

Modeling the Effects of Fishing and Implications for the Design of Marine Protected Areas: Juvenile Fish Responses to Variations in Seafloor Habitat

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Abstract: A number of recent studies have linked post-settlement survivorship of Atlantic cod (*Gadus morhua*) with the complexity of the seafloor to which fish settle. Survivorship is greater in habitats of higher complexity (e.g., pebble-cobble substratum with emergent epifauna > pebble-cobble > sand), where cover provides shelter from predators. Fishing with mobile gear such as bottom trawls and dredges reduces the complexity of seafloor habitats. We used a dynamic model to (1) link patterns in habitat-mediated survivorship of post-settlement juvenile cod with spatial variations in habitat complexity, (2) simulate habitat change based on fishing activities, and (3) determine the role of marine protected areas in enhancing recruitment success. Density-dependent natural mortality was specified as three alternative functional response curves to assess the influence of different predator foraging strategies on juvenile survivorship during the first 12 months of demersal existence. We applied the model to a theoretical patch of hard-bottom substrata and to a case study based on seafloor habitat distributions at Stellwagen Bank National Marine Sanctuary (Gulf of Maine, Northwest Atlantic). Our results demonstrate that patterns in the shape of response surfaces that show the relationship between juvenile cod survivorship and density as well as movement rate were similar regardless of functional response type, that juvenile cod movement rates and post-settlement density were critical for predicting the effects of marine protected-area size on survivorship, and that habitat change caused by fishing has significant negative effects on juvenile cod survivorship and use of marine protected areas can ameliorate such effects.

Modelado de los Efectos de la Pesca y sus Implicaciones para el Diseño de Áreas Marinas Protegidas: Respuesta de Peces Juveniles a Variaciones en el Hábitat del Fondo Marino

Resumen: Estudios recientes han relacionado la sobrevivencia post-establecimiento del bacalao del Atlántico (*Gadus morhua*) con la complejidad del fondo en el que se establecen los peces. La sobrevivencia es mayor en hábitats con mayor complejidad (e.g., substrato con guijarros con epifauna emergente > guijarros > arena) en los que la cubierta protege contra depredadores. La pesca con equipo móvil (e.g., redes de arrastre y dragas) reduce la complejidad de los hábitats del fondo marino. Utilizamos un modelo dinámico para (1) relacionar patrones de sobrevivencia post-establecimiento de juveniles de bacalao con las variaciones espaciales en la complejidad del hábitat, (2) simular cambios en el hábitat con base en actividades pesqueras y (3) determinar el papel de las áreas marinas protegidas en el incremento del éxito en el reclutamiento. La mortalidad natural denso-dependiente se especificó en tres curvas de respuesta funcional alternativas para evaluar la influencia de las distintas estrategias de depredación en la sobrevivencia de juveniles durante los primeros 12 meses de existencia demersal. Aplicamos el modelo a un mosaico teórico de substratos duros y a un estudio de caso basado en la distribución de hábitats de fondo en el Stellwagen Bank National Marine Sanctuary (Golfo de Maine, Atlántico Noroccidental). Nuestros resultados muestran que: a) hay similitud entre los patrones en la forma de superficies de respuesta que tienen relación entre la sobrevivencia de los peces

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juveniles y la densidad así como la tasa de movimiento, independientemente del tipo de respuesta funcional; b) las tasas de movimiento y la densidad post-establecimiento fueron críticas para la predicción de los efectos de la extensión del área marina protegida sobre la sobrevivencia; c) los cambios en el hábitat por actividades pesqueras mostraron efectos negativos significativos en la sobrevivencia de juveniles de bacalao y d) el uso de áreas marinas protegidas puede reducir tales efectos.

Introduction

Attention to the role of seafloor habitat in the dynamics of fish populations has increased recently in both management and scientific communities around the globe. For example, the U.S. Sustainable Fisheries Act of 1996 (the reauthorized Magnuson Fishery Conservation and Management Act) requires that the federal fishery management councils identify essential fish habitat (EFH) for all of the fish and shellfish species for which fishery management plans are enacted (National Oceanic and Atmospheric Administration 1998). The effective designation and ultimate conservation and protection of EFH requires data on fish population dynamics and the ecological influences of habitat on those dynamics for each life-history stage.

Historically, research on exploited offshore fish populations has been directed toward understanding the dynamics of adults and mortality of pelagic eggs and larvae (Anderson 1988), whereas the attention of the management community has focused largely on the management of adults through traditional controls on fishing effort such as limitations on days at sea, gear restrictions, and catch quotas (Sissenwine 1984). Less attention has been directed to the dynamics of early benthic-phase juvenile fish and the role of habitat in mediating post-settlement processes (e.g., Auster & Malatesta 1995; Tupper & Boutilier 1995a; Auster et al. 1997a) and to linkages between patterns in post-settlement juvenile fish survivorship and the alteration of seafloor habitat by fishing activity (Auster et al. 1996, 1998; Auster 1998; Jennings & Kaiser 1998; Lindholm et al. 1998, 1999).

Researchers have observed high densities of settled juvenile cod on the gravel portion of Georges Bank (Lough et al. 1989), on rocky reefs, sea grass beds, and gravel of the nearshore environment in Nova Scotia (Tupper & Boutilier 1995a, 1995b) and over hard bottom in Newfoundland (Gregory and Anderson 1997). Although juveniles settle on less complex habitats such as sand, high post-settlement mortality over habitats with little to no relief leads to low juvenile survivorship (Lough et al. 1989; Tupper & Boutilier 1995a). Similar relationships between juvenile fish and the seafloor habitat of the northwest Atlantic have been observed for silver hake (*Merluccius bilinearis*) on amphipod tubes (Auster et al. 1997a) and cunner (*Tautolagrabus adspersus*) on rocky reefs (Tupper & Boutilier 1997).

Habitat-specific differences in the survivorship of post-settlement juvenile cod have been demonstrated in laboratory experiments (Gotceitas & Brown 1993; Fraser et al. 1996; Gotceitas et al. 1995; Gotceitas et al. 1997; Lindholm et al. 1999). These studies indicate that associations with the vertical relief provided by particular physical substrata (e.g., pebble-cobble and boulder fields) and associated emergent epibionts (e.g., sponges and eelgrass) provide cover from predation and enhance survivorship for post-settlement juvenile cod.

Assessment of the ultimate effect of fishing activity on the seafloor and associated fish communities requires knowledge of the nature and extent of fishing-induced disturbance and their responses to such disturbance. Alteration of seafloor habitat by fishing activity has been demonstrated for a number of marine communities around the world (reviewed by Jennings & Kaiser 1998; Auster & Langton 1999). In the Gulf of Maine, for example, Auster et al. (1996) showed that mobile fishing gear reduces seafloor habitat complexity through removal of epifauna that provide structure, removal of structure-building taxa, and the smoothing of bedforms. On Georges Bank the effect of scallop dredging on the gravel pavement of the northeast peak was quantified, indicating a decrease in the number of species and species biomass in dredged areas (Collie et al. 1997).

Ultimately, the goal of research on the effects of trawling on the seafloor is to predict the range of effects on fish populations given particular management protocols (Auster & Langton 1999) and to evaluate the effects of trawling on the environment and overall biodiversity. We present a dynamic model of early benthic-phase juvenile cod survivorship that captures patterns in survivorship as a function of habitat-mediated predation for a continuous patch of pebble-cobble bottom, and we examine fish population responses to habitat management through the use of Marine Protected Areas (MPAs). We applied a larger model to Stellwagen Bank National Marine Sanctuary (SBNMS) in the Gulf of Maine (Northwest Atlantic), where the distribution of major habitat types is known. Models such as the one we present can improve current understanding of ecological relationships gained from studies at small spatial scales to a point where the implications of a variety of management measures can be investigated and their corresponding effect on fish populations can be evaluated.

Methods

Patch Model

The simple population model (Lindholm et al. 1998) uses a modified Beverton-Holt equation to simulate a population subdivided into n regions, where each region is represented by a particular level of habitat complexity. We interpreted habitat complexity as a measure of the vertical relief and cover from predation provided by a particular substratum (e.g., boulder, pebble-cobble, sand) and any associated emergent epifauna (e.g., sponges, amphipod tubes, cerianthid anemones, shell deposits, biogenic depressions, and burrows). Habitat complexity is uniform within any region i . Each region is either an MPA in which no fishing disturbance occurs or is outside an MPA and altered by fishing activity. We ran the model for 12 months at a monthly time step. Juvenile fish settle to the seafloor in the first period and are then subject to density-dependent natural mortality depending on the region they moved to or settled.

The change in population N_i in region i ($i = 1:16$), measured in number of individuals per month, is

$$\frac{dN_i}{dt} = S_i - m_i N_i + \bar{M}_i, \quad (1)$$

where S_i is the number of fish in a one-time settlement event in region i , $m_i N_i$ represents natural mortality for each region i , and \bar{M}_i is the net movement into and out of any region i .

Coefficients of natural mortality, m_i , are the predator-induced mortality specific to habitats of particular complexity. Relative differences in predator-induced, habitat-mediated juvenile fish survivorship are from laboratory experiments (Lindholm et al. 1999). Density-dependent natural mortality (Fig. 1) is specified as type I, II, and III functional response curves (Holling 1959).

The type I and II functional response curves are, respectively,

$$m_i = \alpha_i x_i + z_i \quad (2)$$

and

$$m_i = \frac{\alpha_i x_i}{1 + \alpha_i x_i} z_i \quad (3)$$

where α_i is a habitat-specific constant, x_i is a measure of the density of juvenile cod in region i , and z_i is a scaling factor. The type III functional response curve is

$$m_i = \frac{\alpha_i x_i^2}{1 + c_i x_i + \beta_i x_i^2} z_i \quad (4)$$

where α_i , β_i , and c_i are habitat-specific constants, x_i is a measure of the density of juvenile cod in region i , and z_i is a scaling factor.

We assumed a density-dependent relationship between local density (of juvenile fish) and natural mortality.

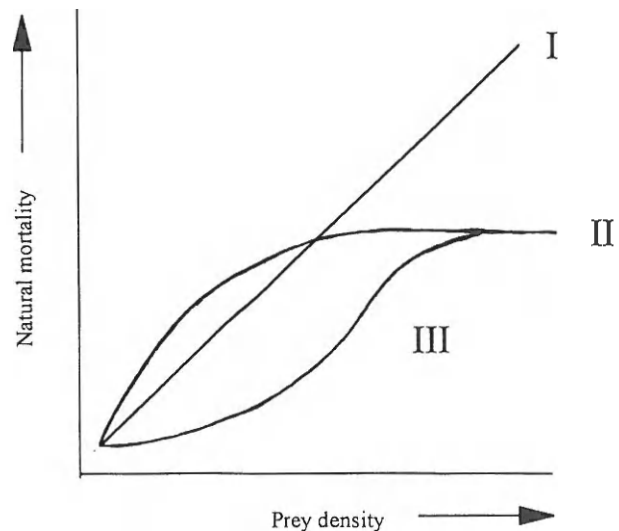


Figure 1. Type I, II, and III functional response curves. The response curves simulate a range of possible predator-prey relationships given a variety of predators, each using different tactics.

Specifications for the functional response curves were based on the relative differences in habitat-specific mortality observed in laboratory experiments (Lindholm et al. 1999). Juvenile mortality for habitats with lowest complexity (unprotected areas) was given a maximum value of 0.98. Mortality for habitats with highest complexity (MPAs) was given a maximum value of 0.32. Any habitat region i that was not in an MPA was subject to alteration by fishing activity. Juvenile fish in unprotected areas lack adequate cover to seek refuge from predation and therefore experienced a corresponding increase in natural mortality over regions within an MPA.

In equation 1, \bar{M}_i is the net per-month movement between any region i and surrounding regions n and is given by

$$\bar{M}_i = \sum v_j N_j - v_i N_i \quad (5)$$

where v_j is the percentage of individuals moving each month from region j to i and v_i is the percentage of individuals leaving region i . Movement occurs in a "rook" pattern in a 4×4 matrix such that individuals move randomly to any adjacent cell (e.g., up, down, to either side, but not diagonally).

Model of Stellwagen Bank National Marine Sanctuary

We expanded the patch model to simulate an open system similar to Stellwagen Bank National Marine Sanctuary (SBNMS). The model grid (176 cells) was superimposed over a sun-illuminated bathymetric map of the seafloor (Valentine et al. 1998), and habitat was classified in 25-km² regions (Fig. 2) based on the highest level

Figure 2. Sun-illuminated bathymetric map showing the boundary of Stellwagen Bank National Marine Sanctuary (SBNMS) and the 11×16 cell model grid.

of complexity present in each region (Table 1). Although the model grid incorporated areas outside the sanctuary (79 cells), only those cells that fell within the SBNMS boundary were included in the analysis.

The change in population N_i in region i ($i = 1:176$), measured in number of individuals per month, is given by equation 1. Natural mortality for this model is given by equation 4, a type III predator functional response curve. Any region i is "unaffected," "affected," or "flat sand or mud." Juvenile cod survivorship was highest in unaffected regions, which are those areas where an MPA was established and fishing-induced alteration of the seafloor did not occur. These regions included pebble-cobble bottom with dense coverage of emergent epifauna and boulder habitats. Here the upper threshold for each mortality curve was 0.32. Affected regions are those areas where no MPA was established and the seafloor had been significantly affected by fishing activity, including pebble-cobble bottom with no emergent epifauna and disturbed boulder habitats. Here juvenile cod survivorship was significantly lower than within regions protected by an MPA. Nevertheless, the physical substrata in these areas provided a measure of cover in the interstitial spaces between pebbles, cobbles, and boulders.

The upper threshold for affected areas was 0.67. Juvenile cod survivorship was lowest for regions categorized as flat sand or mud. This refers to areas in which the relief of the physical substratum provided little to no cover from predation and any emergent epifauna (e.g., cerianthid anemones) had been removed by fishing. These regions also included gravel bottom covered by a layer of sand where emergent epifauna had been removed by fishing. The upper threshold of natural mortality for these areas was 0.93 (Lindholm et al. 1999).

Weak east-west tidal currents are characteristic of Stellwagen Bank, with average current velocities ranging from 0 to 30 cm per second (Valentine & Schmuck 1995). To account for this slight dominance of east-west currents,

movement of juvenile fish in the model occurred both east-west and north-south between adjacent regions, with net east-west movement 20% higher than north-south movement. A three-fold classification scheme for seafloor habitats (modified from Auster 1998) was used to characterize fish habitat for each cell (Table 1).

Due to a lack of empirical data on movement rates of juvenile (0-year) cod, in the model we specified movement rates as the inverse of a habitat complexity score. This assumes that the more complex the habitat the more likely a juvenile cod is to remain in that habitat for biological reasons (e.g., cover from predation; Tupper & Boutilier 1995a) and physical reasons (e.g., refuge from bottom currents; Gerstner 1998). Movement rates were highest ($v_i = 0.7$ fish moving between regions per month) for areas of flat sand or mud, where there was little to no cover from predation and no refuge from bottom currents. Movement rates decreased linearly to 0.3 for pebble-cobble bottom, where interstices provided cover from predation and bottom currents. The lowest juvenile cod movement rates ($v_i = 0.0625$) occurred over unaffected habitats where structure provided by emergent epifauna and boulders provided cover from predation and served as refugia from bottom currents.

Model Assumptions

We made a number of simplifying assumptions that should be considered when our results are interpreted. Juvenile cod settlement occurred in a single pulse in the first month, and settlement was uniform within any region or cell and between all cells in both the patch and Stellwagen Bank models. Juvenile mortality was a density-dependent function of predation, mediated by seafloor habitat quality. The model did not consider food availability, water temperature, salinity, and other biological

Table 1. Habitat classification and specification of juvenile cod movement rates based on a hierarchical classification of fish habitat types on the outer continental shelf of the temperate northwest Atlantic*

| Category | Description | Rationale | Complexity score | Movement rate |
|----------|--|--|------------------|---------------|
| 1 | flat sand or mud | areas with little vertical structure such as depressions, ripples, or epifauna; includes pebble-bottom covered by a thin layer of sand with epifauna removed by fishing activity | 1 | 0.7 |
| 5 | affected pebble-cobble | small interstitial spaces between pebble and cobble; emergent epifauna removed by fishing activity | 5 | 0.3 |
| 6-8 | unaffected pebble-cobble with sponge cover; partially buried, dispersed, or piled boulders | attached epifauna on cobble such as sponges provide additional spatial complexity; boulders provide interstitial spaces, crevices of variable sizes, and attached epifauna | 10-15 | 0.0625 |

* Modified from Auster (1998)

and physical parameters affecting juvenile fish. Differences between an MPA and surrounding areas with respect to mortality were constant for the duration of a model run. Fishing activity directly influenced habitat quality. High natural mortality was interpreted as low habitat quality due to fishing alteration of the seafloor, whereas low natural mortality was interpreted as high habitat quality with little to no alteration by fishing. The effect of fishing activity on seafloor habitat was uniform across any area in which it occurred. Habitat heterogeneity was considered relative only to differences between an MPA and surrounding areas, with habitat quality uniform within a cell. Movement rates were constant for the duration of a model run.

Results of the Patch Model

Juvenile Movement Rate and MPA Size

Patterns in juvenile cod survivorship were first presented as a function of juvenile movement rate and MPA size, with density-dependent mortality expressed by predator functional response curves (Fig. 3). Juvenile movement rates varied from 0 (no movement) to 1.0 (100% of fish in any region i moving to any other regions j each month), and MPA size, or coverage, varied from 0 to 100% of total area. The number of fish settled in each region in the first month was constant for all regions at 10 fish/m². Survivorship was calculated as the number of surviving juvenile cod for any region i per number of fish settled to the same region i and was presented for the end point of a 12-month model run. For each treatment, cells in a 4 × 4 matrix were randomly converted from unprotected to MPA over the course of multiple ($n = 100$) model runs. Results were presented as response surfaces generated from the average of three treatments.

The general shape of the surfaces was nearly identical for each of the three functional response curves within each respective category: total survivorship, survivorship in an MPA, and survivorship outside an MPA. Total survivorship (Fig. 3a–3c) was highest with zero juvenile movement and/or 100% of the seafloor protected by an MPA (9.5% in Fig. 3c). Similarly, survivorship was lowest where juvenile movement rates were high and MPA size was low (close to 0 in Fig. 3a). Because total survivorship was calculated as the sum of surviving fish in all regions of the model, the influence of juvenile movement rate was minimal, with survivorship a near linear function of MPA size.

Habitat-mediated juvenile mortality (type I functional response) was a linear function of juvenile cod density, with a maximum mortality rate of 0.98 fish consumed by predators per month in unprotected areas and a maximum of 0.38 in regions protected by an MPA. Here the influence of juvenile movement rate was significant. Sur-

vivorship was near zero for regions with no MPA (Fig. 3d). For regions where MPA size was small (6–50% of the habitat patch protected), an increase in juvenile movement rate from 0 to 0.1 (10% of fish in a particular region moving to other regions per month) produced a reduction in survivorship ranging from 37% to 66% of its maximum value. Survivorship was low throughout the lower right quadrant of the surface, where movement rates varied from 0.5 to 1.0 and MPA sizes varied from 0 to 50% of habitat protected. Correspondingly, survivorship was highest for the upper right quadrant of the surface, where MPA size was relatively high (50–100%) and movement rates relatively low (0–0.5). Survivorship increased rapidly for MPA sizes of 75% or greater. Here increases in movement produce declines in survivorship that were less severe than was the case for areas with smaller MPAs.

Survivorship in areas protected by an MPA is depicted in Figs. 3e and 3f for the type II and type III predator functional response curves, respectively. Similar to the type I response surface (Fig. 3d), survivorship for type I and II response curves (Fig. 3e & f) was highest in the upper right quadrant of both surfaces and lowest in the lower right quadrant. Survivorship was highest at 4.6% of fish that settle to the MPA in the first period (Fig. 3e), whereas the peak was at 9.5% for the type III response curve (Fig. 3f). Each of the surfaces depicted an exponential decline in survivorship for increasing values of v_i for all MPA sizes of 100% habitat protected or less. The decline was more pronounced at MPA sizes of 50% or less and for values of v_i ranging from 0.1 to 0.5. Survivorship ranged from a maximum of approximately 4.5% to a minimum of 1% for the type II response curve (Fig. 3e) and from 9.5% to 3.9% for the type III response curve (Fig. 3f).

High mortality in unprotected areas (Fig. 3g–i) led to lower survivorship than found in areas protected by MPAs, with maximum survivorship for each surface of approximately 1.42%, 3.3%, and 9.6%, respectively. The highest survivorship was found in the upper right quadrant of each surface, where movement rates were high (0.5 to 1.0) and MPA size was 50% or greater. Fish densities in unprotected areas increased because of movement of fish from nearby MPAs. Similar to survivorship in areas protected by an MPA, the slope of the response surface was steepest with the type I response curve, where mortality was a linear function of juvenile cod density.

Post-Settlement Juvenile Cod Density and MPA Size

We also present patterns in juvenile cod survivorship as a function of post-settlement fish density and MPA size. The number of fish settling to the seafloor in the first period, S_i , was varied from 1/m² to 10/m² in subsequent runs. The size of an MPA was varied from 0 to 100% of a habitat patch protected. Juvenile movement, v_i , was

figure 3. Response surfaces depicting juvenile cod survivorship as a function of rates of juvenile cod movement and size of marine protected area (MPA) for type I, II, and III functional response curves. Results show survivorship for the entire sanctuary (a, b, c), for areas inside the sanctuary protected by MPAs (d, e, f), and for areas inside the sanctuary not protected by MPAs (g, h, i).

held constant at 0.5 for all model runs to isolate the influence of fish density. For each treatment, cells in a 4×4 matrix were converted randomly from unprotected to MPA over the course of multiple model runs ($n = 100$).

We present results as response surfaces generated from the average of three treatments.

Juvenile cod settled to the seafloor in the first month and were immediately subjected to density-dependent

natural mortality, specified by type I, type II and type III predator functional response curves (Fig. 4a–c). For the type I response (Fig. 4a), the peak in survivorship came in the upper left quadrant of the surface at approxi-

mately 4.4%, where density of juvenile cod was lowest ($1/\text{m}^{-2}$) and MPA size was 100%. For MPA sizes of <56%, survivorship was near zero for all juvenile settlement densities, whereas for MPA sizes of >56% survivorship

Figure 4. Response surfaces depicting juvenile cod survivorship as a function of post-settlement juvenile cod densities and size of marine protected area (MPA) size for type I, II, and III functional response curves. Results show survivorship for the entire sanctuary (a, b, c), for areas inside the sanctuary that are protected by MPAs (d, e, f), and for areas inside the sanctuary that are not protected by MPAs (g, h, i).

increased dramatically with increasing MPA size. Here survivorship declined nearly linearly with increasing juvenile cod density.

For the type II and type III functional response curves (Fig. 4a & 4c), both response surfaces had prominent peaks in the upper left quadrant, at approximately 20% (Fig. 4b) and 45% (Fig. 4c). Unlike the type I functional response (Fig. 4a), where the influence of post-settlement fish density was superseded by MPA size, the density-dependent response to low fish density captured by both the type II and type III functional response curves was evident from the slope of the response surfaces. Here survivorship was relatively high at low fish densities where no MPA existed. For the type II response (Fig. 4b), the 7% survivorship evident for $1/\text{m}^{-2}$ and no MPA was equivalent to a fish density of $6/\text{m}^{-2}$ and 100% of the habitat protected. Similar conditions were evident for the type III response (Fig. 4c), with the 25% survivorship at the lowest fish density comparable to survivorship at $3/\text{m}^{-2}$ and 100% habitat protected. Survivorship was a negative exponential function of post-settlement fish densities for each of the two response surfaces at all MPA sizes, with the maximum fish density of $10/\text{m}^{-2}$ and 100% habitat protected.

Juvenile cod survivorship in areas protected by an MPA reflected patterns similar to those of total survivorship for each of the three functional response curves (Figs. 4d–f). The uniform slope of the response surface for the type I response (Fig. 4d) reflected the dominance of MPA size over fish density in determining survivorship in a system where predation exhibited a type I functional response. For type II and III response curves, the response surfaces (Figs. 4e & 4f) indicate the population responses to low fish density and the corresponding increase in survivorship. Survivorship was a negative exponential function of fish density and was zero where no MPA existed. The same patterns in survivorship were shown for unprotected areas surrounding MPAs (Figs. 4g–i).

Model of Stellwagen Bank National Marine Sanctuary

Nonextractive Closed Areas

Patterns of juvenile survivorship within SBNMS were first presented as a function of MPA size, with MPAs interpreted in this case as year-around nonextractive closed areas. The number of fish settling to the seafloor in the first period was uniform throughout SBNMS at 10 fish per 25 m^2 . Juvenile movement rates were specified for each habitat type (Table 1): flat sand and mud, 44 cells; pebble cobble, 30 cells; boulders, 23 cells. For each treatment, mobile fishing gear (e.g., otter and bottom trawls and scallop dredges) was iteratively excluded from

$25,000\text{-m}^2$ sections of hardbottom seafloor within SBNMS over the course of multiple model runs ($n = 53$). To account for variation in juvenile cod survivorship caused by the spatial heterogeneity in habitat distributions, each of the 53 sections of hardbottom seafloor (pebble cobble and boulders) was randomly closed to fishing activity. We present results for the end points of 12-month model runs as the average of three treatments.

Juvenile cod survivorship was presented as a percentage of all fish that settle to hardbottom (Fig. 5a) and as the total number of fish surviving for the entire SBNMS (total), for nonextractive closed areas (MPA), and for unprotected areas within SBNMS (outside; Fig. 5b). Survivorship for the entire SBNMS was shown to be a linear function of MPA size, ranging from 2.5 million surviving fish if no closed areas existed to 9 million fish if 100% of hardbottom seafloor in SBNMS was protected. This was an increase in the number of surviving fish equal to 3.6 times the number that survived in the absence of an MPA. Survivorship within nonextractive closed areas also increased as a linear function of MPA size, ranging from zero where no closed areas exist to 8.2 million fish where 100% of the hardbottom seafloor in SBNMS was protected by closed areas. Survivorship was lowest in unprotected areas, with a linear decrease from 2.6 million fish where no closed areas existed to approximately 900,000 fish where all hard-bottom areas were protected. This decline in total numbers in outside areas occurred as expanding MPAs reduced the total area of unprotected areas.

Survivorship was presented as the number of surviving fish per number of fish that settle to any region i in the first month (Fig. 5b). Here survivorship in areas protected by nonextractive closures exceeded 100% (ranging from 158% to 170%) as fish from surrounding unprotected areas moved into closed areas. Survivorship in unprotected areas varied between 21% (with no closed areas) and 19% (where 98% of hardbottom was protected). Total survivorship throughout SBNMS increased with increasing MPA size as fish from areas surrounding SBNMS moved into protected areas.

Habitat-Specific Representative Closed Areas

We evaluated patterns in juvenile survivorship as a function of the size and orientation of representative closed areas established within SBNMS. We simulated contiguous, rectangular closed areas within SBNMS oriented east-west and north-south and compared them to networks of smaller closed areas (Fig. 6). Three experimental treatments were simulated for representative closed areas that cover 0, 10, 25, 50, and 100% of the SBNMS: (1) contiguous rectangular closed areas oriented east-west (parallel to the major axis of tidal flux); (2) contiguous rectangular closed areas oriented north-south (perpendicular to the major axis of tidal flux); and (3) noncontig-

Figure 5. Juvenile cod survivorship for Stellwagen Bank National Marine Sanctuary as a function of the percent area of hardbottom seafloor habitat closed to mobile fishing gear. Survivorship is reported for the entire sanctuary (total), areas closed to mobile fishing gear (MPA), and areas open to fishing activity (outside): survivorship reported as (a) total number of surviving fish and (b) percentage of fish settled to each region.

uous networks of individual closed areas. For each of the three treatments, representative percentages of the three primary habitats—boulder, pebble-cobble, and flat sand or mud—were protected by the closure. For example, for the treatment in which 10% of the SBNMS was protected, the closed area protected approximately 10% boulder habitat, 10% pebble-cobble habitat, and 10% flat sand or mud. Post-settlement fish density and rates of

natural mortality and fish movement were identical to those of the nonextractive closed areas.

Juvenile cod survivorship was simulated for the entire SBNMS (total), for representative closed areas (MPA), and for unprotected areas within SBNMS (outside). The closed areas (Fig. 6a) consisted of contiguous regions oriented in an east-west direction, parallel to the dominant tidal current. Where no closed areas exist (i.e., total and outside were identical), total survivorship for SBNMS was approximately 28% of those fish that settled to the seafloor in the first period. Total survivorship was a threshold function of MPA size, increasing to 98% where the entire SBNMS was protected. Survivorship within closed

areas exceeded 105% at 10% of the seafloor protected because the combined effect of undisturbed habitat and movement of fish from adjacent regions resulted in a greater number of fish at month 12 than settled to the region in the first month. Here the high survivorship of those fish that settled to the seafloor in a region protected from fishing was augmented by emigration of fish from surrounding areas where fishing had occurred and mortality was high. Survivorship in closed areas declined slightly to 99% and then to 97% as the size of the closed area was increased to 100%. Total survivorship was constant at approximately 27% for all conditions where protection was <100%. Survivorship in outside areas was a positive function of MPA size up to 100% protected, where by definition there was no longer any "outside," or unprotected areas, in SBNMS.

Contiguous closed areas (Fig. 6b) were oriented north-south, perpendicular to the dominant tidal current. Total survivorship was again a threshold function of closed-area size, increasing from 27% to 97% for closed areas of 10% and 100%, respectively. Survivorship in closed areas was highest at 10% habitat protected, with more than 105% of fish surviving by month 12. An increase in closed-area size to 25% of the seafloor protected actually produced a decline in survivorship to 88%. Survivorship in closed areas at 50% and 100% seafloor protected was 98% and 96%, respectively. For unprotected areas of <100%, survivorship was a positive function of MPA size.

Closed areas (Fig. 6c) were networks of noncontiguous habitat patches distributed throughout SBNMS. Total survivorship was 27% for 10% of the seafloor protected, increasing to 97% at 100% of the seafloor protected. At 23%, survivorship in closed areas was lowest for 10% of habitat closed to fishing; it increased to 91%, 100.2%, and 95% for closed areas of 25%, 50%, and 100%, respectively. Survivorship in unprotected areas was a positive function of MPA size for all closed areas of <100%.

Discussion

Habitat disturbance by fishing activities is the dominant anthropogenic effect on the marine environment (Dayton et al. 1995; Watling & Norse 1998). Mobile fishing gear in particular is estimated to affect seafloor habitat with an intensity and spatial extent orders of magnitude greater than other disturbances to the same environment (Watling & Norse 1998). Nevertheless, the effect of habitat alteration on associated fish species in the northwest Atlantic and the rate of recovery of those species in the absence of fishing have yet to be sufficiently quantified for the development of strategic management decisions (Auster et al. 1997b). Lindholm et al. (1999) quantified relative differences in habitat-mediated predation on juvenile cod at the microhabitat scale. In our model we used the results of this small-scale study to

predict the effects of habitat-mediated processes on population responses at the landscape scale (i.e., SBNMS).

Results of the dynamic model demonstrated distinct patterns in juvenile cod survivorship and linked those patterns to seafloor habitat quality and fishing-induced alteration of seafloor habitat. The model of a single patch of pebble-cobble bottom indicated that the vagility of juvenile cod and the density of post-settlement juvenile cod are each significant factors in the survivorship of early benthic-phase juvenile cod, particularly in the context of MPAs designed to protect seafloor habitat. This was true for each of the three simulated forms of density-dependent natural mortality. Further, the case study of SBNMS suggests the utility of nonextractive closed areas for management of fishing-induced alteration of the seafloor. Results of the SBNMS model also suggest that the size and configuration of closed areas and their orientation relative to the dominant tidal-current regime (Fig. 6) may influence patterns in juvenile cod survivorship.

Recent modeling studies have explicitly addressed the use of MPAs for fish conservation and fisheries management in outer continental shelf systems (Polacheck 1990; Holland 1993; Man et al. 1995; Ruth 1995; Nowlis & Roberts 1997; J. S. Nowlis, personal communication). The majority of these models deal primarily with fish as mature, reproductive adults, with early life history often represented in the models by pelagic dispersal of eggs and larvae. Similarly, fish mortality is driven mainly by fishing effort, with no coupling of fish populations to habitat-mediated processes or fishing effects on those processes. In our model, juvenile cod settled to the seafloor in the first period, and settlement was uniform among all habitat types. This is consistent with field observations of juvenile cod in the nearshore environment (Tupper & Boutilier 1995a) and on the northeast peak of Georges Bank (Lough et al. 1989). These studies indicate that settlement occurs over all habitat types, with differences in post-settlement juvenile abundance between habitats attributed to habitat-mediated, predator-induced mortality. Natural mortality is specified in the models as habitat-specific, predator-induced, and density-dependent.

To account for the variety of predator-prey-habitat interactions that occur on the seafloor, we modeled density-dependent juvenile mortality as three functional response curves. The interpretation of the response curves has been widely accepted by ecologists (Peters 1991). Optimal habitat selection (Kramer et al. 1997) indicates that as a habitat becomes saturated, fish move to previously suboptimal habitats. This, coupled with cod settlement over all habitats, suggests that juveniles encounter more than one habitat type and, consequently, more than one predator community. Although each of the three individual functional response curves may be insufficient to characterize these conditions, the comparison of model

results indicates that, although actual survivorship varied, the patterns of survivorship remained similar in all three cases.

Regional species assemblage patterns in the Gulf of Maine can be defined by temperature and depth contours (Overholtz & Tyler 1985; Gabriel 1992), but fish movement at smaller scales in particular habitat types remains highly uncertain. It is precisely for these smaller scales that movement data is required for the design and implementation of MPAs for fish conservation and management. Results from the patch model suggested that juvenile cod survivorship (fish <14 cm total length) is highly sensitive to juvenile movement rates, particularly with respect to the design of MPAs. Where no juvenile cod movement occurs, maximum survivorship within MPAs was constant for all MPA sizes greater than zero. Such site fidelity has been observed among recently settled juveniles in areas of adequate cover (Tupper & Boutilier 1995a). Our model results also indicated that the siting of small MPAs relative to the location of seafloor habitat is critical. For larger MPAs (>50% habitat protected), the influence of movement rate remained significant for juvenile survivorship, but the magnitude of the influence was reduced as the size of the MPAs encompassed a greater portion of the possible range of a juvenile cod.

Practical limitations imposed on MPA designation by real-world constraints in the management process indicate that we must look at the lower half of the response surfaces for juvenile cod survivorship patterns that we might expect to see in the field. It is unlikely that large areas of a given system will be closed for the purposes of fishery management. Rather, smaller areas in the range of 10–20% of a given area protected are far more likely to be implemented (Plan Development Team 1990). Our model suggested that where fish movement is low, increases in survivorship can reach as high as 10% in MPAs (Fig. 3f) and up to 4% in areas surrounding MPAs (Fig. 3i).

The export of fish from MPAs to surrounding harvested populations is important to the fishing community and managers alike. Although our model did not deal explicitly with recruitment to adult populations that are harvested, results indicate that for those conditions in which juvenile movement was high, survivorship was most pronounced in unprotected areas where MPA size was greater than 50%. A greater number of surviving juveniles within an MPA provided a larger supply of fish for areas beyond the boundaries of any MPA. In the real world, an increase in survivorship of 0–4% (Fig. 3g–i) translates into a significant increase in harvested fish as juveniles recruit to adult populations. Where MPA size was <50%, survivorship in unprotected areas was low for all movement rates because sufficient cover from predation was in short supply.

Results from the patch model indicated that survivorship of juvenile cod was highest for populations at low densities, particularly where MPA size was large, with

survivorship significantly lower at higher population densities and for smaller MPAs. This basic relationship, with slight variations, was constant for total survivorship, survivorship in MPAs, and survivorship in unprotected areas and across the three forms of density-dependent mortality. The location of the peak of each response surface confirmed *a priori* expectations, with the minimum modeled density $1/\text{m}^2$ and 100% of the habitat protected (total survivorship and survivorship in an MPA) and 90% of the habitat protected (survivorship in unprotected areas). Atlantic cod populations in the Gulf of Maine and on Georges Bank currently represent a fraction of historical population levels (Clark 1998). The utility of habitat-specific MPAs for the protection of cod at low population densities is a particularly appropriate subject of concern for both conservation and fisheries management.

From a management perspective, these results indicate that the designation of habitat-specific MPAs for areas identified as locations of juvenile cod settlement may produce significant increases in survivorship for populations at low densities. Again, one should look at the lower half (MPA <50% total area protected) of the response surfaces for guidance in identifying the role of habitat for improving juvenile cod survivorship. Survivorship in MPAs that protected 20% of hardbottom seafloor habitat ranged from 0.5% to 19% higher than in areas where no protection existed. Further, survivorship in areas surrounding MPAs reached 25% (Fig. 4i), which suggests that closing 20% of the seafloor can produce increases in cod survivorship of more than 40% relative to conditions in which no closed areas exist.

Results of the model that captures key features of SBNMS suggest that the closure of hardbottom seafloor habitat to fishing with mobile gear can produce significant increases in juvenile cod survivorship. The linear relationship between juvenile cod survivorship (total number of fish) and the closure of hardbottom habitat to mobile fishing gear in the model provides a well-defined management option for fishery managers. Closure of all hardbottom seafloor habitat within SBNMS produced the maximum number of surviving juvenile cod. When 50% of the seafloor was protected, the corresponding reduction in juvenile cod survivorship was approximately 50% of that maximum.

Our results indicate that juvenile survivorship varied with the size, configuration, and orientation of MPAs designed to protect representative samples of flat sand and mud, pebble-cobble, and boulder habitats. Maintenance of habitat diversity is a well-established tenet of conservation biology (e.g., Primack 1993) and is often a consideration in the design of MPAs for the conservation of biological diversity (Jones 1994; Ticco 1995). Given that the fishing industry is a key stakeholder in decisions regarding the use of MPAs for conservation of diversity, understanding the role of MPAs in the dynamics of ecologically important species is critical.

Ballantine (1995) discusses the designation of networks of marine reserves to account for the dispersive propagules of many marine organisms and to capture a diversity of habitat types. Juvenile cod settle on a variety of habitats, from flat sand to boulder reef (Tupper & Routilier 1995a). The relatively weak tidal-current velocities along the bottom, 0–30 cm/second, occurring within the SBNMS influence juvenile cod movement much less than in systems such as Georges Bank where bottom currents can regularly reach 100 cm/second (Valentine & Schmuck 1995). Juvenile cod movement in our model was dominated by the biological imperative of predation avoidance, with net movement between regions only slightly higher along the major axis of the tidal currents. Results of the patch model confirm that for fish at low densities, small MPAs increased juvenile survivorship. Results of the SBNMS model, however, indicate that where 10% of each seafloor habitat was protected, contiguous rectangular MPAs produced significantly higher survivorship than in networked, smaller MPAs.

The ultimate objectives of modeling studies such as ours are to predict fish population responses to habitat alteration and to identify the role of MPAs in the conservation of biodiversity and fishery management. Modeling also provides the opportunity to identify needed laboratory and field research that can be used to further specify key parameter values in the model for more accurate prediction of population responses. The use of nonextractive and habitat-specific MPAs for fisheries management that we modeled is not the only management tool potentially available to conservationist biologists and fishery managers. In the face of continued uncertainty regarding post-settlement ecological processes on the seafloor, such MPAs represent a precautionary or risk-averse approach to management (Ludwig et al. 1993; Auster et al. 1997b), designed to protect diversity in general and fish communities in particular while research continues.

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