

CHAPTER 15

Spatially Explicit Models of Growth Rate Potential

Linking Estuarine Fish Production to the Biological and Physical Environment

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Abstract

Estuaries are high-yield fishing areas that are characterized by spatial heterogeneity in physical and biological conditions. Models of fish production have traditionally been based on systemwide averages of environmental conditions, but habitat heterogeneity can substantially influence fish growth. Growth rate potential (GRP) provides a spatially explicit approach that integrates the heterogeneous nature of estuaries into a simple modeling framework. In this chapter, we describe and illustrate the application of GRP to compare potential growth of two piscivores and to determine the potential growth of a non-native species introduced into an estuary. Acoustically derived prey distributions and temperature profiles were merged in a spatially explicit analysis to estimate and compare GRP of striped bass and bluefish in Chesapeake and Delaware Bays. In this analysis, bluefish grew better in the thermal regimes and prey biomass available during midsummer while striped bass had higher potential growth during fall. This suggests that, although striped bass and bluefish use similar prey resources, they may be thermally and temporally segregated, thereby reducing competitive overlap. In our second example, GRP results indicate that the suitability of Chesapeake Bay for the growth of chinook salmon (a non-native, hypothetical invader) was very low during summer, whereas in October, water temperature and prey availability could possibly support chinook salmon growth. This spatially explicit approach proved to be a valuable tool to study fish production in estuarine systems where heterogeneous conditions can affect populations at systems levels.

Introduction

Estuaries are very productive ecosystems widely recognized as high-yield fishing areas (McHugh 1967). Indeed, more than 50% of the total U.S. fishery harvest includes species that are estuarine or estuarine dependent at some life stage (Houde and Rutherford 1993). The large nutrient- and sediment-rich water plumes of estuaries also influence continental shelf and offshore fisheries (Day et al. 1989). The ecological importance of estuarine habitats to fish includes providing productive feeding areas (Goshorn and Epifanio 1991), spawning sites for adults (Shepherd and Grimes 1983), and nursery grounds for larvae and juveniles (Greco and Targett 1996). Many estuaries are impacted by anthropogenic activities such as changes in land-use patterns, nutrient enrichment, contaminant loading, recreational and commercial fisheries, shipping, general recreation, and aquaculture. Such activities can lead to biological and physical alterations to the environment that can adversely affect fish production.

Fish production depends on changes in the number of individuals in populations over time (caused by mortality, migration, and recruitment), and in growth rates of individuals within the population. The growth rate of an individual fish is a highly pliant, species- and size-specific response to environmental conditions and food availability. Growth is an important parameter, since high growth has been linked to improved survivorship and larger size at age (Houde 1987). Growth rate is also directly related to reproductive potential because larger females often produce more and larger eggs, which can enhance larval survival (Monteleone and Houde 1990).

Models of population production are typically based on mean conditions (water temperature, prey density) over large areas, but recent work suggests that local biological and physical processes that occur at relatively small spatial scales can significantly affect population processes including trophic interactions, mortality, and system-level production (see Kotliar and Wiens 1990). Traditional models of fish production have also assumed homogeneity and constancy of the environment, but natural systems are neither homogeneous nor constant in time and space. Systemwide averages of predator and prey abundances that do not incorporate spatial heterogeneity of the environment may be insufficient for understanding production dynamics or predator-prey interactions. Moreover, heterogeneity in the environment results in a mosaic of rate-determining habitats that often have nonlinear effects on the ecological and physiological processes that regulate fish growth and survival. For example, systemwide averages of water temperature and prey density may be meaningless to fish growth rate if the overlap in the distribution of predator and prey populations across a rate-determining heterothermal environment is not considered. Rose and Leggett (1990) showed that correlations in the spatial

distribution of Atlantic cod (*Gadus morhua*) and their prey, capelin (*Mallotus villosus*), were positive, negative, or insignificant depending on the scale of observation. Since predator-prey and foraging models are sensitive to scale effects (Wiens 1989), scale-dependent linkages of biological function to the biological and physical structure must be evaluated to understand the mechanisms regulating production processes and dynamics in aquatic systems (Legendre and Demers 1984; Carpenter 1988).

Because of inherent difficulties in measuring underwater spatial and temporal heterogeneity, there have been relatively few studies of spatial processes in aquatic systems. However, recent advances in underwater remote sensing techniques (such as Doppler current profilers, optical plankton counters, underwater acoustics) now provide sufficient spatial information about aquatic environments to formulate and test hypotheses. The development of techniques for continuously measuring phytoplankton and zooplankton provides a framework to define the spatial characteristics and dynamic linkages between biology and physics at lower trophic levels (Bennett and Denman 1985). For fish, underwater acoustics provide one of the few means to continuously measure fish abundances across large bodies of water. Acoustic techniques have been applied routinely for fish stock assessment (see Brandt et al. 1991) and have also been used to directly measure spatial patchiness of fish distributions and its correlation with physical structure (Nero et al. 1990). The spatial information inherent in acoustic data can also be integrated in spatially explicit ecological models of fish production.

Spatially explicit modeling of fish growth rate potential has recently been proposed as a quantitative tool for linking species- and size-specific production to the physiological and behavioral requirements of fish, and to the prevailing biological and physical conditions of the environment (Brandt et al. 1992; Mason et al. 1995). Growth rate potential is defined as the expected growth rate of a predator if placed in a particular volume of water with known physical (temperature) and biological (food resources) characteristics. Thus, growth rate potential reflects the individual's response to environmental conditions, metabolic requirements, and overall activity level. This measure has advantages over simply measuring fish growth in the field in that it (1) provides a measurement of the environment itself; (2) is a mechanistic and process-based approach that allows interpretation of the causes of changes in growth rate; (3) is independent of the actual predator distribution and actual growth rates; and (4) allows predictions of the potential responses of a native or non-native species introduced into a new habitat.

In this chapter, we (1) review the application of spatially explicit models of growth rate potential to functionally define and quantify fish growth with respect to the physiological needs of targeted fish species; and (2) show with examples how this approach might be applied to estuarine fisheries issues.

Our first example compares the pelagic environment of two economically and ecologically important species, striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) in Chesapeake Bay and Delaware Bay. In this example, we compare the pelagic environment for these two predatory species across estuaries and seasons and evaluate the degree of growth rate potential overlap between species. Our second example includes a determination of the suitability of Chesapeake Bay for chinook salmon (*Oncorhynchus tshawytscha*) as an example of a hypothetical species introduction and to illustrate how growth rate potential does not require the predator to be present in the modeled environment.

General Approach

Spatial Modeling

Spatial complexity is an inherent and scale-dependent attribute of pelagic ecosystems (Legendre and Demers 1984; Wiens 1989), yet it is often ignored in studies of biological processes and production, particularly at higher trophic levels. Biological processes that occur at relatively small spatial scales (1–10 m³) may significantly affect production at the whole-system level (Kotliar and Wiens 1990). For example, Lasker (1978) showed that survival and growth of larval northern anchovies (*Engraulis mordax*) depended on the existence of food patches, whereas average values of prey density would lead to starvation. Therefore, the distribution of a predator and its prey across heterogeneous environments may strongly influence the predator's consumption, growth, and, by extension, overall production at the ecosystem level.

By coupling spatially explicit modeling with remote-sensing techniques (underwater acoustics) that provide a high-resolution view of the environment (see Brandt et al. 1992), the bias associated with standard spatially averaged models can be overcome. Incorporating the spatial environment into a modeling framework has improved our understanding of how production processes and predator-prey interactions respond to the underlying biological and physical structure of the environment (Carpenter 1988).

Spatially explicit models of fish growth rate potential have been used for a wide variety of applications and environments. These models have been used to (1) evaluate growth and habitat quality of adult salmonines in the North American Great Lakes (Goyke and Brandt 1993; Mason et al. 1995; Hondorp and Brandt 1996); (2) map seasonal patterns of striped bass growth rate (Brandt and Kirsch 1993) and bay anchovy (*Anchoa mitchilli*) planktivory (Luo and Brandt 1993; Luo et al. 1996) in Chesapeake Bay; (3) evaluate effects of thermal fronts on fish growth (Brandt 1993); and (4) assess

the effects of spatial scale of observation on fish growth by borrowing approaches used in landscape ecology (Brandt and Kirsch 1993; Brandt and Mason 1994; Mason and Brandt 1996). The spatially explicit modeling approach has been extended to include individual-based models and ideal free distributions to predict habitat selection of foragers in spatially complex environments (Tyler and Hargrove 1997; Tyler and Rose 1997; Tyler and Brandt in review). Most of these studies have shown that fish growth is sensitive to the spatial heterogeneity of physical and biological characteristics of environments, and that scales of sampling and modeling critically affect interpretations of biological process.

Model Structure

Spatially explicit models subdivide the habitat into small homogeneous volumes or cells. Each cell is treated individually and is characterized by its own set of measured or simulated attributes including water temperature, prey density, and prey size. The same process-oriented simulation models are run in each cell to produce a growth rate potential, but each cell is parameterized with its own attributes. Fish growth rate potential in each cell is defined by the relationship between the supply of prey afforded by the habitat (prey density and sizes) and the amount of prey that the predator could consume (predator demand) based on its physiological capabilities under the environmental characteristics (water temperature) of each cell. Thus, predator growth rate potential within each cell depends on the innate growth potential of the predator and on the constraints imposed by the habitat in the cell. These constraints include inadequate prey availability, suboptimal water temperatures, and foraging limitations.

The grid model has a particular volume of water, V_i , as the basic cell unit. In our case, the number and size of the cells are determined by water depth, horizontal extent of sampling, and the technological limitations of underwater acoustic sampling. Field measures of prey density (D_i), prey size (S_i), and interpolated water temperature (T_i) for each cell i are used as inputs to foraging and growth (bioenergetics) models that are run in each cell. The high-resolution prey data are acquired with acoustic techniques that measure fish densities and sizes throughout the water column on a near-continuous basis (MacLennan and Simmonds 1992; Brandt 1996). The foraging submodel computes predator consumption rate potential (C_i) from measured prey densities and sizes. The bioenergetics model estimates predator growth rate potential (G_i) from the consumption rate and the physiology of the predator. Results are displayed as cross-sectional maps of predator growth rate potential in each cell as if the predator were to occupy that particular volume of water. Recent developments in interactive data visualization (see Platt and Sarbhvendraiah 1989) allow

to illustrate the spatial relationships of fish growth rates. Brandt et al. (1992) provide a general introduction and discussion of the overall approach.

Bioenergetics Model

Fish growth rates are highly sensitive to water temperature and food supply (Bartell et al. 1986) and thus, bioenergetics models are useful for evaluating the effects of changes in temperature and prey abundances on consumption, growth, and ultimately trophic interactions (Brandt and Hartman 1993). Bioenergetics models are species-specific, energy-balance approaches that describe the flow of energy through an individual fish and how that energy is partitioned among consumption (foraging), growth (somatic and reproductive), and losses (respiration, egestion, excretion, and specific dynamic action). Bioenergetics models can be used to estimate food consumption based on observed growth rates, thermal history, and diet, or alternately to simulate growth of fish under different conditions of diet, prey availability, or water temperature. We use the "Wisconsin" bioenergetics model (Kitchell et al. 1977; Hanson et al. 1997) to compute a fish's growth rate potential under given environmental conditions. This model has been used for a wide variety of applications to fisheries management and ecology (Ney 1993; Brandt and Hartman 1993). Sensitivity analyses (Bartell et al. 1986) and model validation studies (Rice and Cochran 1984; Beauchamp et al. 1989) have shown that bioenergetics models generally provide accurate and robust estimates of fish consumption and growth.

A species-specific bioenergetics model is run in each cell to determine the growth rate potential of an individual fish that might occupy that cell. Growth rate (G_i) of an individual fish in cell volume V_i depends on consumption (C_i), metabolic costs (R_i), and the energy losses due to excretion (U_i), egestion (F_i), and specific dynamic action (H_i):

$$G_i = C_i - (R_i + F_i + U_i + H_i).$$

Consumption and respiration are influenced nonlinearly by the water temperature (T_i) in the cell volume and the weight (W) of the predator, and energy losses (U_i , F_i , and H_i) are typically expressed as proportions of food consumed. We assume equal energy densities (J g^{-1}) for prey and predator since sensitivity analyses have shown bioenergetics models to be insensitive to energy density (Bartell et al. 1986).

Foraging Model

Several foraging models can be used to define the relationship of prey density to predator consumption (Stephens and Krebs 1986). Generally, foraging is modeled as a random process whereby the predator randomly encounters

prey, and prey are assumed to be randomly distributed. Normally, the latter occurs only in a small local volume or cell. To simplify the problem of spatial patchiness of the prey, we reduce the scale of observation to a volume of water sufficiently small so as to assume randomly distributed prey. Our approach does not assume discrete food patches, but rather uses a nearly continuous spatial measure of food density determined with underwater acoustics. The predator consumption rate (C_i) is a general function of encounter rate (E_i , the number of prey encountered per unit time) and the combined probabilities (k) of prey detection (recognition), attack, capture, and ingestion (Fuiman and Gamble 1989):

$$C_i = E_i \cdot k$$

We define the latter combined probabilities (k) as foraging efficiency.

Predator encounter rate with prey is assumed to depend directly on predator reaction distance (RD), the distance at which an individual prey is recognized), swimming speeds of the predator (v) and prey (u , $u < v$), and prey density (D_i) (Gerritsen and Strickler 1977). We generally apply the encounter rate model developed by Gerritsen and Strickler (1977):

$$E_i = \frac{\pi(\text{RD})^2}{3} \cdot \frac{3v^2 + u^2}{v} \cdot D_i$$

Predator consumption rate (C_i) is constrained by water temperature and weight-dependent maximum consumption (C_{max}); that is, an individual fish cannot consume more than it can physiologically contain, assimilate, and evacuate in a single day. Feeding rate is thus bounded by a maximum consumption function.

Measurements of Prey Density

Underwater acoustics provide one of the few means to obtain high-resolution and near-continuous measures of the spatial distribution of fish density over large areas. This technique can effectively sample pelagic ecosystems that are often characterized by short-term dynamics and extreme spatial patchiness through the water column (Brandt 1996). General reviews of acoustics can be found in MacLennan and Simmonds (1992), Brandt (1996), and Medwin and Clay (1998). Acoustic systems sample the water column by sending repetitive pulses (for example, 3 pulses s^{-1}) of sound in a directed beam downward through the water column as the survey vessel moves across the surface. Acoustic pulses are generated by short (0.2–1.0 ms) bursts of high-frequency (for example, 12–420 kHz) voltage from a beam-forming array of pressure transducers. The resulting pressure wave propagates from the transducer at the speed of sound in water. When the sound wave encounters a fish,

or any other acoustic scatterer, an echo is reflected from the target and received at the surface. Echoes contain information on the number of targets, target location, and target size. The strength of an echo can be related to the biomass of the target. Since sound travels in sea water at ca. $1,500 \text{ m s}^{-1}$, the entire water column can be sampled quickly, and a continuous map of fish densities can be obtained. Acoustic data are combined into cells by defining the depth intervals and horizontal distances over which data are pooled.

Application Examples

The above model produces spatial arrays of fish growth rate potential that define the environment from the point of view of the predator. We provide two examples of applications from estuarine systems: (1) a comparison of growth rate potential for striped bass and bluefish in two Atlantic Coast estuaries, the Chesapeake Bay and Delaware Bay; and (2) a determination of growth rate potential for chinook salmon in Chesapeake Bay as an example of a hypothetical species introduction.

Striped Bass and Bluefish Growth Potential in Chesapeake and Delaware Bays

Chesapeake Bay and Delaware Bay are large, productive estuaries that support extensive commercial and recreational fisheries. These estuaries are highly dynamic ecosystems (as exhibited, for instance, in changes in commercial catches, increasing hypoxia in bottom waters of Chesapeake Bay), and they are constantly influenced by management activities (nutrient-loading reductions, enhancement or restoration of fisheries production). Any perturbations to these ecosystems that affect lower trophic levels could eventually be manifested in the higher trophic levels occupied by economically important fishes (bottom-up control; Carpenter 1988). Similarly, changes in overall predator consumption rates caused by changes in the environment (such as the seasonal cycle of water temperatures or increased hypoxia) or in the abundance of predators (such as stocking, migration, mortality) could cause subsequent changes in lower trophic levels (top-down control; Carpenter et al. 1985). Many of the ecologically and economically valuable fishes of these two estuaries are piscivores that depend on the pelagic environment for survival. Although some progress has been made toward understanding the upper trophic levels in these ecosystems (see Baird and Ulanowicz 1989), the functional linkages between prey abundances, environmental characteristics, and predator production remain to be quantitatively defined.

For this example, we evaluate the growth rate potential of a 2 kg striped bass and a 2 kg bluefish in Chesapeake Bay and Delaware Bay. Striped bass

and bluefish support valuable recreational and commercial fisheries in these two estuaries, and their abundance in Atlantic Coast estuaries has fluctuated in the last few decades (NMFS 1997). Both predators commonly feed on the same prey fish species, namely bay anchovy, Atlantic menhaden (*Brevoortia tyrannus*), Atlantic silversides (*Menidia menidia*), Atlantic croaker (*Micropogonias undulatus*), and spot (*Leiostomus xanthurus*) during their estuarine residency (Hartman and Brandt 1995a), and thus competitive interactions likely occur between these two species. Our modeling approach can provide an evaluation of the estuarine environment and potential competitive overlap for these two estuarine predators.

We use the species-specific bioenergetics models developed by Hartman and Brandt (1995b) for these two species based on laboratory experiments. Striped bass and bluefish differ in their basic energetics (figure 15-1): under unlimited food availability, striped bass is capable of positive growth from 5 to 31°C , whereas positive growth for bluefish occurs at water temperatures of $10\text{--}33^\circ\text{C}$. Also, optimal temperature ranges for maximum growth differ between species ($13\text{--}19^\circ$ and $19\text{--}24^\circ\text{C}$ for striped bass and bluefish, respectively). Although bluefish are capable of higher individual consumption than striped bass, this is somewhat offset by higher metabolic costs for bluefish (Hartman and Brandt 1995b).

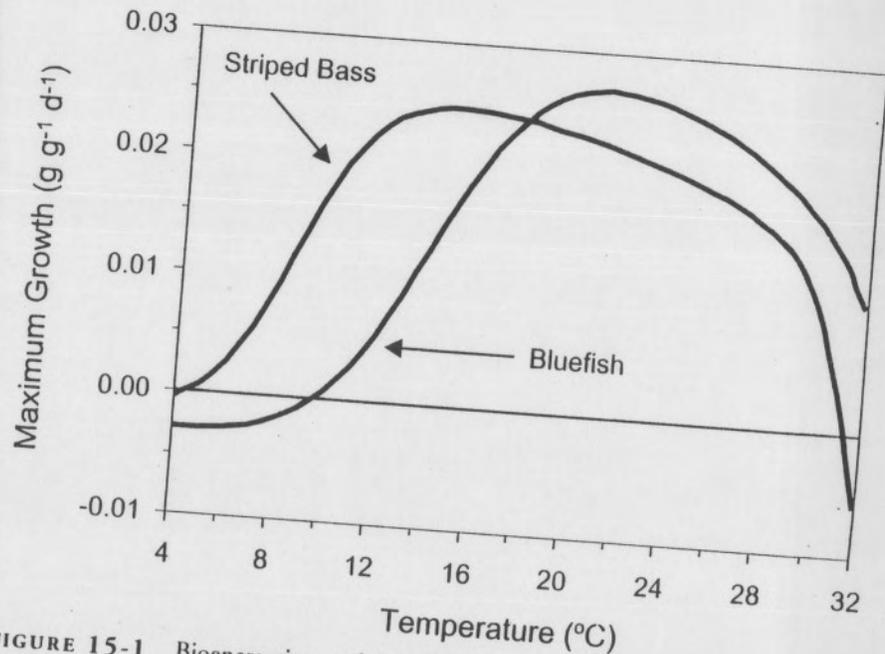


FIGURE 15-1 Bioenergetics model predictions of maximum growth rates for a 2 kg striped bass and a 2 kg bluefish at various water temperatures and under conditions of unlimited food availability.

Field measurements of prey density and water temperature were made at night during July and October 1996. Sampling was conducted along lateral transects taken in the mesohaline, middle portion of each estuary (Chesapeake Bay: 37°46'N, 76°10'W; Delaware Bay: 39°08'N, 75°13'W). Transect lengths were 14 km in Chesapeake Bay and 5 km in Delaware Bay. Water temperatures were interpolated from profiles taken with conductivity-temperature-depth sensors (CTD) at the beginning and end of each transect, and at two additional equidistant points along the transects in Chesapeake Bay. Prey densities were measured with underwater acoustics. The acoustic methods are detailed in Brandt (1990) and Barry et al. (1997) and are summarized here. Acoustic data were collected continuously along each transect using a split-beam 120 kHz Simrad echosounder. The transducer was mounted on a 2.5-m-long aluminum vessel towed near-surface (1.5 m) along the research vessel at speeds of 2.0–2.5 m s⁻¹. Digital information was stored directly in a personal computer and processed using the processing software Digital Echo Visualization and Information System (DEVIS 3.0) developed by Jech and Luo (in review). This system processes digital acoustic data and translates integrated echo and individual target information into two-dimensional matrices of fish density and fish size. Fish densities (fish m⁻³) were measured throughout the water column using narrow depth intervals (0.5 m) and averaged over constant time intervals (15 sec, ~30–40 m). Fish size (total length) was computed from measured target strengths using Love's (1977) equation for clupeid fishes. Fish densities were converted to fish biomass (g m⁻³) using species-specific length-weight relationships (Hartman and Brandt 1995c) applied to the mean fish size and fish density within each cell. The acoustic data were screened for prey too small or too large to be consumed by predators. Prey size ranges were determined from diet data for Chesapeake Bay (Hartman 1993); they were set to 40–250 mm for striped bass and 40–300 mm for bluefish. Species composition was assessed with 2–4 midwater trawls taken near the acoustic transects. Bay anchovy comprised 80% and 95% of total fish caught in midwater trawls in Chesapeake Bay during July and October, respectively. Atlantic croaker and spotted seatrout (*Cynoscion nebulosus*; July only) comprised most of the remaining fish caught. In Delaware Bay, more than 99% of all fish caught in midwater trawls during both July and October were bay anchovy.

We estimated growth rate potential for each species, estuary, and time of year using the GRP Map Maker software developed by Tyler (1998). This software integrates field measures of prey density and water temperature with bioenergetics and foraging model parameters to produce spatially explicit estimates of growth rate potential within each cell along our acoustic transects. The results are displayed as maps of growth rate potential as a function of horizontal position and water-column depth along the transect.

Given the different foraging behaviors of bluefish and striped bass, some of the foraging model parameters differed between species. Predator weights were converted to total length to facilitate use in the foraging model. A 2 kg predator corresponded to a total length of 567 mm for striped bass and 584 mm for bluefish (K. J. Hartman, unpublished data). Swimming speeds (body length s⁻¹; BL s⁻¹) of striped bass and bluefish were set at 1.0 and 1.25 BL s⁻¹, respectively. The higher swimming speed for bluefish was based on their perceived higher relative mobility in comparison with striped bass (Freadman 1979). Data on the reactive distances (RD) of striped bass and bluefish are unavailable, so we assumed that RD was one body length (BL) for all encounter rate calculations. Foraging efficiencies (k) for these two species under field conditions are unknown. We assumed that the probability of prey detection, attack, and capture were each equal to 0.10, and that the probability of prey ingestion once captured was equal to 1.0. Thus, the product of these probabilities (that is, foraging efficiency) was set to 0.001.

The overall relationship of fish growth rate potential to prey density and water temperature (color plate 4) shows that growth rate potential can be determined if any combination of temperature and prey density are known. Positive growth can occur only if water temperature is within the range for positive growth, and prey density is high enough for food consumption to exceed metabolic and waste losses. If prey density exceeds the level necessary for maximum consumption at any given water temperature, surplus food does not contribute to additional growth.

Temperature and prey fish distribution. Water temperatures varied seasonally and between estuaries but were relatively uniform (range <2.5 °C) within transects (color plate 5). During July, water temperatures were higher in Chesapeake Bay (24.5–26.7 °C) than in Delaware Bay (21.4–23.0 °C). By contrast, water temperatures were very similar between Chesapeake Bay and Delaware Bay during October (15.2–16.2°C) and varied by <1°C within each estuary. Water temperatures during July corresponded to the range where bluefish are capable of higher growth rates than striped bass, whereas temperatures during October were more favorable to striped bass growth (figure 15-1).

Prey fish biomass was higher in October than in July for both estuaries (color plate 6). During July in Chesapeake Bay, prey fish were scattered relatively evenly throughout the upper half of the transect (0–15 m), but there was virtually no prey in the deeper water. The absence of prey in deeper water was likely due to hypoxic conditions at those depths (dissolved oxygen <1 mg l⁻¹). Hypoxia did not occur in Delaware Bay, and prey were distributed throughout the transect during July. Transect-wide mean prey fish biomass

during July (table 15-1) was lower in Chesapeake Bay (0.11 g m^{-3}) than in Delaware Bay (0.17 g m^{-3}). Similarly, only 10% of the environment sampled in Chesapeake Bay during July contained prey fish (that is, 685 of 6,758 cells with biomass $> 0 \text{ g m}^{-3}$), compared to 24% for Delaware Bay (table 15-1). During October, patterns of prey biomass were more similar between estuaries, and the highest levels occurred in the deeper channel areas. Although mean prey fish biomass differed between estuaries during October (0.33 and 0.20 g m^{-3} for Chesapeake Bay and Delaware Bay, respectively), the proportion of the environment with prey fish was similar for both estuaries (46% for Chesapeake Bay and 43% for Delaware Bay; table 15-1).

Growth rate potential. For both estuaries, striped bass growth rate potential was highest during October (color plate 7), due to better temperatures for growth and higher prey fish biomass. During July, striped bass growth rate potential was low across most of the transects in both estuaries, and a few higher growth rate potential levels were limited to areas with elevated levels of prey biomass. Only 1–3% of the environments could support positive growth during July (table 15-1). Although prey biomass was similar between estuaries in July, mean striped bass growth rate potential was higher in Delaware Bay because lower temperatures were better for striped bass growth. During October, striped bass growth rate potential was high in the deeper channel areas of both estuaries where prey fish biomass was also highest. Approximately 11–14% of all cells supported positive growth (table 15-1),

TABLE 15-1

Mean and percentage of cells with positive prey biomass and growth rate potential for Chesapeake Bay and Delaware Bay during July and October 1996.

Measurement	Chesapeake Bay		Delaware Bay	
	July	October	July	October
<i>Biomass</i>				
Mean	0.107	0.330	0.171	0.195
% cells greater than 0	10.1	45.6	23.8	42.9
<i>Striped Bass Growth Rate Potential</i>				
Mean	-0.011	-0.003	-0.008	-0.003
% cells greater than 0	1.5	13.8	2.5	11.2
<i>Bluefish Growth Rate Potential</i>				
Mean	-0.015	-0.005	-0.011	-0.005
% cells greater than 0	1.7	13.4	2.7	10.8

and 5% of the transects in both estuaries contained prey biomass levels that were high enough for striped bass to achieve maximum food consumption and hence maximum growth rate potential.

Bluefish growth rate potential did not follow the same pattern as for striped bass (color plate 8). The highest levels of growth rate potential for bluefish in both estuaries occurred during July, but they were limited to a few areas with elevated levels of prey biomass. Mean bluefish growth potential in July was slightly higher in Delaware Bay since water temperatures were closer to the optimal level for bluefish growth (table 15-1). Only 2–3% of all cells could support positive growth during July, but most of these cells had prey biomass high enough for bluefish to achieve maximum growth. During October, bluefish growth rate potential was high in the deeper channel areas where prey fish biomass was also highest. Highest growth rate potential during October was lower than during July because of cooler water temperatures, which were less favorable for bluefish growth. Nonetheless, about 11–13% of the environment supported positive growth (table 15-1). In general, bluefish reached higher growth rate potential levels during July because of favorable water temperatures, but higher prey biomass during October resulted in a larger proportion of the environment being suitable for positive growth.

For both species, transect-wide averages of growth rate potential were always negative (table 15-1), even though spatial maps of growth rate potential displayed numerous areas with positive growth. This exemplifies the importance of having spatially explicit information on distributions of water temperature and prey biomass. Simply using average values of water temperature and prey density across the environment would lead to the erroneous conclusion that the habitat could not support positive growth for striped bass or bluefish. Positive growth by these two species in Chesapeake Bay and Delaware Bay is likely linked to the existence of areas with appropriate food resources and environmental conditions.

Growth rate potential overlap. Because striped bass and bluefish feed on similar prey fish species during their estuarine residency (Hartman and Brandt 1995a), they may be competing for food resources. Indeed, distributions of growth rate potential for striped bass and bluefish were often similar across environments; that is, cells with elevated growth rate potential for one species usually had elevated growth rate potential for the other species as well. To quantify the extent of growth rate potential overlap between striped bass and bluefish, we compared growth rate potential levels between species and for each environment. Cells were color coded (light blue for

bluefish and yellow for striped bass) according to which species had the highest growth rate potential. Only cells with positive growth rate potential were included in this analysis.

In both estuaries, growth rate potential was higher for bluefish than for striped bass across transects during July (color plate 9). The warm water temperatures during July in both estuaries were more favorable for bluefish growth. During October, striped bass had higher growth rate potential than did bluefish in about 56% and 52% of cells with positive growth in Chesapeake Bay and Delaware Bay, respectively. Cooler water temperatures during October were more favorable for striped bass growth than for bluefish growth. At water temperatures of 15–16°C, bluefish growth is largely limited by their reduced maximum possible consumption rates. Although prey fish biomass was high during October, bluefish growth was restricted by the temperature-related physiological limits imposed on maximum consumption. However, at prey fish biomass concentrations that were suboptimal for both species (that is, 0–1 g m⁻³), bluefish had higher growth rate potential. Higher growth rate potential for bluefish in those cells was largely due to their more active foraging behavior in the model, which enabled them to search a larger volume and encounter more prey in a given amount of time. In turn, higher encounter rates resulted in higher consumption rates and a higher growth rate potential.

Measures of growth rate potential support the concept that fish use of estuaries may be driven by both thermal physiology and prey availability. Striped bass were better suited to the thermal regimes and prey biomass available during October, while their growth potential during July was limited by high water temperatures. In contrast, thermal conditions were suitable for bluefish during July but were limiting maximum growth rate potential during October even though prey biomass was relatively high. Such patterns of growth rate potential for these two estuarine species are consistent with their reported use of Atlantic Coast estuaries. Bluefish typically inhabit estuaries when water temperatures are above 15°C (usually May to October) and they overwinter in the coastal waters off the southeastern United States from November to April, where temperatures are more favorable during that time (Kendall and Walford 1979). Bluefish grow rapidly during their summertime estuarine residency, and age-1 and age-2 fish can double their weight between June and October (Hartman and Brandt 1995a). Striped bass are annual residents of Chesapeake Bay and Delaware Bay, and their highest growth rates typically occur during spring and fall with little or no growth during summertime (Hartman and Brandt 1995a). Although striped bass and bluefish likely compete for similar prey in estuaries, competitive overlap may be reduced by their different thermal physiologies.

Growth Rate Potential for Chinook Salmon in Chesapeake Bay: Example of Species Introduction

Because growth rate potential is based on environmental conditions and predator physiology and because it is independent of actual predator distribution and growth rates, this approach can be particularly useful to evaluate the potential response (for instance, growth) of a species that has been purposefully or accidentally introduced into an habitat. One can evaluate the suitability of a particular environment for a species based simply on measurements of the environment's thermal structure and prey distribution. Estimates of growth rate potential can reveal whether conditions are adequate to allow introduced individuals to achieve positive growth and for the population to be sustained or to expand.

To illustrate the application of growth rate potential models for species introductions, we estimated growth rate potential for a 2 kg chinook salmon in Chesapeake Bay as a hypothesized case of the introduction of a non-native species into a new ecosystem. We estimated chinook salmon growth rate potential during July and October at the same mesohaline transect used above for Chesapeake Bay. Growth rates were calculated using the bioenergetics model for chinook salmon developed by Stewart and Ibarra (1991). We assumed that chinook salmon in Chesapeake Bay would be piscivorous predators of pelagic fish, and hence that our acoustic estimates of prey fish biomass would be adequate representations of prey availability. We also assumed that the foraging behavior of chinook salmon would be similar to that of bluefish and used similar foraging parameters.

Chinook salmon growth rate potential. Maps of growth rate potential indicate that chinook salmon growth in the Chesapeake Bay would differ greatly between seasons (color plate 10). During July, chinook salmon would not be capable of achieving any positive growth since water temperatures at that time are well in excess of the maximum temperature (20°C) for chinook salmon positive growth. However, favorable water temperatures and sufficient prey fish biomass during October resulted in positive chinook salmon growth rate potential in 6% of the environment. Water temperatures in Chesapeake Bay during October were near the optimal growth range (9–15°C) for chinook salmon growth.

Our results indicate that chinook salmon could perhaps survive and grow in Chesapeake Bay when water temperatures are below 20°C (November to May) and if prey biomass is adequate. However, no positive growth could occur from June to October because of excessive water temperature and the absence of cool-water refuges. Although we used an unlikely species for stocking in Chesapeake Bay, this analysis provides an example of how

growth rate potential models can be used to evaluate the potential response of an introduced species to its new environment. This approach can be particularly useful for a species targeted for reintroduction into a rehabilitated environment.

Summary and Future Applications

Spatially explicit models of fish growth rate potential provide a mechanism for linking biological and physical environments, and for defining the distributional patterns of the aquatic environment at different spatial scales. By coupling high-resolution data on prey density, prey sizes, and thermal structure with bioenergetics and foraging models, the spatially explicit modeling approach goes beyond the simple (but essential) correlation of biological and physical structures to model the expected functional responses of fishes to their physical and biological habitats. This type of approach may be particularly useful in heterogeneous habitats where density-dependent (biological) and density-independent (physical) processes occurring at relatively small spatial scales can substantially affect population processes and production at the system level (Possingham and Roughgarden 1990).

Growth rate potential modeling has a wide range of possible applications. As we have shown with our examples, this approach provides a robust means for comparing growth potential for targeted species among habitat and time of year. Similarly, comparisons can be made between species that occupy a similar habitat, making it possible to evaluate the seasonal and spatial overlap in growth potential of competing species. Growth rate potential also provides a relative measure of ecological efficiency for fish under a specific set of habitat characteristics. That is, by comparing actual growth rates and habitat use with predictions from growth rate potential models, it is possible to assess the ecological efficiency of the species within that particular environment. A highly efficient predator in areas of the environment that contain optimal water temperatures and prey density will maximize its growth rate. By contrast, a less efficient predator located in areas with suboptimal conditions of temperature, prey, or both may have lower growth rates.

The transformation of prey fish density and size into estimates of consumption rate for calculation of growth rate potential remains the least well-known component to quantify growth rate potential (Bartell et al. 1986; Mason et al. 1995). In our examples, we assumed a constant reactive distance ($RD = 1$ body length) and foraging efficiency ($k = 0.001$) in the foraging model. Certainly, the reactive distance of a predator will change in response to diet and seasonal light levels and turbidity (Benfield and Minello 1996), and foraging efficiency will vary as a function of prey

size, prey species, predator experience, hunger level, and predator preference (Stephens and Krebs 1986). Light level at depth, prey size structure, and prey species composition often differ greatly within and among estuaries and likely affect growth rate potential estimates. Future investigations should address behavioral interactions between predators and their prey, and how changes in the physical environment (such as water temperature or turbidity) influence the intensity of predator-prey interactions.

Despite existing model limitations, the spatially explicit approach provides a solid foundation for evaluating species-specific habitat needs based on the physiological requirements of targeted species. Our approach provides information on the physiological response of fishes that cannot be determined from prey abundance, prey size, or water temperature alone. Complex spatial details of the biological and physical environment are explicitly considered for the evaluation of growth rate potential. Extensive high-resolution and remote-sensing data are now routinely collected by agencies throughout the world. Data from such monitoring programs can provide the information necessary for quantifying and assessing changes in species- and size-specific fish growth rate potential in estuaries.

We contend that growth rate potential models are useful tools to help us understand the relationships between prey supply and predator demand in aquatic systems and to forecast the effects of proposed management actions. Possible effects of stocking decisions, population fluctuations, invasion by exotics, nutrient reduction strategies, and weather can be modeled with the approach outlined in this chapter. If planktivorous fish abundances decline in Chesapeake Bay (as they have in the last decades), the pelagic community may change greatly. Spatial models can help assess how changes in the fish communities and the environment will affect piscivore production and the health of the ecosystem. As such, growth rate potential can also serve as an indicator of ecosystem health or habitat quality in which maximum growth rate reflects the highest habitat quality.

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