Contents lists available at ScienceDirect

### **Ecological Modelling**

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



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#### ARTICLE INFO

Article history: Received 3 October 2014 Received in revised form 29 April 2015 Accepted 3 May 2015 Available online 28 May 2015

Keywords: Simulation modeling Bottom-up forcing Predator-prey dynamics Functional response Reproductive numerical response

### ABSTRACT

Bottom-up control within ecosystems is characterized, in part, by predator populations exhibiting growth and recruitment changes in response to variability in prey density or production. Annual prey availability can vary more than 10-fold in marine ecosystems, with prey experiencing a dramatic increase or pulse in production within some years. To assess the bottom-up effects of such pulses on predator growth, production, and fisheries management, we developed an age-specific, predator-prey simulation model (parameterized for summer flounder, Paralichthys dentatus) based on simple hypothesized mechanisms for consumption, growth, and population dynamics. Pulses in each of the three modeled prey groups (small crustaceans, forage fish, larger fish prey) generated different magnitudes of change in predator weight-atage (w), spawning stock biomass (S), fishery yield (Y), and recruitment (R), due to ontogenetic differences in growth potential and dietary composition across predator age classes. Increases in productivity of small forage fishes generated the greatest gains in predator w, S, Y, and R, relative to pulses of the other prev groups. Median increases in R following a prey pulse were minimal (<4%) except under high fishing rates that stimulated a stronger compensatory response in the population (8–11% increase in R), demonstrating the interactive role of top-down and bottom-up effects on predator productivity. Seasonal migration patterns determined the degree of spatiotemporal overlap of predators with the spatially constrained pulses in prey production. Prey pulses reduced the median time required for depleted populations to be rebuilt by 0-5% following declines in fishing pressure. Reductions in time to recovery were highly variable due to recruitment stochasticity, but stock recovery was more sensitive to the severity of harvest control measures than to availability of the non-limiting prey. Understanding the relative magnitudes of such bottom-up processes, particularly in the presence of varied fishing pressure can aid in developing ecosystem approaches to fisheries management that account for such ecological interactions more explicitly. © 2015 Elsevier B.V. All rights reserved.

#### 1. Introduction

Bottom-up control in ecosystems is characterized by the regulation of higher-trophic-level productivity and variability by processes acting on lower trophic levels. Although other forms of control (top-down and wasp-waist) can be dominant in some systems or under certain conditions (Hunt and Stabeno, 2002; Cury and Shannon, 2004; Hunt and McKinnell, 2006), empirical evidence supports bottom-up structuring of various marine ecosystems (Aebischer et al., 1990; Verheye, 2000; Chavez et al., 2003; Frederiksen et al., 2006). Theoretically, a simple mechanism supporting such bottom-up control can consist of four steps: (1)

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http://dx.doi.org/10.1016/j.ecolmodel.2015.05.002 0304-3800/© 2015 Elsevier B.V. All rights reserved. environmentally mediated increases in prey production and density, (2) enhanced foraging by predators, (3) improved growth, survival, and fecundity of predators, and (4) greater recruitment to the following generation of the predator population. The relationship between predator density and prey density that would link the two ends of this mechanistic progression has been described in terrestrial literature as a predator's reproductive numerical response (Solomon, 1949; Holling, 1959). For marine fishes, direct empirical support for such a mechanism is stronger for steps 1-3 (e.g., McGowan et al., 1998; Ringuette et al., 2002; Castonguay et al., 2008), but wanes through its progression to step 4 (e.g., Mcfarlane and Beamish, 1992; Beaugrand et al., 2003). Thus, at broad scales, support for reproductive numerical responses by fishes tends to be more correlative in nature (Aebischer et al., 1990; Ware and Thomson, 2005; Frank et al., 2007), with the mechanistic components corroborated empirically at smaller spatiotemporal scales or supported theoretically.







Two of the main difficulties in linking prey and predator densities at system-wide scales involve the high degree of interannual variability in predator-prey populations and the adaptive foraging behaviors of most fishes. Populations of fishes and other organisms commonly experience 10-fold variability in recruitment, but variations can be even more drastic (>100-fold) as recruitment and mortality are influenced by a complex suite of climatic, oceanographic, ecological, and anthropogenic factors (Rothschild, 1998; Hunt and Stabeno, 2002; Houde, 2009). Importantly, an aggregation of ameliorative conditions in some years can cause dramatic increases, or pulses, in production (Holland et al., 1987; Rothschild, 1998; Jung and Houde, 2004b). These pulses in production can be targeted and consumed heavily by predators, especially by relatively opportunistic fishes that can switch to these prey as they become more available (Ringuette et al., 2002; Castonguay et al., 2008). However, the ability of predators to exploit pulses in prey production is partially mediated by ontogenetic changes in diets and food preferences (Scharf et al., 2000). Years of abrupt failures in prey production or recruitment can also have important consequences for predator populations (Gjøsæter et al., 2009). Understanding a predator's growth and numerical responses to the large inherent variability in prey production can be an important component to characterizing the trophodynamic mechanisms controlling fisheries production.

The potential benefits of increased prey production to predators can interact with top-down fishing pressure and be influenced by spatiotemporal overlap of the interacting species. For exploited predator populations, fishery removals are a dominant source of mortality, and a reproductive numerical response could be dissipated by the harvest of any surplus predator production that results from prey pulses. Movement of predatory populations also has the potential of obscuring any bottom-up effects, given that prey production can be regionally confined. For example, many marine fishes have life histories dependent on estuaries, in which prey production can be greater relative to alternative offshore habitats (Beck et al., 2001; Able, 2005). Thus, the degree of movement between estuarine and offshore regions could influence predator–prey overlap, predatory growth, and the numerical response.

In this study, we evaluated the population-scale consequences of increased prey availability on a predator stock using a mechanistic, multi-species simulation model, parameterized for summer flounder, Paralichthys dentatus. The age-specific, spatial, predator-prey model linked consumption, growth, and population dynamics. Summer flounder was chosen as the model predator because its fishery and ecology (e.g., migration, ontogenetic diet shifts, life history) are representative of other exploited marine groundfish, and because there is evidence that the species is responsive to pulses in prey production. This species has supported a large fishery in the northwest Atlantic Ocean, and overfishing led to significant declines of the stock, reaching record lows in the late 1980s (Terceiro, 2002). After establishing a rebuilding plan and implementing regulations, the stock recovered and was declared rebuilt in 2010 (Terceiro, 2011). Based on research from the Chesapeake Bay (the largest estuarine nursery area serving the coastal summer flounder population), summer flounder demonstrated strong episodic increases in prey consumption likely driven by prey availability (Buchheister and Latour, 2015b). These annual periods of increased consumption were also correlated with larger weightat-age for summer flounder (Buchheister, unpublished data).

Our simulation model provided a controlled virtual environment for examining questions regarding the potential populationscale response to pulses in prey production. We were specifically interested in examining the relative effects of three different prey groups that are consumed and targeted at varying rates through ontogeny, as is common in the diets of many fishes (Latour et al., 2008; Buchheister and Latour, 2015a). Multiple modeling scenarios were used to address three major research questions: (1) How do pulses in productivity of different prey populations influence the growth, production, and reproductive numerical response of a migratory predator? (2) How do fishing rates and migration patterns interact with a population's ability to harness regionally localized increases in prey production? (3) What influence would these prey pulses have on rebuilding timelines of an overfished predator population? Understanding the relative magnitudes of these bottom-up processes, particularly in the presence of varied fishing pressure can aid in developing ecosystem approaches to fisheries management that account for such ecological interactions more explicitly (Link, 2010a).

#### 2. Methods

#### 2.1. Base model formulation

We developed a spatial, age-specific simulation model that consisted of linked population, growth, and consumption models. Within the population model, the key abundance changes modeled were decreases in abundance due to fishing and natural mortality, movement between regions, and additions through recruitment (Fig. 1). The model was parameterized to represent the summer flounder stock along the Northeast U.S. Atlantic coast, from North Carolina to Maine. We coded the model for two linked spatial domains or ecosystems (region 1 – nearshore estuaries and bays; region 2 - offshore continental shelf waters) to account for the strong migration of the species between these habitats. Summer flounder were modeled with 8 age-classes from age-0 to age-7+, following the convention of recent stock assessments (Terceiro, 2011). We treated time discretely, using a seasonal (3-month) time-step to account for the highly seasonal dynamics of summer flounder movement, spawning, and growth. Within each time step, the order of processes proceeded with recruitment, mortality, consumption, growth, and movement, with the census taken at the end of each season. Model simulations were conducted for 55 years under various scenarios (see Section 2.2) following a 25-year burn-in period. All symbols for the simulation model are defined in Table 1. Model equations are presented in Table 2 and referenced by Tx.y, with x denoting the table number and y indicating the



**Fig. 1.** Diagram of predator–prey simulation model. Major mechanistic processes are labeled (C – consumption, G – growth, R – recruitment, I – net immigration, F – fishing mortality losses, M – natural mortality losses).

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