ranged from 0.015 to $0.025 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6b, dotted line) during summer and fall. The same fish would reach 28 g (132 mm) by the end of the year (Fig. 6c, dotted line). At growth rates greater than $0.01 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6a, dashed line), the percentage of habitat was reduced to 10% to 50% of the bay, and the average growth rate increased to 0.02 – $0.035 \text{ g g}^{-1} \text{d}^{-1}$ (Fig. 6b, dashed line). A 1-g menhaden growing under these conditions would reach about 60 g (165 mm) by the end of the year (Fig. 6c, dashed line). Data from fish surveys conducted in lower Chesapeake Bay by Virginia Institute of Ma-

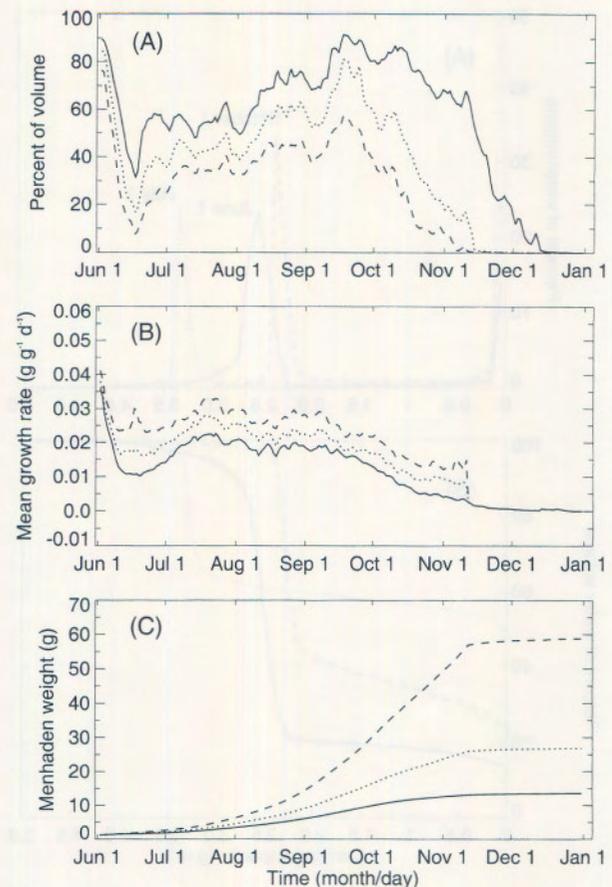


Fig 6. Temporal distribution of percent of water volume (A), mean growth rate (B), and weight of the Atlantic menhaden (C) at three different growth rates: solid line growth rate $> 0.0 \text{ g g}^{-1} \text{d}^{-1}$, dotted line growth rate $> 0.005 \text{ g g}^{-1} \text{d}^{-1}$, dashed line growth rate $> 0.01 \text{ g g}^{-1} \text{d}^{-1}$.

rine Sciences (Bonzek et al. 1992) show that the sizes of young-of-the-year menhaden ranged from 120 to 160 mm (25 to 60 g) in November and December. Since age-0 menhaden achieved end of year weights in the field similar to those obtained in the model when growth rate potential was $> 0.005 \text{ g g}^{-1} \text{d}^{-1}$, we could define the menhaden habitat for use in carrying capacity estimates as those cells with growth rate potential equal to or greater than $0.005 \text{ g g}^{-1} \text{d}^{-1}$.

SPATIALLY-EXPLICIT CARRYING CAPACITY

Similar to growth rate potential, carrying capacity is generally low near the mouth of Chesapeake Bay due to low phytoplankton production of oceanic water, and is low in deeper water due to low light intensity and dissolved oxygen (Fig. 4b). In early summer (June 1, Fig. 7), carrying capacity ranged from 0 to 4.0 g m^{-3} (0 to 3.42 fish m^{-3}) over the entire bay and 80% of the bay had car-

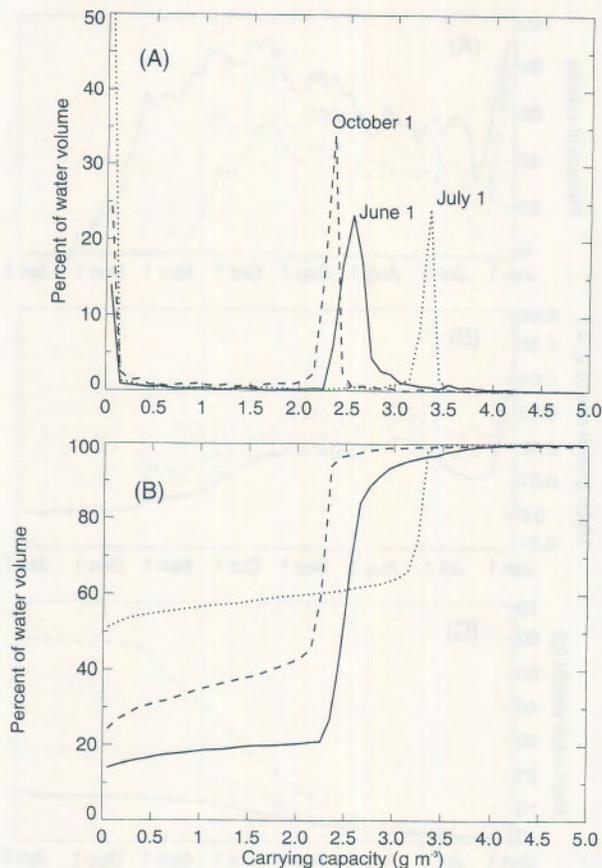


Fig. 7. Frequency (A) and cumulative distribution (B) of the carrying capacity (g m^{-3}) of Chesapeake Bay for Atlantic menhaden on June 1 (solid line), July 1 (dotted line), and October 1 (dashed line).

rying capacity greater than 2.0 g m^{-3} . On July 1 (Fig. 7), 50% of the bay had zero carrying capacity for juvenile menhaden while 40% of the bay had carrying capacity greater than 2.0 g m^{-3} ($0.823 \text{ fish m}^{-3}$). During fall (October 1, Fig. 7), the capacity differences between cells decreased; 25% of the bay had zero carrying capacity and 60% of the bay had carrying capacity greater than 2.0 g m^{-3} ($0.088 \text{ fish m}^{-3}$). Another measurement of menhaden habitat quantity is the percentage of the bay (habitat volume) where carrying capacity is greater than zero (Fig. 8a). The volume of menhaden habitat where positive carrying capacity exists is over 90% in early June and drops to the minimum volume in mid June (40%), then increases gradually during the summer and fall (Fig. 8a).

If we integrate the carrying capacity of each cell over the entire bay for each day, we obtain the daily total carrying capacity (on a weight basis) of Chesapeake Bay for the menhaden (Fig. 8b). The weight-based carrying capacity may not be a good measurement in an ecological sense because mor-

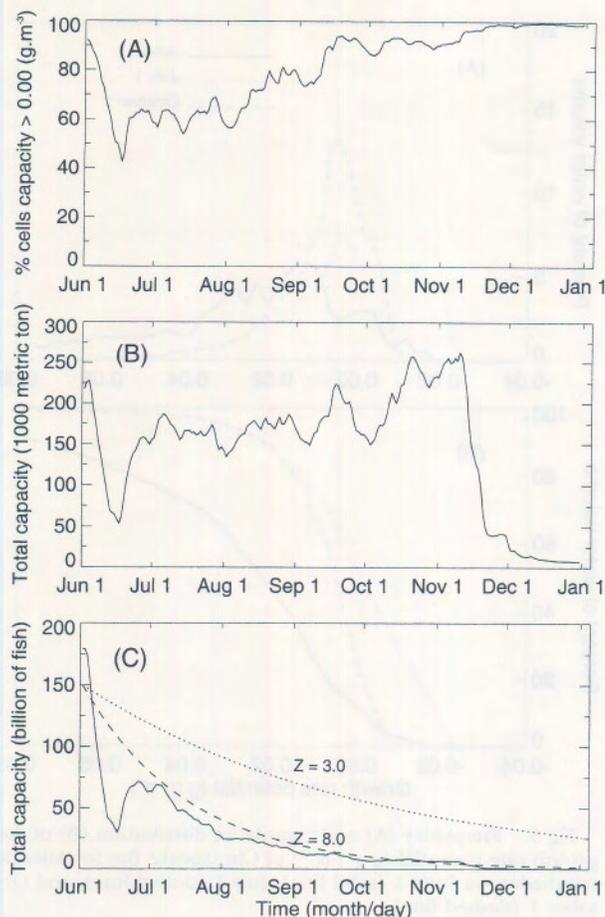


Fig. 8. Temporal distribution of the carrying capacity of Chesapeake Bay for the Atlantic menhaden. (A) Percent of water volume with carrying capacity $> 0 \text{ (g m}^{-3}\text{)}$, (B) total carrying capacity in 1,000s of metric ton, (C) total carrying capacity in billions of fish. The two lines with $Z = 3.0$ and $Z = 8.0$ indicate the exponential decline curves used as a visual reference for the changes in carrying capacity.

tality and migration are operating on individual organisms. The individual-based carrying capacity can be derived by dividing the weight-based carrying capacity by the average weight of an individual fish on each day (Fig. 8c). Results indicated a carrying capacity of over 175 billion fish in early June, but that number declined rapidly to the bottleneck level of 30 billion fish by mid June. Carrying capacity increased to over 50 billion age-0 menhaden from late June through mid July. From mid July through the end of the year, carrying capacity for age-0 menhaden continued to decline to levels below the early June bottleneck level. On November 1, just before menhaden emigrate to coastal waters to overwinter, the carrying capacity for age-0 menhaden was 10 billion fish. This can be considered a second bottleneck period that may

limit the recruitment potential of Chesapeake Bay for menhaden.

Discussion

The objective of this study was to link a bioenergetics model with a 3-D water quality model, and to develop a methodology for evaluating the spatial and temporal patterns of growth and carrying capacity. We used the Atlantic menhaden as an example here. The seasonal trends and spatial patterns are the important results not actual values of growth and carrying capacity for the Atlantic menhaden because we had to make many simplifying assumptions due to lack of data. Our results indicated large spatial and temporal variations in growth rate potential and carrying capacity of Chesapeake Bay for age-0 Atlantic menhaden. The spatial and temporal variations of growth rate potential and carrying capacity are results of non-linear model functional interactions (i.e., foraging and metabolism) of phytoplankton production, temperature, and dissolved oxygen distributions. Phytoplankton density determines the trend of the spatial and temporal distribution, while temperature is the modifier of the distribution and dissolved oxygen concentration is a limiting factor of the distribution (Figs. 1 and 4).

Other studies (Kemmerer 1980; Friedland et al. 1989; Friedland et al. 1996) showed that the Atlantic menhaden are able to respond to gradients of phytoplankton biomass and modify their distribution patterns to match those created by phytoplankton biomass. Compared with the traditional method of estimating carrying capacity (a single value for a given system), the spatially-explicit method of estimating carrying capacity has many advantages. Spatial patchiness of growth rate potential and carrying capacity characterize the quality and quantity of habitat for Atlantic menhaden in Chesapeake Bay. Spatially-explicit carrying capacity not only gives the total carrying capacity (when integrated) of the system, but also tells when and where different carrying capacities occur. Temporal changes in growth rate potential and carrying capacity portray factors that might influence the dynamics of Atlantic menhaden in Chesapeake Bay.

Comparison of predicted growth with the growth of the Atlantic menhaden observed from the field suggests that menhaden must occupy areas where growth rates were greater than 0.005 or $0.01 \text{ g g}^{-1} \text{ d}^{-1}$ throughout the growing season (June to November) to achieve observed weights (25–60 g, Bonzek et al. 1992; Fig. 6c) at the end of the year. The difference in the mean growth rates of the two habitat classes (> 0.005 or $> 0.01 \text{ g g}^{-1} \text{ d}^{-1}$) is small 0.003 – $0.005 \text{ g g}^{-1} \text{ d}^{-1}$ (Fig. 6b),

but it can produce large differences in menhaden weight (25 to 60 g) at the end of the year (Fig. 6c).

The bioenergetic parameters of Atlantic menhaden used in this study were derived from laboratory and field samples (Rippetoe 1993), and also some were adopted from Hewett and Johnson (1987). The suitability of the parameters could be questionable. For example, the highest SDA in Hewett and Johnson (1987) was 0.172 for omnivores and carnivores. The SDA could be higher for herbivores. For the juvenile and adult Atlantic menhaden, as a filter feeder, their diets are constituted almost entirely of phytoplankton and detritus (Lewis and Peters 1984), so the SDA could be higher for the Atlantic menhaden. On the other hand, since it is a filter feeder, zooplankton do contribute a small percentage of the diet (Durbin and Durbin 1981; Lewis and Peters 1984; Keller et al. 1990). Since zooplankton have much higher caloric values compared to phytoplankton and detritus, we could underestimate the caloric intake by the Atlantic menhaden. The lower SDA value and omitted portion of zooplankton in the diet might cancel out each other in some portions.

A comparison of predicted carrying capacity of Chesapeake Bay from this study with estimated recruitment of age-0 menhaden for the entire east coast, suggests that Chesapeake Bay could nurse most of the recruits of the entire Atlantic menhaden stock. Estimates of the number of age-0 Atlantic menhaden for the entire stock from 1955 to 1986 from virtual population analysis methods ranged from 1.2 to 18.6 billion fish (Ahrenholz et al. 1987; Vaughan and Merriner 1991). Seasonal trends in carrying capacity from the model suggest the greatest potential for limitation occurs during mid June and fall. Considering the fall carrying capacity of 10 billion menhaden, Chesapeake Bay appears capable of supporting the annual recruitment of menhaden for the Atlantic coast. Under the conditions assumed by the model, the bottleneck in Chesapeake Bay carrying capacity for menhaden is not expected to affect menhaden recruitment level.

The gradual decline of carrying capacity in late summer and fall (Fig. 8c) can be explained by the natural seasonal succession of the ecosystem. As the menhaden grow larger in the fall, each individual fish will consume more food and require more space than earlier in the season. The habitat would support fewer individuals later in the season, and as the season progresses, some menhaden will be eaten by large predators such as striped bass, bluefish, and weakfish (Hartman and Brandt 1995) or will migrate out of the bay (Friedland and Haas 1988). The decline of carrying capacity can be

quantified by an exponential function: $N_t = N_0 e^{-8t}$ (where t is time in year, Fig. 8c).

In our model, we assumed that only 10% of phytoplankton production (fp) can be consumed by the menhaden throughout the bay and throughout the simulation period (June 1 to December 31), and that other organisms (such as zooplankton and benthic filter-feeders) and detrital pathways account for 90% of the production. Our assumption may not be correct but it should not affect the conclusions of the study (spatial and temporal variations in carrying capacity and the carrying capacity of Chesapeake Bay is larger than the typical recruits of the entire Atlantic menhaden stock). On the spatial and temporal variations issue, if we varied fp over space and time in our simulation, it would result in more variations in space and time according to the variance rule of statistics (i.e., $\sigma_{x+y}^2 = \sigma_x^2 + \sigma_y^2$). On the carrying capacity issue, our assumption of 10% of phytoplankton production being consumed by menhaden is close to the 6–9% estimated by Peters and Scharf (1981) for the coastal age-0 menhaden population.

Our 10% assumption is conservative compared to the amount of phytoplankton production that may be available for menhaden after accounting for grazing by other grazers and inputs to detritus. Baird and Ulanowicz (1989) estimated that in spring, summer, and fall 64%, 63%, and 50% of phytoplankton production was available to grazers with the remainder entering detrital pathways. White and Roman (1992) reported that grazing by the zooplankton community integrated over the entire water column could remove 12% (May), 44% (August), and 20% (October) of the daily primary production in the bay. This would leave approximately 52%, 19%, and 30% of spring, summer, and fall, respectively, phytoplankton production available for consumption by menhaden, bivalves, and other grazers. Gerritsen and Irvine (1994) reported that suspension feeding bivalves could consume between 10% (in deep water) and 50% (in shallow water) of annual phytoplankton production. Eastern oyster (*Crassostrea virginica*), the major suspension feeding bivalve in Chesapeake Bay, has experienced declines in filtering capacity in Chesapeake Bay and in 1988 this capacity was estimated to be less than 1% of daily phytoplankton production (Newell 1988). Although the amount of phytoplankton production that is consumed by grazing bivalves is not presently available, it appears that an assumption of 10% of phytoplankton production available for menhaden grazing is probably conservative.

This study demonstrates how environmental and fish biological models can be combined in a way which describes the potential for the assessment of

habitat quality and quantity of an estuarine ecosystem, and how large amounts of data can be integrated into models potentially useful to fishery and environmental managers. While the model could benefit from additional development, the present results are valuable and highly relevant to environmental and fishery management, and improve our understanding of how environmental processes may affect fish growth and distribution. This model shows the dynamic nature of spatial and temporal patterns in carrying capacity for an important estuarine fish and points to potential bottleneck periods where changes in the ecosystem may most influence carrying capacity of menhaden. The model can be used to test how nutrient reduction, global warming, and point or nonpoint source nutrient loadings may affect habitat quality and carrying capacity of Chesapeake Bay for the Atlantic menhaden, and the approach described in this study may be used to study other species and ecosystems.

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APPENDIX 1. Abbreviations and symbols used in the spatial growth and carrying capacity model.

Symbol	Description	Unit
ACT _{ij}	Temperature dependence of activity parameter	dimensionless
CC _{ij}	SPatially-explicit carrying capacity for spatial cell i and day j	g m ⁻³
chl _a _{ij}	Chlorophyll <i>a</i> concentration for spatial cell i and day j	mg m ⁻³
con _{ij}	Conception rate for spatial cell i and day j	g d ⁻¹
cons _{ij}	Weight specific conception rate for spatial cell i and day j	g g ⁻¹ d ⁻¹
DO _{ij}	Dissolved oxygen concentration for spatial cell i and day j	mg l ⁻¹
eff(L)	Size dependence of phytoplankton retention efficiency	dimensionless
fp	Fraction of phytoplankton production consumed	dimensionless
f(G _{ij})	Growth rate dependent scale function	dimensionless
f(DO _{ij})	Dissolved oxygen dependent scale function	dimensionless
G _{ij}	Spatially-explicit growth rate potential for spatial cell i and day j	g g ⁻¹ d ⁻¹
gap(L)	Size dependent mouth open area	mm ²
L	Fish total length	mm
pb _j	Daily phytoplankton production to biomass ratio for day j	d ⁻¹
ph _{ij}	Phytoplankton biomass density for spatial cell i and day j	g m ⁻³
T _{ij}	Water temperature for spatial cell i and day j	°C
u(T, L)	Temperature and size dependent swimming speed	m s ⁻¹
Wt	Fish weight	g
WQM	Water quality model	