

**Abstract**—Increasing interest in the use of stock enhancement as a management tool necessitates a better understanding of the relative costs and benefits of alternative release strategies. We present a relatively simple model coupling ecology and economic costs to make inferences about optimal release scenarios for summer flounder (*Paralichthys dentatus*), a subject of stock enhancement interest in North Carolina. The model, parameterized from mark-recapture experiments, predicts optimal release scenarios from both survival and economic standpoints for various dates-of-release, sizes-at-release, and numbers of fish released. Although most stock enhancement efforts involve the release of relatively small fish, the model suggests that optimal results (maximum survival and minimum costs) will be obtained when relatively large fish (75–80 mm total length) are released early in the nursery season (April). We investigated the sensitivity of model predictions to violations of the assumption of density-independent mortality by including density-mortality relationships based on weak and strong type-2 and type-3 predator functional responses (resulting in depensatory mortality at elevated densities). Depending on postrelease density, density-mortality relationships included in the model considerably affect predicted postrelease survival and economic costs associated with enhancement efforts, but do not alter the release scenario (i.e. combination of release variables) that produces optimal results. Predicted (from model output) declines in flounder over time most closely match declines observed in replicate field sites when mortality in the model is density-independent or governed by a weak type-3 functional response. The model provides an example of a relatively easy-to-develop predictive tool with which to make inferences about the ecological and economic potential of stock enhancement of summer flounder and provides a template for model creation for additional species that are subjects of stock enhancement interest, but for which limited empirical data exist.

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## Coupling ecology and economy: modeling optimal release scenarios for summer flounder (*Paralichthys dentatus*) stock enhancement

G. Todd Kellison

David B. Eggleston

Department of Marine, Earth, and Atmospheric Sciences,  
North Carolina State University  
Raleigh, North Carolina 27695-8208

Present address (for G. T. Kellison, contact author): National Park Service/Biscayne National Park  
9700 SW 328<sup>th</sup> St, Homestead, Florida 33033

E-mail address (for G. T. Kellison): todd\_kellison@nps.gov

Commercially important marine fish and invertebrate populations are declining worldwide in response to overexploitation and habitat degradation (Rosenberg et al., 1993; FAO 1998). This reduction in harvestable fishery resources has stimulated increasing interest in the use of hatchery-reared (HR) animals to enhance wild stocks (Munro and Bell, 1997; Travis et al., 1998; Cowx, 1999; Kent and Drawbridge, 1999). Unfortunately, many stock enhancement programs proceed before ecological concerns are adequately addressed (Blankenship and Leber, 1996), and without the identification of goals or the evaluation of the success of enhancement efforts (Cowx, 1999). If fishery managers can satisfactorily determine that enhancement efforts will have no ecologically significant negative ramifications, then managers should establish specific, quantifiable goals and objectives of enhancement efforts as part of a responsible approach to stock enhancement (Blankenship and Leber, 1996; Heppell and Crowder, 1998). Once such goals have been established, managers should identify stocking approaches that will lead to the most cost-efficient realization of enhancement goals—a process that can be accomplished with the aid of coupled ecological and economic models. Although numerous (advanced) models (conceptual and species-specific) exist to predict the biological and ecological impact of alternative enhancement scenarios (e.g. Botsford and Hobbs, 1984; Salvanes et al., 1992; Barbeau and Caswell, 1999; Sutton et al., 2000),

there are few models (of which we are aware) that have attempted to link the biological and ecological results of stocking efforts (e.g. addition of biomass to a stocked population) with the economic costs associated with various release scenarios (e.g. Botsford and Hobbs, 1984; Hobbs et al., 1990; Hernandez-Llamas, 1997; Kent and Drawbridge, 1999). Such a link is critical to the responsible use of funding to rebuild or manage fisheries, and for the comparison of predicted costs of enhancement versus alternative management techniques.

In North Carolina, there has been recent interest in stock enhancement with summer flounder (*Paralichthys dentatus*) (Waters, 1996; Rickards, 1998; Waters and Mosher, 1999; Burke et al., 2000; Copeland et al.<sup>1</sup>) because of a combination of heavy commercial and recreational exploitation, established techniques for mass hatchery-rearing (Burke et al., 1999), and considerable knowledge of summer flounder life history (Powell and Schwartz, 1977; Burke et al., 1991; Burke, 1995). Nevertheless, there have been no large-scale release experiments (and subsequent collection of data) by which to make empirical inferences about stock enhancement potential for this species. We present a compartmental model, parameterized from mark-recapture field experiments,

<sup>1</sup> Copeland, B. J., J. M. Miller, and E. B. Waters. 1998. The potential for flounder and red drum stock enhancement in North Carolina. Summary of workshop, 30–31 March, 1998, 22 p. [Available from North Carolina State Univ, Raleigh, NC 27695.]

**Table 1**

Range of numbers of summer flounder (*Paralichthys dentatus*) released (and resulting postrelease densities), sizes-at-release, and dates of release simulated in the model.

Number released	Postrelease density	Size-at-release	Dates of release
100–400,000	0.001–4.0	30–80 mm	1 April–15 July

that incorporates size of fish released, date-of-release, and number of fish released to calculate 1) predicted numbers of survivors and 2) economic costs associated with varying release scenarios under density-independent mortality. We investigated the sensitivity of model predictions to violations of the assumption of density-independent mortality because there is abundant evidence that mortality rates, or processes underlying mortality rates (e.g. growth), are affected by density-dependent relationships in the wild (see, for recent examples, Buckel et al., 1999; Bystroem and Garcia-Berthou, 1999; Jenkins et al., 1999; Kimmerer et al., 2000). We did so by repeating model simulations under varying density-mortality relationships (depensatory in nature at elevated densities), using experimental evidence from our own field studies and published observations for similar species to parameterize density-mortality relationships. Additionally, we used a scenario in which the density-mortality relationship changed over time to make inferences about the effect of more complex density-mortality relationships on postrelease mortality of juvenile summer flounder. Finally, we generated predicted temporal patterns of field densities under varying density-mortality relationships and compared them with observed (in the field) patterns to determine whether model output under the considered density-mortality relationships matched actual patterns in the field. The model provides an example of a relatively easy-to-develop predictive tool with which to make inferences about the ecological and economic potential of stock enhancement with summer flounder and provides a template for model creation for additional species that are subjects of stock enhancement interest, but for which limited empirical data exist.

## Materials and methods

### Background

In North Carolina, wild summer flounder recruit to shallow-water estuarine nursery habitats from February to May, after which small juvenile (20–35 mm total length [TL]) densities range from ~0.1 to 1.0 fish/m<sup>2</sup> (Burke et al., 1991; Kellison and Taylor<sup>2</sup>). Juveniles subsequently make an ontogenetic habitat shift to deeper waters (Powell and Schwartz, 1977), apparently after reaching a total length

of ~80 mm (Kellison and Taylor<sup>2</sup>). By mid-July, densities of juvenile summer flounder in the shallow water nursery habitats are near zero (Kellison and Taylor<sup>2</sup>).

### Model pathway

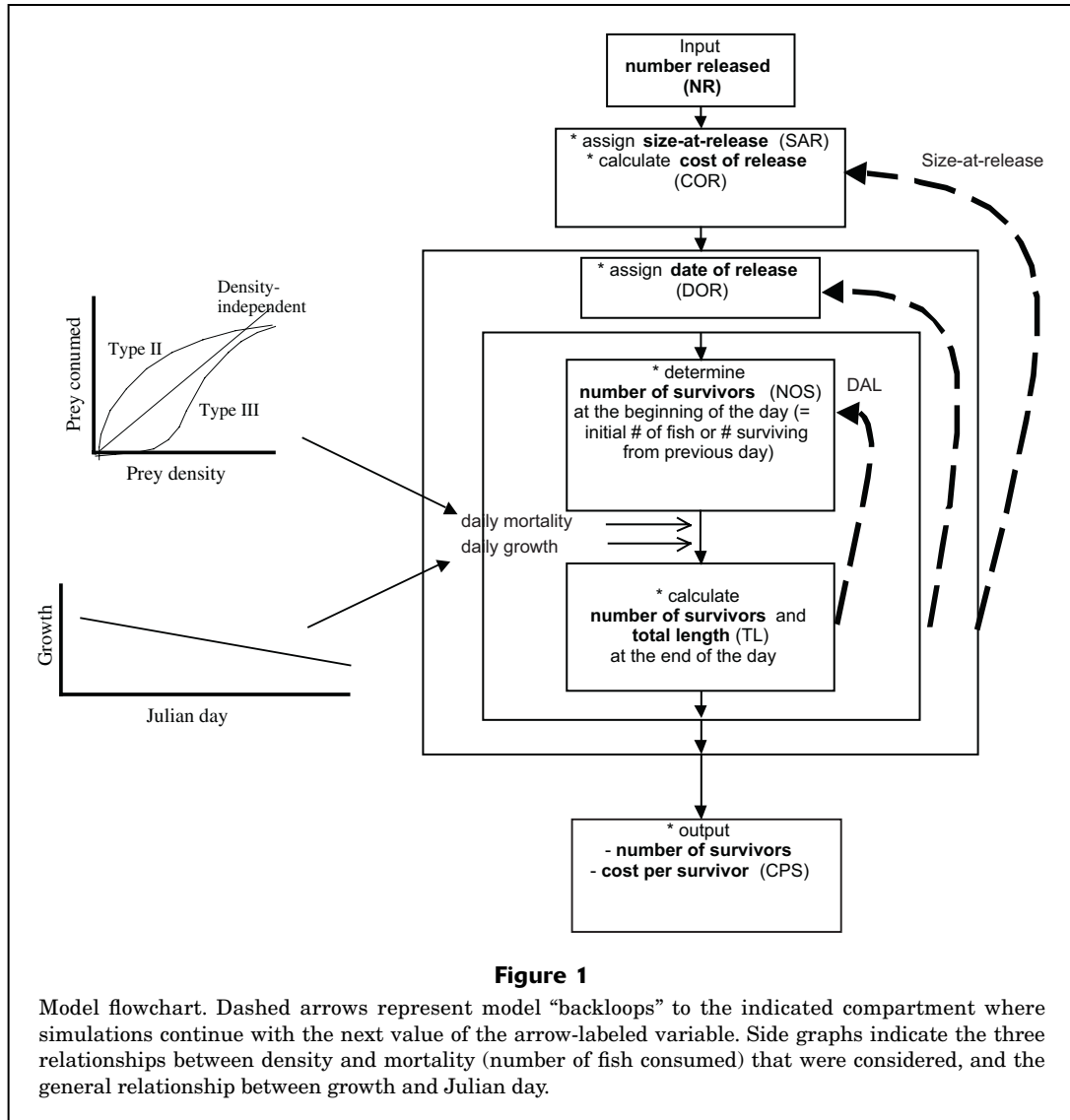
Our compartmental model simulated the daily mortality and growth of different-size hatchery-reared (HR) fish released in the field over a 105-day period (1 April to 15 July, based on observed field abundances) in a hypothetical release habitat of 10 hectares. The model predicted the percentage of released fish surviving and economic cost-per-survivor under 2730 release scenarios for a specified number of fish released (see below). To begin the model, a value of number of fish released (NFR) ranging from 100 to 400,000 (Table 1) was chosen (Fig. 1), resulting in postrelease densities (assuming even postrelease distribution) of 0.001–4.0 fish/m<sup>2</sup>. These values included a range of densities of juvenile summer flounder observed in wild nursery habitats (~0–1 fish/m<sup>2</sup>; mean ~0.05 fish/m<sup>2</sup>; Kellison and Taylor<sup>2</sup>), but also included unusually high densities (>1 fish/m<sup>2</sup>) in order to examine how such release strategies would affect model output (we did not examine densities >4 fish/m<sup>2</sup> because of a lack of data on fish response to resource limitation likely to occur as densities increased past values for which we had empirical growth data). Each group of NFR was initially assigned a “size-(TL) at-release” of 30 mm (the smallest size-at-release simulated in the model), after which a size-dependent economic cost associated with the release of the 30-mm-TL fish was calculated (see below). The release group was then assigned a minimum Julian “day of release” of 92 (corresponding to 1 April, the earliest release date simulated in the model). A range of Julian days of release was included in the model because field-estimated growth rates were dependent on Julian day (Kellison, 2000), and growth rates are potentially important to the determination of mortality rates (Rice et al. 1993). With this model, we then calculated daily mortality and growth (described below) in the hypothetical release habitat over the number of days at large (DAL), where

$$DAL = 197 \text{ (the Julian day corresponding to 15 July)} - 92 \text{ (Julian release day),}$$

and output a number of survivors and a calculated cost-per-survivor (CPS), where

$$CPS = \text{cost associated with release} \div \text{predicted number of survivors,}$$

<sup>2</sup> Kellison, G. T., and J. C. Taylor. 2000. Unpubl. data. Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695-8208.



**Figure 1**

Model flowchart. Dashed arrows represent model “backloops” to the indicated compartment where simulations continue with the next value of the arrow-labeled variable. Side graphs indicate the three relationships between density and mortality (number of fish consumed) that were considered, and the general relationship between growth and Julian day.

for the initial release scenario of fish size = 30 mm TL, Julian day = 92, and an NFR input determined by the modeler). The model then looped back to the “date-of-release” step and simulated the release of the 30-mm-TL fish for Julian release days 93–197, outputting a predicted number of survivors and cost-per-survivor for each release date. The model then repeated all previous steps under sequentially larger size-at-release scenarios, looping back to the “size-at-release” step and simulating the release of fish ranging in size from 32–80 mm TL fish in steps of 2 mm TL. The model output was a predicted number of survivors and economic cost-per-survivor for each release day (92–197) for each size-at-release (Fig. 1). Thus, for each input NFR, there were 26 size-at-release possibilities  $\times$  105 Julian days of release possibilities, which resulted in 2730 simulations, each of which resulted in a predicted number of survivors and cost-per-survivor for that particular release scenario. For each input NFR, the results from the 2730 simulations were plotted on two response surfaces, with an  $x$ -axis of

size-at-release, a  $y$ -axis of date-of-release, and a  $z$ -axis of either 1) predicted number of survivors (NOS), or 2) cost-per-survivor (CPS), to identify release scenarios resulting in the maximum predicted number of survivors and minimum cost-per-survivor, respectively. The scenarios resulting in the maximum predicted number of survivors and minimum cost-per-survivor were not necessarily identical.

#### Calculation of mortality, growth, survival, and economic costs associated with release

During each day at large (DAL), released fish were subjected to a density-independent daily mortality rate of 0.02153, derived from postrelease mark-recapture data of HR summer flounder (Kellison et al., 2003b). In deriving this value, mean postrelease densities were used to estimate a total number of survivors from experimental releases. Daily survival was then calculated with the equation

$$NFR \times S_D^{DAL} = NOS,$$

where  $NFR$  = number released;

$S_D$  = daily survival;

$DAL$  = days at large (from release date until Julian day 197); and

$NOS$  = estimated number of survivors.

Daily mortality ( $M_D$ ) was then calculated from the equation

$$M_D = 1 - S_D.$$

At the end of each simulated day, all fish that were alive increased in growth according to the equation

$$G_D = -0.0061 \times \text{Julian day} + 1.2487,$$

which was derived from mark-recapture data (Kellison, 2000), and in which  $G_D$  is daily growth in millimeters. Fish reaching 80 mm TL during the model (i.e. by 15 July) were considered to make an ontogenetic habitat shift to deeper waters. These fish were then subjected to one half year of natural mortality to simulate mortality-related losses from deeper-water habitats ( $M=0.28$ ; Froese and Pauley, 2001). Remaining fish, now having survived ~one year of natural mortality, were considered to be survivors (available to the commercial fishery), which is a conservative assumption because 1-yr-old summer flounder are only partially recruited to the commercial fishery. All fish not reaching a total length of 80 mm were assumed to perish.

To determine size-dependent economic costs of fish production, we used the following regression equation derived for Japanese flounder (*Paralichthys olivaceus*) by Sproul and Tominaga (1992) because equivalent economic data for summer flounder were unavailable:

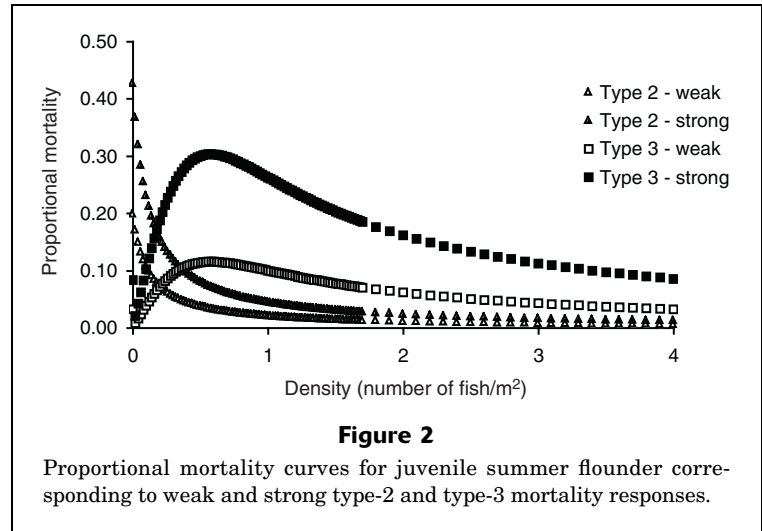
$$C_{PF} = 14.24 + 1.234 \times TL,$$

where  $C_{PF}$  = the cost per fish in Japanese yen (¥); and  
 $TL$  = the total length of the HR fish.

Costs were then converted into US\$ by using an exchange rate of 106.7¥ per 1 US\$ (universal currency converter). We feel use of this cost-of-fish-production equation is appropriate because the Japanese flounder is closely related and similar in life history traits to the summer flounder (Tanaka et al., 1989; Burke et al., 1991), resulting in similar optimal rearing practices for hatchery-reared Japanese and summer flounder (Burke et al., 1999), and thus likely similar rearing costs. Additionally, the scale of Japanese flounder hatchery production is similar to, or greater than, other government subsidized hatchery production programs (e.g. red drum in Texas, cod in Norway [Svåsand, 1998]).

### Density-mortality relationships

We tested the sensitivity of the model results (optimal predicted number of survivors and cost-per-survivor estimates under varying NFRs) to violations of the assumption



of density-independent mortality by incorporating varying types and strengths of density-dependent mortality (depensatory in nature at elevated densities; see below) into the model. As a basis for these sensitivity analyses, we assumed that predation was the driving mechanism underlying the postrelease mortality of HR summer flounder under the densities examined (Kellison et al., 2000; Kellison et al., 2003b). Thus, we made daily mortality rates correspond to either a type-2 or type-3 predator functional response (Holling, 1959; see Lindholm et al., 2001 for example), in which proportional mortality due to predation decreases with increasing density (type-2 response) or increases initially with increasing density, reaches a zenith, and then decreases with increasing density (type-3 response) (Fig. 2). Both type-2 and type-3 responses result in decreasing (depensatory) mortality at elevated prey densities due to predator satiation. We did not include scenarios in which mortality increased at elevated densities (as would be expected when densities reached those likely to result in resource limitation) because we did not include in the model elevated release densities likely to result in resource limitation. We parameterized the daily mortality curves so that each response (type 2 or 3) incorporated the daily mortality rate of 0.02153. These mortality curves contain mortality values that are within ranges reported in the literature for other species of juvenile marine fishes (Bax, 1983; Houde, 1987; Nash, 1998; Rose et al., 1999). To make further inferences about the importance of density-dependent mortality to model results, we included a 1) weak and 2) strong form of each functional response (types 2 and 3) (Fig. 2), as well as scenarios in which the response shifted temporally from 3) type 2 to 3, and 4) type 3 to 2 at the midpoint of the nursery season (Julian day 145). We included both the weak and strong forms of the type-2 and type-3 functional responses to determine the extent to which variation in the strength of the functional response would affect model predictions. The strength of the functional response could vary because of annual variation in the presence or abundance of prey or because predators could affect the density-mortality relationship (see, for example, Hansen et al., 1998).

For example, a strong positive (compensatory) density-mortality relationship driven by predators might become weaker in years when predator abundance was lower than average. We included the temporally shifting functional response scenarios to determine the extent to which temporal variation in the form of the functional response would affect model predictions. Temporal variation in the form of the functional response might occur because of temporal changes in the predator community, or because of changing predator-prey size dynamics (e.g. Stoner, 1980; Black and Hairston, 1988). For example, as the nursery season for summer flounder progresses, proportionately greater numbers of juveniles grow to sizes at which they are capable of preying on smaller juveniles (Kellison, personal obs.). If cannibalistic summer flounder exhibit a different predatory functional response from that of the predator guild community predominating earlier in the season, then the density-mortality relationship may change seasonally.

We replicated all model simulations over each of the six density-mortality relationships (weak and strong types 2 and 3, and shifting patterns [type 2 to 3 and type 3 to 2]) to determine optimal release scenarios (maximum number of survivors, minimum cost-per-survivor) under each relationship. We then compared results to those obtained under density-independent mortality to make inferences about the importance of density-mortality relationships to model results.

#### Correspondence between predicted and observed temporal abundance patterns

Different density-mortality relationships may result in distinct temporal patterns of abundance (e.g. rapid versus more gradual declines in abundance) depending on initial densities. We generated predicted patterns of temporal field abundance of juvenile summer flounder under density-independent mortality and four additional density-mortality relationships (governed by weak and strong type 2 and 3 functional responses) and under varying initial densities (0.1, 0.3, and 0.5 fish/m<sup>2</sup>) to examine whether the different density-mortality relationships would result in distinct temporal patterns of abundance. We used 1998–99 field data and logarithmic or polynomial regression models to generate curves that best fitted (based on  $r^2$  values) observed (from natural nursery sites) temporal declines in abundance under varying initial densities. We compared the best-fit curves to those predicted by the model under density-independent and four additional density-mortality relationships. These comparisons allowed us to make qualitative inferences about which density-mortality relationship(s) resulted in the best match between predicted and observed temporal patterns of abundance.

#### Model assumptions

The assumptions of the model are the following:

- 1 Daily mortality is independent of size. Although there is strong evidence that mortality of fishes in the wild is size-dependent (Lorenzen, 2000), particularly in regard

to the importance of size to susceptibility to predation (see, for example, Elis and Gibson, 1995; Furuta, 1999; Manderson et al., 1999), we found no evidence (from recaptures of released hatchery-reared fish) of size-selective daily mortality for juvenile summer flounder ranging in size from ~30–80 mm TL in shallow-water nursery areas (Kellison et al., 2003a). Implications for violations of this assumption are addressed in the “Discussion” section.

- 2 Daily growth is independent of fish density. We based this assumption on field experiments that indicated no growth limitation at densities roughly equal to the maximum densities explored in the model (Kellison et al., 2003b). Similar findings (i.e. no food-limitation or density-dependent growth) have been reported for similar-size plaice in shallow-water nursery habitats (van der Veer and Witte, 1993).
- 3 Economic cost per fish ( $C_{PF}$ ) is independent of the number of fish acquired for release (i.e. within the range of numbers of fish released in model simulations, there is no decrease in cost per fish as the number of fish acquired from the production hatchery for release increases). This assumption is likely to be valid over changes in numbers of fish released common to stock enhancement programs (Sproul and Tominaga, 1992) but may not be valid as numbers released change over orders of magnitude because of economy of scale (Adams and Pomeroy 1991; Garcia et al., 1999).
- 4 There is no emigration from the release habitat until fish exhibit an ontogenetic shift in habitat at 80 mm TL. Although pre-ontogenetic habitat shift emigration may not truly be zero, we feel that it is also unlikely that pre-ontogenetic habitat-shift emigration accounts for more than a minimal amount of loss of released fish from the habitat of release, as supported by several points. First, rates of pre-ontogenetic shift emigration in wild juveniles are apparently low (Kellison and Taylor<sup>2</sup>), suggesting that large-scale spatial migrations may not be part of the behavioral repertoire of early juvenile summer flounder. Second, irregular temporally replicated sampling outside of experimental release sites resulted in zero captures of emigrating hatchery-reared fish (Kellison et al., 2003b). Third, emigration rates of closely related HR Japanese flounder (*Paralichthys olivaceus*) are reported to be very low (Tominaga and Watanabe, 1998). In combination, these points suggest that our zero emigration assumption is appropriate.
- 5 Fish that do not grow to 80 mm TL during the model period (i.e. by 15 July) do not survive. Although this assumption cannot be examined with our field data, data do show that juvenile summer flounder are absent from shallow-water nursery habitats by mid to late July (Kellison et al.<sup>3</sup>). Thus, all fish have either perished or made ontogenetic habitat shifts to deeper habitats by this time. Our field observations suggest that the deeper habitats to which larger flounder

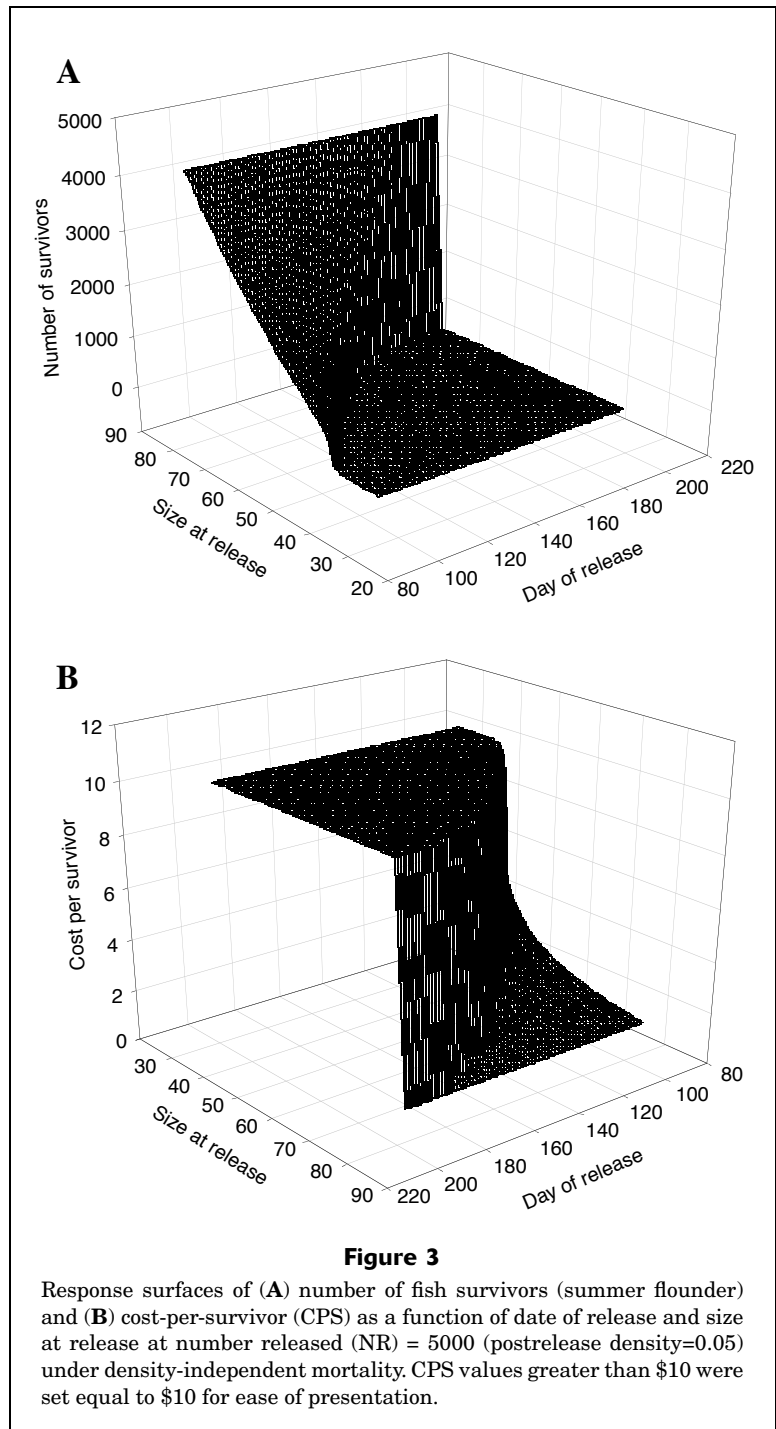
<sup>3</sup> Kellison, G. T., J. C. Taylor, and J. S. Burke. 2000. Unpubl. data. Department of Marine, Earth, and Atmospheric Sciences, North Carolina State Univ., Raleigh, NC 27695-8208.

make ontogenetic habitat shifts are inhabited by relatively high densities of potential predators (e.g. blue crabs, age 1+ flounders, red drum [*Sciaenops ocellatus*], searobin [*Prionotus* sp.], and lizardfish [*Synodus* sp.]), which may be considerably less abundant in shallow-water habitats. These relatively large and abundant predators would presumably expose small migrating fish to high rates of predation (see, for example, Elis and Gibson, 1995; Furuta, 1999; Manderson et al., 1999). This assumption is supported by research with the congener Japanese flounder (*Paralichthys olivaceus*). Although a range of sizes of hatchery-reared Japanese flounder may survive within relatively shallow nursery habitats, fishes less than 90 mm TL moving into relatively deep waters are poorly represented in subsequent age classes, most likely due to predation-induced mortality (Yamashita et al., 1994; Furuta, 1999).

- 6 There is no relationship between length of rearing period (time spent in the hatchery environment) and probability of postrelease mortality related to behavioral deficits (Olla et al., 1998). Hatchery-specific selection pressures may result in HR fish that are behaviorally selected to survive in the hatchery and not in the wild (see Olla et al., 1998; Kellison et al., 2000; for discussion). We assume that behavioral deficits are not exacerbated with time spent in the hatchery (i.e. behavioral deficits are equal for all sizes-at-release).

## Results

The most important factor affecting the number of survivors (and therefore percent survival) was size-at-release because the greatest numbers and percentages of survivors were always produced by releasing the largest fish possible (80 mm TL in the model). Number of survivors decreased with decreasing size-at-release and with increasing Julian day of release (Fig. 3A). The cost-per-survivor (CPS) was also most affected by size-at-release, such that CPS decreased with increasing size-at-release (Fig. 3B). CPS generally increased with increasing Julian day of release (Fig. 3B), although this effect was less important than the effect of size-at-release. Because mortality was originally assumed to be density-independent, the optimal cost-per-survivor did not vary with the number of fish released (Fig. 4), and the relationship between number of fish released and number of survivors was linear (Fig. 4), such that the maximum number of survivors were generated from the greatest number of fish released (NFR=400,000).

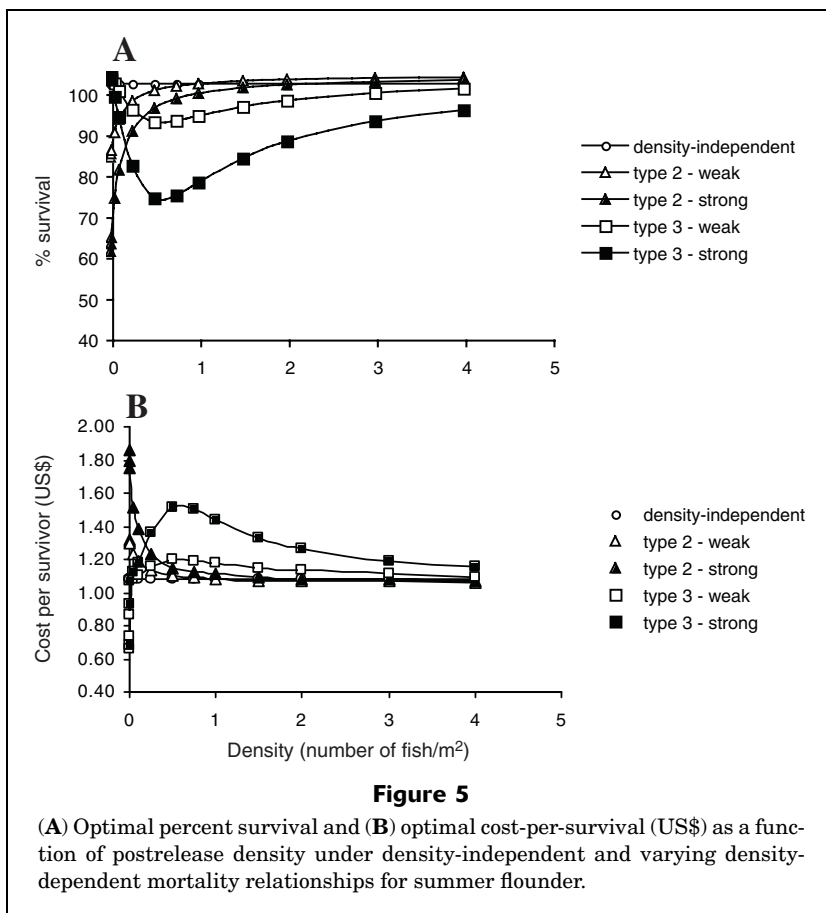
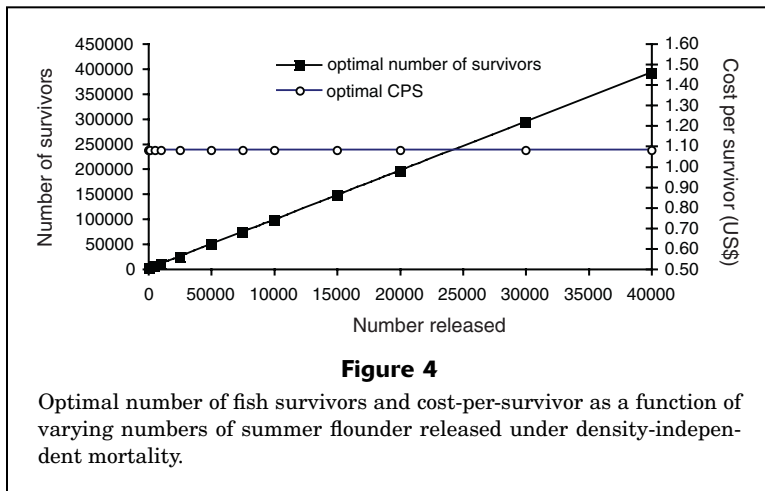


### Sensitivity of model predictions to violations of density-independent mortality assumption

Model results varied considerably under the various density-mortality relationships (Fig. 5, A and B), indicating the importance of knowledge of the relationship between numbers of fish released (density) and mortality in the wild to predicting optimal release scenarios. Variation in model output was dependent on the type and strength of

the density-mortality relationship. For example, at postrelease densities of 0.5 fish/m<sup>2</sup> (NFR=50,000), survival of released flounder under density-independent mortality was ~28% higher than that predicted under strong type-3 mortality, but only ~2% higher than that predicted under weak type-2 mortality (Fig. 5A). At postrelease densities of 0.001 fish/m<sup>2</sup> (NFR=100), survival of released flounder under density-independent mortality was ~41% higher

than that predicted under strong type-2 mortality, but ~2% less than that predicted under strong type-3 mortality (Fig. 5A). In contrast, when postrelease densities were relatively high, there was less of an impact of density-mortality relationship on postrelease survival and costs associated with stock enhancement. For example, at postrelease densities of three fish/m<sup>2</sup> (NFR=300,000), survival of released flounder differed by less than 4% between density-independent, weak or strong type-2, and weak type-3 mortality, although survival under strong type-3 mortality was ~9% less than that predicted under density-independent mortality and ~11% less than that predicted under strong type-2 mortality (Fig. 5A). Thus, the model results were most sensitive to violations of the assumption of density-independent mortality at low densities of fish released in the field.



**Type-2 mortality** As with density-independent mortality, the most important factor affecting number of survivors and cost per survivor under type-2 mortality was size-at-release (Fig. 6, A and B). In all simulations, the greatest number of survivors was produced by releasing the largest fish possible. Number of survivors decreased with increasing Julian day of release (Fig. 6A). There was a considerable interaction between size-at-release and number of fish released, such that low postrelease densities were subjected to relatively high proportional mortality. Thus, when fish were released in low numbers and at small sizes, the fish were subjected to relatively high proportional mortality rates for long periods of time (while they grew towards the 80-mm-TL ontogenetic shift size) and consequently produced few or no survivors (Fig. 6A). Optimal release scenarios under strong type-2 mortality produced substantially lower (>40% in some cases) percent survival (and therefore substantially higher cost-per-survivor) estimates at low to moderate numbers released (NFR=100–50,000; postrelease density=0.001–0.5 fish/m<sup>2</sup>) than under density-independent mortality (Fig. 5, A and B). Differences in percent survival estimates (and thus cost-per-survivor estimates) between density-independent survival and weak or strong type-2 mortality declined to less than 5% when the numbers released increased to 25,000 (postrelease density=0.25 fish/m<sup>2</sup>) under weak type-2 mortality and 75,000 (postrelease density=0.75 fish/m<sup>2</sup>) under strong type-2 mortality (Fig. 5A). Thus, model predictions under density-independent mortality differed most from predictions under mortality governed by

a type-2 predator functional response when postrelease densities were relatively low.

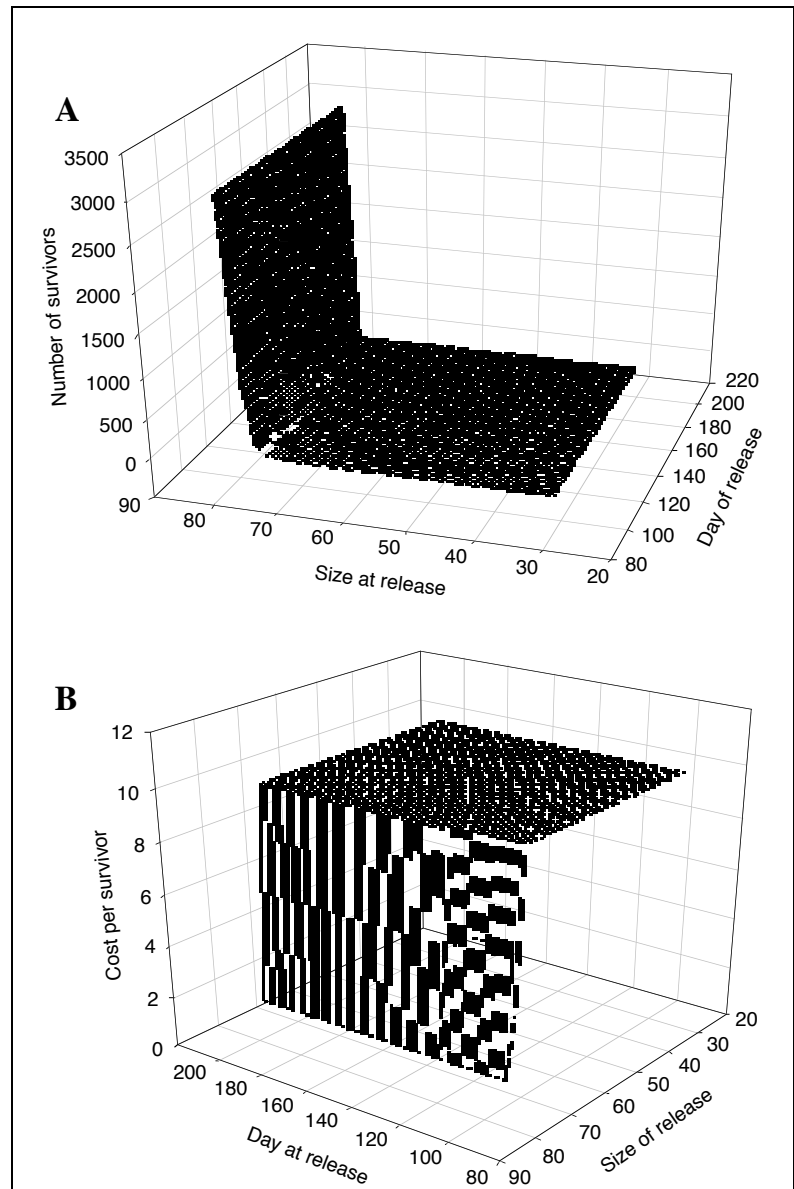
**Type-3 mortality** As in all other simulations, the most important factor affecting number of survivors under type-3 mortality was size-at-release, such that the greatest numbers of survivors were always produced by releasing the largest fish possible (Fig. 7A). Number of survivors decreased with increasing Julian day of release (Fig. 7A). Percent survival was considerably lower (>25% in some cases) under type-3 mortality than under density-independent mortality at moderate to high numbers released (NFR=10,000–400,000) (Fig. 5A).

In nearly all simulations, the lowest CPS values were produced by releasing the largest fish possible (Fig. 7B). The exceptions to the “large size = optimal CPS” rule occurred when postrelease densities were small (corresponding to numbers released of 100, 500, and 1000) and the mortality curve was type 3 (weak or strong). In these instances, mortality was sufficiently low at low release densities (Fig. 7B) so that the difference in overall survival between small- and large-released fish was small enough to be overridden by the increased cost of the larger fish, and the minimum CPS was obtained when small (42–44 mm TL) fish were released (e.g. Fig. 7B).

At low numbers released (NFR=100–1000), optimal cost-per-survivor was considerably lower (>45% in some cases) under type-3 mortality than under density-independent mortality (Fig. 5A). As NFR increased, CPS under type-3 mortality became greater (~40% in some cases) than that achieved under density-independent mortality (Fig. 5B).

#### Temporal shift in functional response from type 2 to type 3, and from type 3 to type 2

The optimal numbers of survivors under varying numbers released were identical, and optimal CPS values nearly identical, when the form of the functional response changed from a type 2 to a type 3, and from a type 3 to a type 2, midway through the juvenile nursery season (Fig. 8, A and B). The differences at low postrelease densities between optimal CPS values under shifting type 2 to type 3 and type 3 to type 2 scenarios (Fig. 8A) occurred because initial mortality under the type-3 functional response was sufficiently low that the difference in overall survival between small- and large-released fish was small enough to be overridden by the increased cost of the larger fish (Fig. 8A). The minimum CPS was obtained when small (42–44 mm TL) fish were released (in all other cases, optimal results were obtained when size-at-release was maximized) (Fig. 8A). The major difference between the two shifting scenarios is that the



**Figure 6**

Response surfaces of (A) number of fish (summer flounder) survivors and (B) cost-per-survivor (CPS) as a function of date of release and size at release at number released (NR) = 5000 (postrelease density=0.05) under a strong type-2 functional response. CPS values greater than \$10 were set equal to \$10 for ease of presentation.

release dates producing optimal results for a given number of fish released varied depending on the direction of the shifting functional response. For example, when the functional response shifted from a type 2 to a type 3, a release of 100,000 HR organisms achieved optimal results when release occurred early in the season (Julian day  $\leq 145$ ) (Fig. 9A). When the functional response shifted from a type 3 to a type 2, a release of 100,000 HR summer flounder achieved optimal results only when releases occurred later in the season (Julian day  $> 145$ ) (Fig. 9B). When the

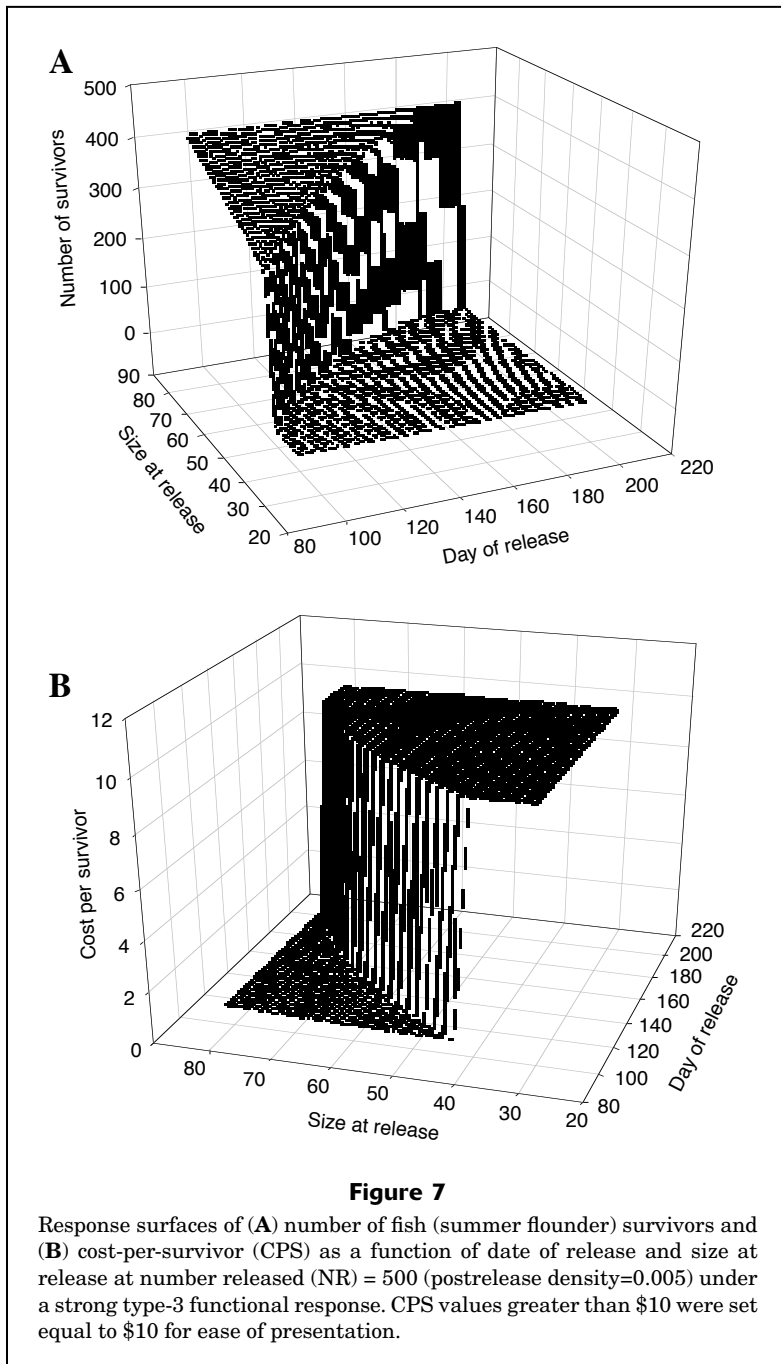


functional response shifted from a type 3 to a type 2, releasing 100,000 HR organisms prior to Julian day 146 resulted in markedly decreased survival (and therefore increased CPS) compared to results obtained from releases after day 146 (e.g. releasing on Julian day 92 resulted in a decrease in number of survivors and an increase in CPS of 22.8% and 29.7%, respectively) (Fig. 9B). Thus, date-of-release had a significant effect on the results (and therefore in determining optimal release strategies) when the relationship between density and mortality changed temporally, suggesting that the presence of a temporal shift in the func-

tional response of the predator guild would have considerable effects on the number of survivors and CPS for stock enhancement efforts with juvenile summer flounder.

#### Correspondence between predicted and observed temporal abundance patterns

Under the assumption of a type-2 functional response, predicted declines in juvenile summer flounder density over time were rapid when initial density was relatively low (i.e. 0.1 fish/m<sup>2</sup>) (Fig. 10, A and B). These predictions contrast with those observed in the field, in which declines at relatively low initial densities were gradual (compare Fig. 10A and 10B to Fig. 10F). Under the assumption of a type-3 functional response, predicted declines were rapid when initial density was relatively high (i.e. 0.5 fish/m<sup>2</sup>) (Fig. 10, C and D). These results generally contrast with those observed in the field, in which declines at relatively high densities were much less rapid than those predicted under a strong type-3 functional response, and somewhat less rapid than those predicted under a weak type-3 functional response (Figs. 10F and 11). Under density-independent mortality, there was little difference in predicted declines in juvenile summer flounder density over time between the three initial density levels (0.1, 0.3, and 0.5 fish/m<sup>2</sup>); in each case there was a gradual decrease in density over time (Fig. 10E). These results were similar to those observed in the field, although declines at relatively high densities in the field were somewhat more rapid than those predicted under density-independent mortality (compare Figs. 10E and 10F). Thus, a density-mortality relationship lying between that generated under density-independence and that generated under the weak type-3 functional response in the model would most closely predict the temporal declines observed in the field.



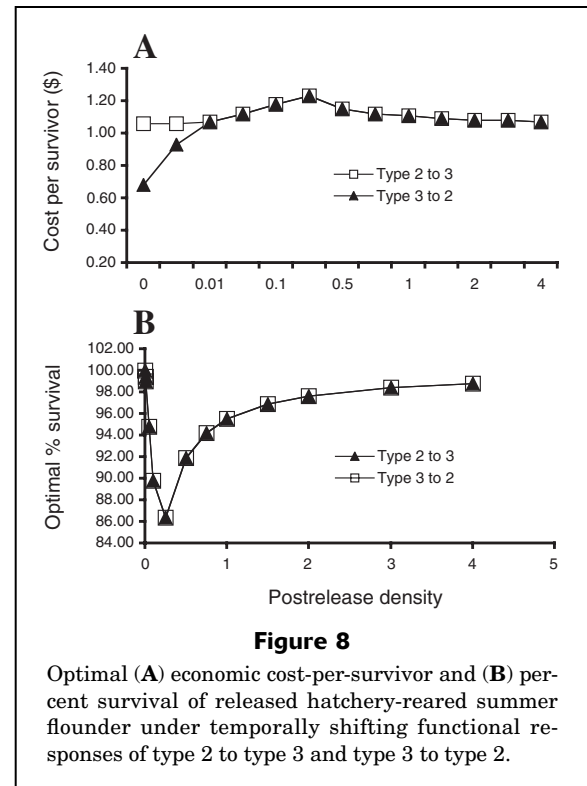
## Discussion

### Implications for stock enhancement of summer flounder

Regardless of the relationship between density and mortality, size-at-release was the most important variable in the model affecting survival and costs associated with stock enhancement of summer flounder. The model predicts that under all release scenarios, 1) survival will be maximized and 2) costs associated with stock enhancement (i.e. cost per survivor) will be minimized when HR fish are released at the largest size possible. From a survival standpoint, these results are not

surprising. Larger fish spend fewer days than smaller fish in the wild nursery habitats before making an ontogenetic habitat shift to deeper waters and thus are susceptible to daily natural mortality for fewer numbers of days than are smaller fish. Thus, total mortality of smaller fish is greater than that of larger fish. Additionally, although we chose to make mortality independent of size in the model, abundant literature suggests that natural mortality (especially due to predation) may decrease with increasing size by mechanisms such as enhanced resistance to starvation, decreased vulnerability to predators, and better tolerance of environmental extremes (Sogard, 1997; Hurst and Conover, 1998; Lorenzen, 2000). Thus, the difference in predicted survival between 1) relatively large and relatively small fish and 2) fish released early versus late in the season in our model would be even greater if larger summer flounder suffered lower natural mortality than smaller fish. Furthermore, the daily mortality estimate used in the density-independent simulations and to parameterize the different types of density-mortality relationships may have been an underestimate of daily mortality (Kellison, 2000). If a greater estimate of daily mortality had been used, the difference in predicted survival between relatively large and relatively small fish in our model would have been further exacerbated because smaller fish spend longer amounts of time in the model growing to the 80-mm-TL ontogenetic shift size. These conclusions are supported by empirical research demonstrating that relatively large released HR fish suffer lower mortality than relatively small HR fish released in the field (e.g. Yamashita et al., 1994; Leber, 1995; Willis et al., 1995; Tominaga and Watanabe, 1998; Svåsand et al., 2000).

Although the survival predictions of the model (total mortality decreases with increasing size-at-release) are not surprising, the economic (cost-per-survivor) predictions were unexpected. The paradigm for stock enhancement strategy is that the rearing of relatively large fish for release is cost prohibitive, so that mass releases of relatively small, inexpensive-to-rear fish are a better strategy than the release of larger, expensive-to-rear fish (Kellison, personal obs.). Thus, relatively small juveniles are released in virtually all current stock enhancement programs (e.g. Russell and Rimmer, 1997; Masuda and Tsukamoto, 1998; McEachron et al., 1998; Svåsand, 1998; Serafy et al., 1999). Nevertheless, large-scale hatcheries and grow-out facilities are using ever-increasing technology to minimize the costs associated with the production of relatively large fishes (Sproul and Tominaga, 1992). Thus, for species for which 1) hatcheries are capable of producing relatively large fish at relatively low costs (as is likely for summer flounder), and 2) postrelease survival rates increase with release size, release scenarios utilizing the largest fish possible may maximize the potential (i.e. produce maximum survival at minimum costs) of stock enhancement efforts. In these cases, the "small fish maximize stock enhancement potential" paradigm might be replaced with a "large fish maximize potential" paradigm. As a caveat, this "large fish" strategy may be limited by spatial limitations of hatcheries in producing large numbers of relatively large fish. Because reared fish generally must



be kept below critical densities in hatchery environments because of water quality and fish interaction issues (e.g. cannibalism), larger fish necessarily require more space than smaller fish for rearing. If the demand for space to rear large quantities of large fish can be realized, then the model simulations indicate that stock enhancement strategies in which size-at-release is maximized will produce the maximum number of survivors.

Although not as important as size-at-release, Julian day of release had a significant effect on survival and cost-per-survivor in the model, such that enhancement efforts were always more successful (more survivors, lower costs) when fish were released at the earliest Julian day possible. These results occurred because growth in the model decreased with increasing Julian Day. Although the mechanisms underlying this decrease in growth with increasing Julian day are unknown, they may be related to decreased prey availability or metabolic efficiency as temperatures increase with increasing Julian day (Malloy and Targett, 1994a, 1994b; Fujii and Noguchi, 1996; Howson, 2000). Thus, for a given size-at-release, fish released earlier in the season experienced greater growth rates than fish of the same size-at-release released later in the season and therefore reached the 80-mm-TL ontogenetic shift size faster (over a period of fewer days) than fish released later in the season. Thus, fish released earlier in the season were susceptible to natural mortality for fewer days than fish released later in the season and therefore suffered lower total mortality. These results emphasize the importance of knowledge of possible time-dependent growth in the field prior to stock enhancement efforts.

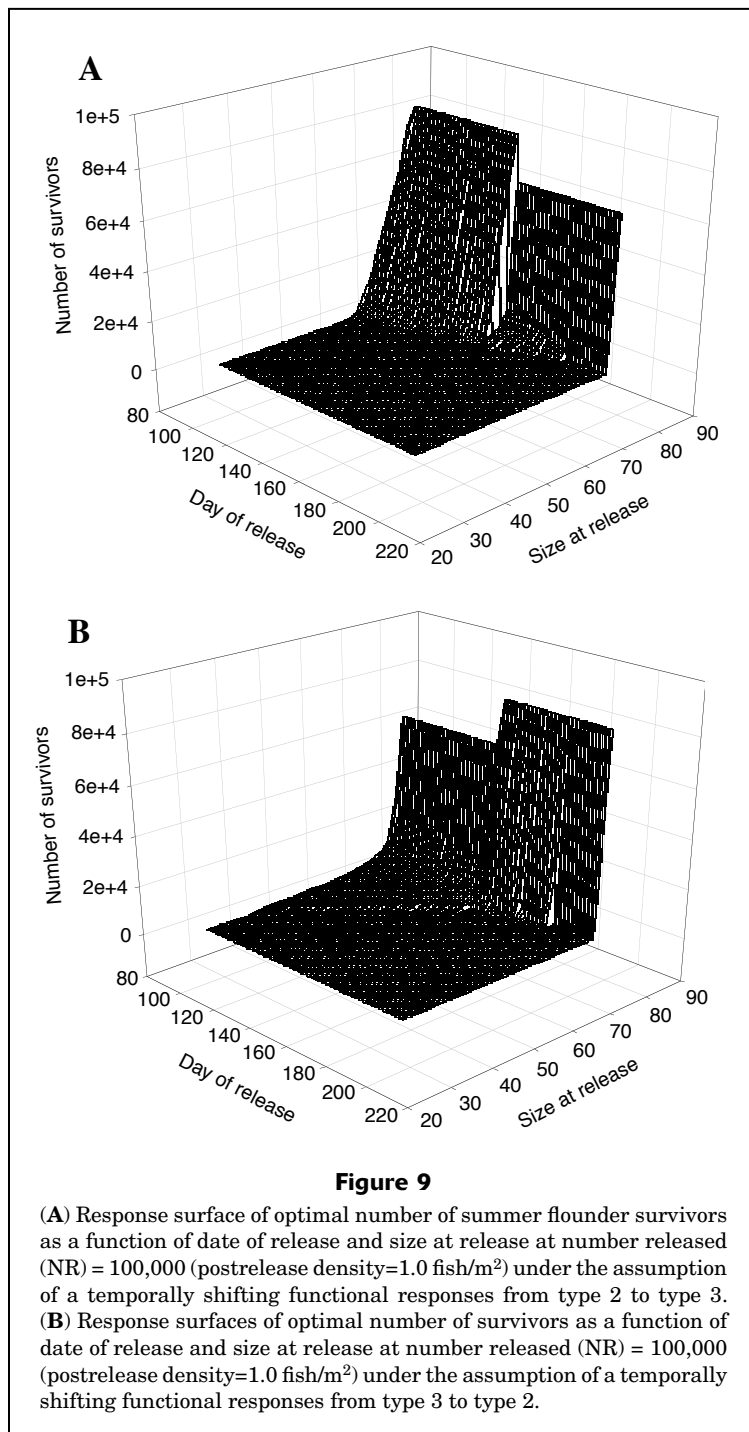
### Is density important? Effects of varying density-mortality relationships

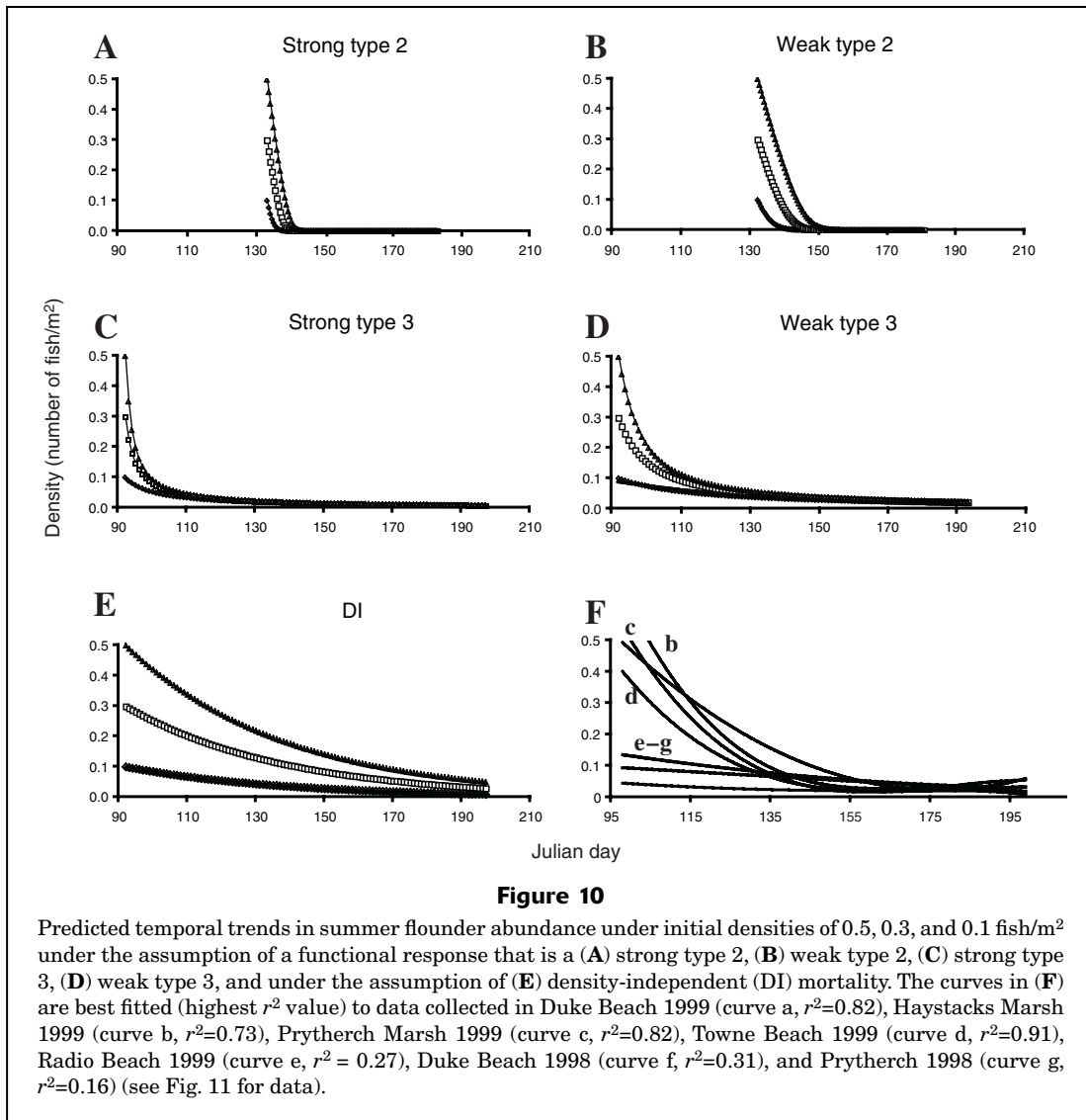
Our results suggest that the relationship between density and mortality has the potential to significantly affect optimal release scenarios associated with stock enhancement efforts. Because the original simulations were performed under density-independent mortality, the number of survivors originally increased linearly with the number

released, resulting in a density-independent cost-per-survivor. Thus, when mortality is independent of density (over a given range of densities) for a target species for stock enhancement, managers will maximize the number of survivors produced by releasing the greatest number of fish possible within that range for a given size class. When mortality varied with density of released fish, the number of survivors and cost-per-survivor depended on the density-mortality relationship. In some cases, optimal results (maximum survival and minimum cost) differed depending on whether the response variable was number of survivors or cost-per-survivor. Under the assumption of a strong type-3 functional response and under relatively low postrelease densities, survival was optimized (maximized) by releasing the largest fish (80 mm TL) possible; however, cost-per-survivor was optimized (minimized) by releasing smaller fish (42–44 mm TL). This result occurred because mortality at low postrelease densities was sufficiently low that the difference in total mortality attributed to the longer “susceptibility” period of the smaller fish was insufficient to override the economic advantage of releasing smaller fish. Simulations under shifting functional responses (type 2 to type 3 and type 3 to type 2) produced optimal results similar to those obtained when nonshifting type-2 or type-3 functional responses were employed because densities were generally reduced to such low numbers by the time the shift occurred that the changing density-mortality relationship was inconsequential. Importantly, when functional responses shifted temporally, the predicted number of survivors and economic cost per survivor was at times very dependent on date of release, suggesting that identifying or ruling out shifting functional responses in the wild may be critical to accurate prediction of response variables (survivors and economic costs) associated with stock enhancement. Although we are not aware of reports in the literature of shifting functional responses in the wild, we are also not aware of studies that have tested for such a phenomenon, possibly because of the logistical difficulties inherent in identifying a shifting functional response.

### Correspondence between predicted and observed temporal abundance patterns

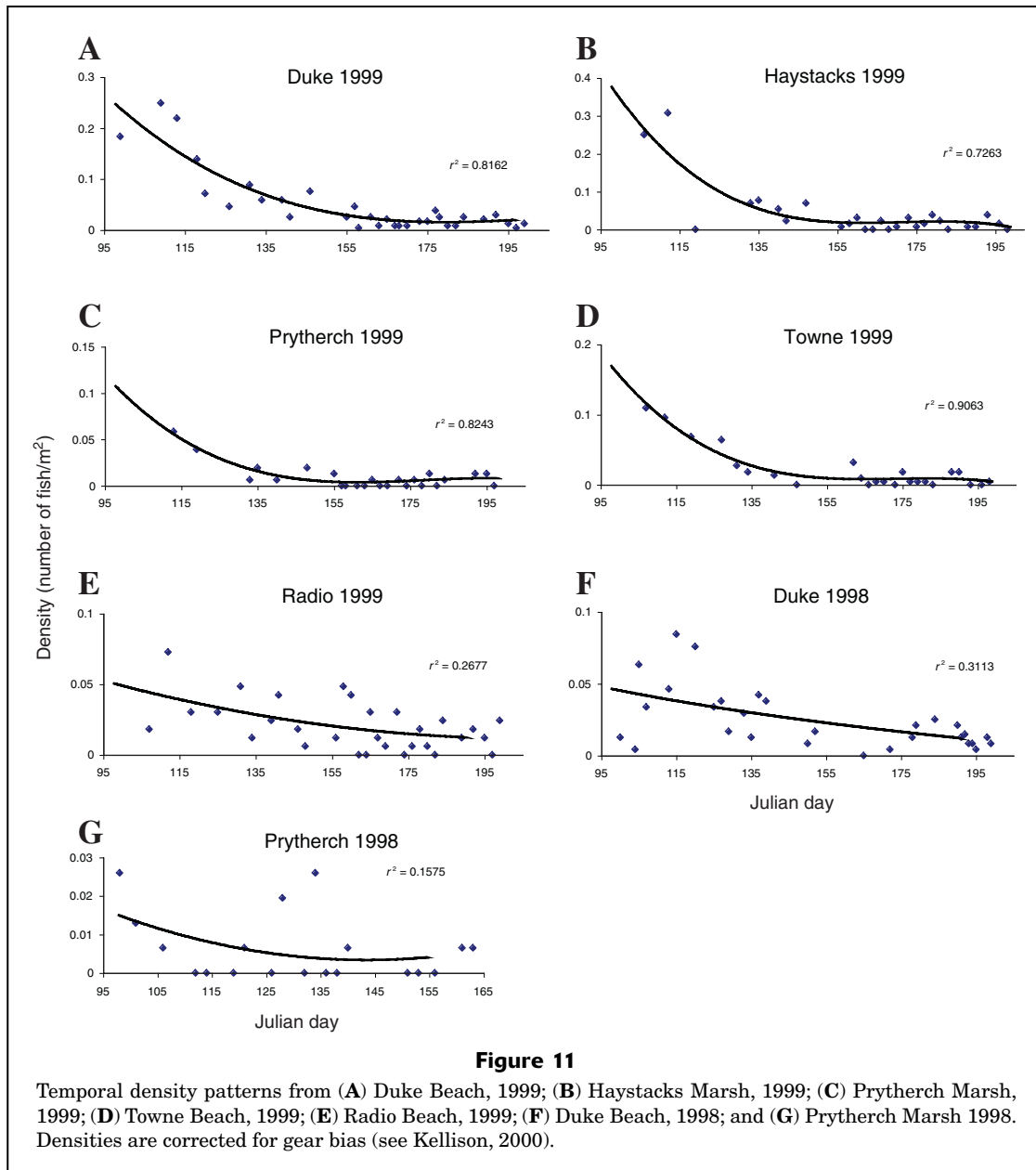
Predictions of field abundance patterns of juvenile flounder density over time were noticeably different under density-independent mortality and density-dependent mortality governed by type-2 and type-3 functional responses. For example, our simulations predict that fish density should decrease rapidly under relatively low initial densities if the functional response is type 2, decrease rapidly at relatively high initial densities if the functional response is type 3, and





gradually decrease regardless of initial density if mortality is density independent. From examinations of temporal abundance patterns from several nursery sites (see Kellison et al., 2003b, for site descriptions), it is evident that observed declines at relatively low initial densities are similar to predicted declines under both density-independent mortality and a weak type-3 functional response; whereas observed declines at relatively high initial densities are somewhat less gradual than predicted under density-independent mortality, but somewhat more gradual than predicted under the weak type-3 functional response. These results suggest that model predictions made under the assumption of a weak type-3 response may give reasonably accurate but conservative predictions of juvenile summer flounder mortality and economic costs associated with stock enhancement for comparison with alternative management methods. As a caveat, although we found no evidence of size-dependent daily mortality over the range of fish sizes examined in this study, it is very likely that

such a relationship exists to some extent (Sogard, 1997; Lorenzen, 2000). Incorporating size-dependent mortality into the model would decrease the slopes of the predicted temporal abundance curves but should not change the conclusion that the observed data lie somewhere between values predicted under density-independent mortality and those governed by a weak type-3 functional response, respectively. Additionally, because the portions of the curves used to delineate between temporal abundances expected under density-independent versus varying density-mortality relationships are from early in the growth season (later parts of the curve converge on very low densities) and because nearly all fish in these portions of the curves are at sizes well below that at which ontogenetic emigration occurs, the exclusion of emigration from these simulations should not affect the general conclusions reached. These issues could be clarified with further field trials to investigate the dependence of daily mortality rates on fish size.



### Model utility and implications

Although model results varied considerably under the various density-mortality relationships, the overall predictions that survival would be maximized and economic costs minimized when relatively large fish were released early in the season were unaffected by the density-mortality relationship. These results suggest that managers may use this model to make inferences about optimal release scenarios even if density-mortality relationships are unknown. Additionally, these results have important implications for the cost efficiency of stock enhancement programs. Managers can use the model to determine

the release scenarios under which they can 1) maximize the number of survivors, given a financial limit (e.g. given a budget of  $x$  dollars, what release scenario or scenarios will produce the greatest number of survivors?), and 2) minimize costs, given a goal of number-of-survivors-produced (e.g. given a goal of producing  $x$  survivors, what release scenario or scenarios will be most cost efficient?).

In conclusion, the compartmental model used in this study provides an example of a relatively easy-to-develop predictive tool with which to make inferences about the ecological and economic potential of stock enhancement, in relation to alternative management approaches, to rebuild depleted fisheries.

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