Simulation modelling as a tool for examining the consequences of spatial structure and connectivity on local and regional population dynamics

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An understanding of the mechanisms underlying population persistence makes fisheries management more effective. A model framework is described, which can test hypotheses about spatial structure and connectivity within and between populations and their influence on the productivity (spawning-stock biomass, SSB), stability (variation in SSB), resilience (time to rebuild SSB after environmental disturbance), and sustainability (maximum sustainable fishing mortality and yield) of systems. The general model consists of linked age-structured submodels that incorporate the unique demographics and dynamics of population components, along with the degree and type of connectivity between them. The flexibility of this framework is illustrated with three case studies examining (i) spatial structure within a population of white perch, (ii) different types and degrees of connectivity between populations of Atlantic herring, and (iii) spatial heterogeneity and connectivity within a stock of Atlantic cod. System variance is reduced by abundant, stable population components, and the asynchronous responses of those components. Components with high productivity contributed disproportionately to the resilience of systems. Increased synchrony of component responses to environmental forcing decreased the stability of the overall system. Simulation modelling is a useful approach to evaluate the consequences of spatial structure and connectivity, and can be used to understand better the productivity and dynamics of local and regional populations.

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Introduction

The study of fish population dynamics has historically focused more on understanding the temporal than the spatial dynamics of populations. Hjort's (1914) work examining fluctuations in the abundance of fish stocks in northern Europe was influential in directing research in fisheries science on temporal variability of populations, i.e. in determining what leads to year-class variation. The examination of fluctuations in populations, ranging from interannual to multidecadal time-scales, continued to be a research focus throughout the twentieth century (Houde, 2008), and typically involved simplifying assumptions about the spatial structure of populations. This simplified view was evident in stock assessment science wherein populations were typically considered to be a single unit with homogeneous characteristics, i.e. the unit stock concept described by Cadrin and Secor (2009). Recently, there has been increased recognition of the importance of spatial structure and connectivity on the productivity and dynamics of local and regional populations (Andrews et al., 2006; Heath et al., 2008; Cadrin and Secor, 2009; Secor and Kerr, 2009; Kerr et al., 2010).

Spatial structure within, and connectivity between, local and regional populations may play an important role in the resilience and persistence of fish stocks (Kerr et al., 2010). Identifying the mechanisms of these biological phenomena is critical to understanding how populations will respond to climatic oscillations and exploitation. Factors including oceanography and fish behaviour (i.e. spawning and larval behaviour) are important in the structuring of unique spawning populations (Sinclair, 1988), and dispersive capabilities, local population density, fitness costs, and environmental conditions can be significant factors in determining the spatial dynamics within populations (Hanski, 1999). Spatial structuring within fish populations (e.g. phenotypic population structure) is often attributed to an individual's behavioural response (e.g. resident vs. migratory) to their fitness relative to environmental conditions (Jonsson and Jonsson, 1993). The connectivity between populations may be maintained through dispersal during the larval period or juvenile/adult straying, a dispersive behaviour that can be triggered by density-independent (i.e. environmental conditions) or -dependent factors (i.e. local population density). Alternatively, the connectivity may occur through entrainment during the juvenile/adult stage, whereby individuals from one population are socially drawn into another during periods of spatial overlap (McQuinn, 1997; Corten, 2002). Because of the role spatial structure and connectivity may play

in population- and metapopulation-level processes, there is a critical need for the development of tools to incorporate these phenomena into models to better understand the local and regional population dynamics and to improve management decisions.

Simulation modelling is a useful and flexible approach that can be used to explore a diversity of ecological and applied questions about fish populations, and serves several important roles. Deterministic simulation is the basis of many traditional management reference points, and stochastic simulation has been used extensively for risk analysis (reviewed by Smith *et al.*, 1993). The operating model concept is used to evaluate stock assessment models, and the approach has been extended to management strategy evaluation (MSE; Butterworth and Punt, 1999; Wilberg *et al.*, 2008). For example, Ricker (1958) simulated reproductively isolated populations of Pacific salmon in variable environments to determine optimal harvest strategies for mixed-stock fisheries. More recently, the application of simulation modelling in fisheries science has been expanded to examine a broader set of questions, exploring a range of ecological issues related to fish (Porch *et al.*, 2000; Heath *et al.*, 2008). Specifically, we show that simulation models can be used as an experimental framework with which to test hypotheses about the likely mechanism and consequences of connectivity between and spatial structure within local and regional fish populations. Our focus is to bring biological realism to a dynamic model of a population, incorporating the best available empirically derived data, to examine how structure and connectivity influence population- or metapopulation-level attributes. The approach draws from the landscape ecology literature, which has a long history of study of spatial patterns and their impact on landscape-level processes (Turner, 1989). Because the development of a simulation model is iterative, the process of constructing and running it helps to inform concepts of how the system works and understanding of the processes, phenomena, and scales at which spatial structure and connectivity have a significant impact (Turner, 1989; Peck, 2004).

The goal of our research was to illustrate the flexibility of an age-structured simulation model framework for examining the consequences of spatial patterns and connectivity on population processes, responses that would be extremely difficult if not impossible to explore based on field observations alone. Using three case studies, we examined the consequences of (i) spatial structure within an estuarine-dependent population of white perch (*Morone americana*), (ii) different types and levels of connectivity between populations of Atlantic herring (*Clupea harengus*), and (iii) spatial heterogeneity and connectivity within the Gulf of Maine Atlantic cod (*Gadus morhua*) management unit.

Methods
Model framework
The generalized model framework used in all three case studies was an age-structured model that incorporated the unique demographics and dynamics of population components, along with the extent and type of connectivity between them. The flexibility of this framework allows for incorporation of multiple spawning components or subcomponents with either unique or shared stock–recruit relationships. Using this approach we can incorporate patterns in recruitment variability based on a mechanistic understanding of environmental forcing on recruitment (e.g. correlation in recruitment with freshwater flow conditions; Kerr *et al.*,

2010) of the population component or, when this is unknown, we can simulate recruitment variability in a more simplistic manner, emulating the pattern in the available recruitment indices or model estimates over time. The focus of the approach is to use simulation models as a tool in the identification and understanding of local and regional population structure.

The model framework for white perch and Atlantic herring is described below, and further information on model structure and details of parameter estimation for the white perch and Atlantic herring case studies is provided in Kerr *et al.* (2010; white perch) and Secor *et al.* (2009; Atlantic herring). The details of the Gulf of Maine Atlantic cod model are described in the Gulf of Maine Atlantic cod subsection.

The population model for white perch consisted of two behavioural contingents (residents and migrants, aged 1–12 years) linked through a common stock–recruitment relationship. Recruitment or abundance of white perch aged 0 (N_0) was calculated from

$$N_0 = \frac{B_1 \text{SSB}_{\text{pop}}}{B_2 + \text{SSB}_{\text{pop}}} + \varepsilon, \tag{1}$$

where SSB_{pop} is the spawning-stock biomass of the overall population (i.e. the sum of the SSBs of resident and migratory contingents), B_1 is the maximum number of recruits produced, and B_2 controls the rate at which the asymptote, or maximum recruits per spawner, is reached (Beverton and Holt, 1957). The error term (ε) was modelled as a normally distributed random deviate ranging up to 10% of the maximum number of recruits. At age 1, the population diverged into resident and migratory groups that were modelled with their respective contingent-specific vital rates, and independent recruitment dynamics that were driven by environmental conditions (i.e. streamflow) and random variation.

The metapopulation model for Atlantic herring consisted of two age-structured spawning components (ages 1–9), each with its own stock–recruit relationship. The populations were patterned after a subordinate Irish Sea and a dominant Celtic Sea population. Recruitment-at-age 1 (R) was calculated by a hockey-stick-type stock–recruit model:

$$R = \begin{cases} \gamma \text{SSB} & \text{if SSB} < \text{SSB}^* \\ \gamma \text{SSB}^* & \text{if SSB} \geq \text{SSB}^* \end{cases}, \tag{2}$$

where γ is the slope and SSB^* the spawning-stock biomass that triggers an asymptotic response in recruitment (Barrowman and Myers, 2000). Variation in the number of recruits was included, and the magnitude was scaled to achieve a coefficient of variation (CV) in age-1 recruitment equal to 40% (based on a time-series of estimates of recruitment from a stock assessment; ICES, 2008) for both populations, with random variation driving the subordinate population, and the North Atlantic Oscillation (NAO) index driving variation of the dominant population.

The SSB of white perch and Atlantic herring was calculated as a function of the number-at-age, weight-at-age, and maturity-at-age of the study species:

$$\text{SSB}_{(t)} = \sum_{a=0}^{a=\infty} N_{a(t)} W_a P_a, \tag{3}$$

where $N_{a(t)}$ is the average number of fish aged a at time t, W_a the average spawning weight (kg) of a fish aged a years, and P_a is the average fraction of fish aged a that are mature. A length–weight relationship was used to estimate the weight-at-age of white perch:

$$W_a = \alpha L_a^{\beta}, \qquad (4)$$

where L_a is the length-at-age, α a proportionality constant, and β is the allometric coefficient. Length-at-age was estimated from von Bertalanffy growth models specific to each population component:

$$L_a = L_\infty\left[1 - e^{-k(a-a_0)}\right], \qquad (5)$$

where L_∞ is the asymptotic size, k defines the rate at which the curve approaches the asymptote, and a_0 is the hypothetical age at which the size of the fish is zero. The average weight-at-age of Atlantic herring was based on field-collected data for the period 1998–2007 (ICES, 2008). The proportion of fish mature-at-age was determined from maturity ogives (Atlantic herring; ICES, 2008) or maturity length-at-age relationships (white perch; Mansueti, 1961).

Abundance-at-age for older ages of white perch and Atlantic herring was calculated from

$$N_{a+1(t+1)} = N_{a(t)}e^{-Z_a}, \qquad (6)$$

where N_a is age-specific abundance, and Z_a is the total adult annual mortality of the population or behavioural contingent.

Gulf of Maine Atlantic cod

Atlantic cod in the Gulf of Maine management area (ages 1–11+) were modelled as three interconnected substocks: Massachusetts Bay, Ipswich Bay, and coastal Maine. The substock model is a portion of a larger model that will ultimately include spatial structure within and connectivity between cod populations within the Gulf of Maine and Georges Bank management units. The results of the substock model were contrasted with a model in which Gulf of Maine cod were modelled as a single stock, the current management perspective. Our simulations expand upon those developed for Gulf of Maine cod by Reich and DeAlteris (2009) by defining spatial structure according to biological knowledge of the primary spawning components within the Gulf of Maine

management unit, based on patterns of genetic variation and tagging data, determining vital rates, and recruitment dynamics within substocks from field observations, and using the stock–recruit relationship from the stock assessment to constrain both models. Life history parameters, including growth (calculated from von Bertalanffy growth models) and maturity (calculated from maturity ogives), were estimated on a substock and single-stock basis from data collected during the Northeast Fisheries Science Center (NEFSC) stratified random bottom trawl survey (Table 1). Fish length and weight were measured on board. Age and maturity stage were determined for subsamples. Multiple years (2000–2007) of data were pooled to estimate life history parameters, because of insufficient annual sample sizes. Only data from spring surveys, which are conducted during or closer to spawning periods than autumn surveys, were used to minimize errors in stock identification. The Gulf of Maine management area for Atlantic cod was defined by NMFS statistical areas, and substocks were defined using knowledge of spawning components derived from tagging studies (Howell *et al.*, 2008; Tallack, 2009), and genetics (Wirgin *et al.*, 2007; Breton, 2008).

Recruitment or abundance-at-age 1 (N_1) was calculated using a modified Beverton–Holt curve (Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish, 2002):

$$R = \frac{4z_{max}R_{max}\text{SSB}}{\text{SSB}_{max}(1 - z_{max}) + \text{SSB}(5z_{max} - 1)}, \qquad (7)$$

where SSB_{max} is the maximum observed stock size, R_{max} the maximum expected recruitment, and z_{max} is the steepness of the curve. Parameter estimates for SSB_{max}, R_{max}, and z_{max} were available for Gulf of Maine cod (Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish, 2002) were used directly in the single-stock model, and modified for use in the substock model (Table 1). In the substock model, the values of R_{max} and SSB_{max} were divided by the relative magnitude of the average recruitment index (number per survey tow) and the SSB index (in kg per survey tow) of each substock. This form of the Beverton–Holt relationship allowed for a common steepness parameter among substocks.

Table 1. Parameter estimates and sources of data used in the single-stock (Gulf of Maine management unit) and substock (including Massachusetts Bay, Ipswich Bay, and coastal Maine spawning groups) age-structured models of Atlantic cod.

		Value			
Parameter	**Definition**	**Gulf of Maine management unit**	**Massachusetts Bay**	**Ipswich Bay**	**Coastal Maine**
M[a]	Natural mortality	0.20	0.20	0.20	0.20
R_{max} (thousands)[a]	Maximum expected recruitment	8 983	3 493	4 802	688
S_{max} (t)[a]	Maximum observed stock size	77 500	40 447	23 341	13 811
z_{max}[a]	Steepness of the stock–recruit curve	0.74	0.74	0.74	0.74
L_{inf} (cm)[b]	Asymptote of growth model	145.77	138.71	164.15	133.95
k (year^{-1})[b]	Rate at which growth model approaches asymptote	0.11	0.12	0.10	0.14
a_0 (cm)[b]	Length at age 0 in growth model	−0.22	−0.26	−0.08	0.01
α(cm kg^{-1})[b]	Length–weight parameter	0.000003	0.000003	0.000003	0.000003
β[b]	Length–weight parameter	3.28	3.28	3.28	3.28
c[b]	Maturity ogive parameter	−4.97	−5.04	−4.44	−5.35
d[b]	Maturity ogive parameter	1.52	1.53	1.30	1.77

[a]Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish (2002).
[b]Estimated from NEFSC survey data (2000–2007).

Table 2. Parameter estimates included in the Atlantic cod substock model.

	Massachusetts Bay	Ipswich Bay	Coastal Maine
Massachusetts Bay		0.39	0.24
Ipswich Bay	0.05		0.15
Coastal Maine	0.01	0.02	

Values above the diagonal are correlations in age 1 recruitment indices, and values below the diagonal are estimated straying rates (the proportions of individuals that stray annually (ϕ)).

Recruitment and spawning-stock indices were developed for each substock from data collected in the NEFSC spring bottom trawl survey for the years 1970–2007. Using substock age–length keys, the length frequency of fish was converted to age frequency, and the number of fish aged 1 per tow (i.e. catch per unit effort, cpue) was calculated and averaged for each year. The CV of age 1 cpue within substocks and correlation in year 1 cpue between substocks was calculated and used to scale the magnitude of recruitment variability and correlation in recruitment between substocks (Table 2). An index of SSB was also calculated based on an annual mean weight of catch per tow within each substock region.

The SSB was calculated in the same manner described for white perch and Atlantic herring. In Atlantic cod substock models, the connectivity between stocks was included as stray fish (derived from other substocks), with straying rates estimated from pairwise F_{st} values between substocks (Wirgin *et al.*, 2007; Breton, 2008), following Wright (1951; Table 2). Straying rates are probably underestimated, because pairwise F_{st} values included both neutral and non-neutral markers, and effective population size was estimated as maximum recruitment at age 1 for substocks (R_{max}). Abundance-at-age for ages 2–10 was calculated from

$$N_{i,a+1(t+1)} = (N_{i,a(t)}\rho_i + N_{j,a(t)}\phi_{ji} + N_{k,a(t)}\phi_{ki})e^{-M-(s_a)F}, \quad (8)$$

where N_a is the age-specific abundance of each substock (i, j, k), ρ the proportional fidelity of fish in a substock, ϕ the proportional movement of fish between substocks, M the natural mortality, s_a the age-specific selectivity into the fishery, and F is the fishing mortality. Abundance-at-age for the age 11+ group was calculated from

$$N_{i,a+1(t+1)} = (N_{i,a(t)}\rho_i + N_{j,a(t)}\phi_{ji} + N_{k,a(t)}\phi_{ki})e^{-M-(s_a)F}$$
$$+ (N_{i,a+1(t)}\rho_i + N_{j,a+1(t)}\phi_{ji} + N_{k,a+1(t)}\phi_{ki})e^{-M-(s_{a+1})F}. \quad (9)$$

Population response variables

The population response variables of interest varied across the three case studies according to the hypotheses being tested. Population and metapopulation productivity were calculated as the grand mean SSB across years and simulations. Stability of populations and behavioural contingents was calculated as the grand mean coefficient of variation (CV is the standard deviation divided by the mean) of SSB across years and simulations. Metapopulation stability was calculated by weighting the CV of population components by the respective SSB and taking into account the extent to which variance was dampened as a consequence of independence between components, a metric termed

the portfolio effect (Secor *et al.*, 2009). Resilience was calculated as the number of years it takes to rebuild a population above mean SSB after a period of poor recruitment, taken as 5 years when recruitment is at 10% of the maximum level. Sustainability with respect to fishing was calculated as the maximum long-term average yield and the fishing mortality that produces maximum sustainable yield (MSY).

Simulations

A series of 500 stochastic simulations, each conducted over a 150-year period (only the last 100 years were used in analyses, to allow models to approach an equilibrium), was performed for each simulated scenario.

White perch

In these simulations, we examined the population-level consequences of partial migration, whereby resident and migratory behavioural groups, or contingents, were present within a population. Specifically, we evaluated the impact of changes in (i) contingent representation, the average proportion of the population that recruits to each contingent each year, and (ii) correlation in interannual age 1 abundances between contingents, i.e. recruitment synchrony, on the stability, productivity, and resilience of the overall population.

Atlantic herring

These simulations were used to examine the impact of different types and levels of connectivity between Atlantic herring populations on the productivity and stability of each population and the overall metapopulation. Model scenarios of connectivity between two populations included the straying scenarios, such as (i) density-independent straying (uni- and bidirectional) and (ii) density-dependent straying, and the entrainment, scenarios, such as (a) density-dependent entrainment (individuals of the subordinate population are drawn into the dominant population), (b) density-dependent entrainment with a reserve or portion of the population protected from entrainment, (c) density-dependent entrainment in strong year classes, and (d) density-dependent entrainment in strong year classes with a reserve. These scenarios were compared with a baseline model in which there was no connectivity between local populations.

Atlantic cod

In these simulations, we examined the consequences of spatial structure, including spatial differences in vital rates and independent recruitment dynamics of spawning components within a management unit of Atlantic cod on the productivity, stability, and sustainable yield of the stock. Model scenarios included several levels of fishing mortality ($F = 0–1.0$) applied to the single-stock and substock models.

Results
Spatial structure within an estuary-dependent population of white perch

Using the flexible structure of the simulation model, we constructed a population model with two subcomponents (resident and migratory contingents), linked through a common stock–recruitment function, with each component having unique demographics and independent responses to changes in streamflow dynamics. The model allowed us to explore population-level

dynamics and to characterize important features of the population, including productivity, stability, and resilience.

Through simulation modelling, we found that the population metrics examined (productivity, stability, resilience) were most sensitive to the proportional representation of behavioural contingents in the population, and less sensitive to the correlation in recruitment between the two contingents. An increased representation of the migratory contingent within the population resulted in an increased productivity and resilience, but decreased stability (Figure 1). Conversely, an increased representation of the resident contingent increased the stability within the population, but decreased the productivity and resilience (Figure 1). Negative correlation in the recruitment dynamics between contingents increased the productivity and dampened the variance in population biomass (Figure 1). A high positive correlation in recruitment also increased the productivity, but it reduced the stability within the population. Across scenarios, variation in the correlation in recruitment had little impact on the resilience of the population. Overall, our analysis using simulation modelling revealed that resident and migratory contingents played different roles in the dynamics of the population. The resident contingent is consistently present and contributes to population stability. The dispersive contingent has more variable dynamics, but is more highly productive and contributes to population resilience.

Different types and extents of connectivity between populations of Atlantic herring

Through modifying the basic model framework, we simulated the metapopulation dynamics of two herring populations, with independent stock−recruitment functions linked through straying or entrainment. Each spawning component had unique demographics, with one population's recruitment variability tied to the NAO and the other modelled in a stochastic manner. Using

this construction, we explored the consequences of different types and levels of connectivity between constituent populations to productivity and stability. Kell *et al.* (2009) employed a similar simulation framework to a more applied question, examining the consequences of population structure of herring west of the British Isles (including the Irish and Celtic Sea herring populations) to recovery and management.

Our results revealed that straying and entrainment scenarios had a notable impact on the productivity and stability of local populations, but through different mechanisms. Regional population dynamics were not as heavily impacted as local ones, but all connectivity scenarios resulted in decreased metapopulation productivity. Density-independent straying (uni- and bidirectional) decreased the productivity within the dominant population owing to the removal of individuals, i.e. strays (Figure 2). The stability of the dominant population also decreased in density-independent straying scenarios because of the random nature of removals from, and additions to, the population. Both productivity and stability increased in the subordinate population, because that population predominantly received immigrants through straying. Metapopulation dynamics were not heavily impacted, but they did exhibit slight decreases in productivity and stability. Density-dependent straying operated as a negative feedback, whereby strong year classes were removed from the dominant population and transferred to the subordinate population. This resulted in decreased productivity, but increased stability in the dominant population (dampened variance through straying during years of high abundance; Figure 2). Both productivity and stability increased in the subordinate population and decreased in the metapopulation. Entrainment generally operated as a positive feedback, whereby the dominant population gained members from the subordinate population when the dominant population abundance was high. Therefore, the productivity
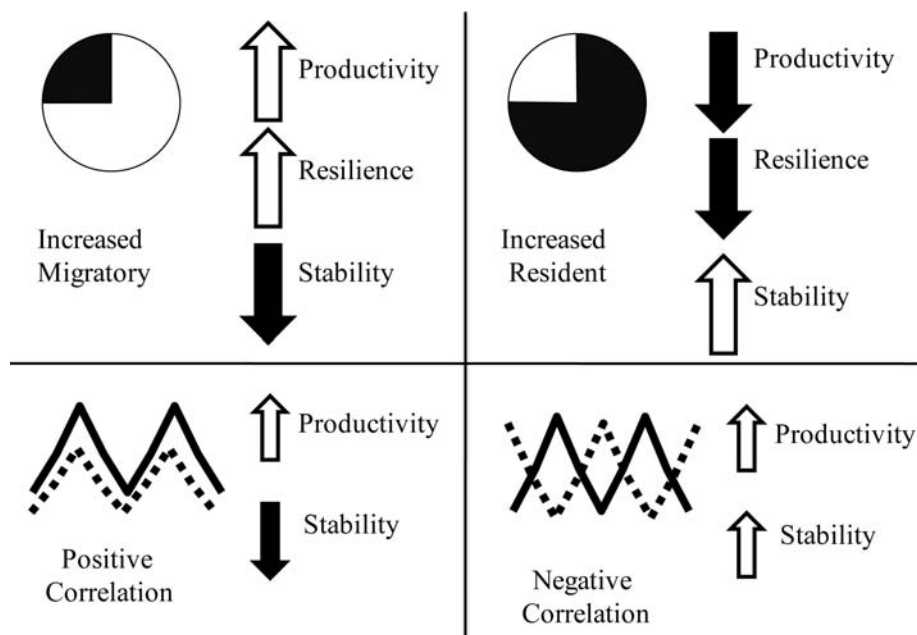

Figure 1. Summary of the results of white perch simulation modelling, examining the impact of changes in (i) contingent representation (average proportion of the population that recruits to each contingent each year) and (ii) correlation in interannual abundance of fish aged 1 year between contingents (i.e. recruitment synchrony) on the stability, productivity, and resilience of the overall population. Figure reproduced from Kerr *et al.* (2010), with permission.

Figure 2. Summary of results of Atlantic herring simulation modelling, examining the impact of different types and levels of connectivity between populations of Atlantic herring on the productivity and stability of each population and the overall metapopulation.

increased in the dominant population and decreased in the subordinate population, as well as in the metapopulation. In general, the stability decreased at a local population level, but tended to increase at a regional level across entrainment scenarios (Figure 2). As more individuals from the subordinate population were entrained when the dominant population density was high, the oscillations in abundance between the populations tended to be out of phase, contributing to a greater portfolio effect, or dampening of variance in the overall metapopulation. However, when a portion of the subordinate population was "protected" from entrainment, the stability increased in the subordinate population and decreased at a metapopulation level, although this was an artefact of reduction of the subordinate population to a static reserve level (Figure 2). Overall, it appears that the connectivity through straying had the effect of increasing synchrony, thus reducing the independence of local populations and resulting in greater variability in the overall metapopulation. The connectivity through entrainment had the effect of increasing asynchrony between local populations, resulting in a more stable metapopulation.

Spatial heterogeneity and connectivity within the Gulf of Maine Atlantic cod management unit

In this case, we contrasted a model based on the single-stock management paradigm with a substock model that incorporated our knowledge of the biological structure existing within the management unit. Each substock possessed an independent stock–recruitment function, unique vital rates, and recruitment dynamics. Populations were connected through straying during the juvenile and adult stages (ages 2–11+). This adaptation of the model framework represents an applied usage, examining the impact of spatial structure on productivity and sustainable yield from the fishery.

Across simulations with differing intensities of fishing mortality, the productivity and yield of the substock model averaged 43% and 46% higher than that of the single-stock model, respectively (Figure 3). The greater productivity of the substock model appears to be attributable to inclusion of spatially explicit differences in vital rates and recruitment dynamics. The inclusion of substock structure also dampened the variance in overall SSB (the mean portfolio effect across fishing mortality scenarios was 40%) compared with the single-stock model (no portfolio effect), demonstrating that independence in recruitment between substocks resulted in an increased stability at a regional level. As expected, the productivity of both single-stock and substock models decreased with increasing fishing pressure, the rate of decrease being approximately the same for the two forms of the model (substock slope = −2.6, single-stock slope = −2.7; Figure 3). The MSY of the substock model was 15 664 t and of the single-stock model was 11 249 t (Figure 3). An implicit assumption of the single-stock model is that the distribution of fishing effort is homogenous ($F_{MSY} = 0.3$), whereas in the substock model, the fishing mortality at MSY varied based on the productivity of the substock. Therefore, by considering spatial
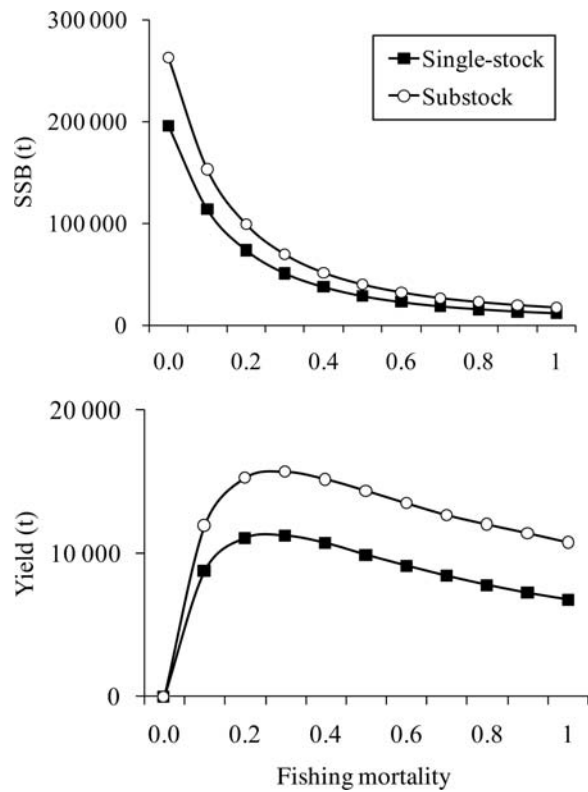
Figure 3. Spawning-stock biomass and yield for the single-stock and substock models of Gulf of Maine Atlantic cod across fishing mortality scenarios.

heterogeneity and connectivity within the Gulf of Maine management unit, our simulations suggest that the system can produce a greater yield.

Individual substocks varied in their productivity, with the Ipswich Bay substock the most productive, followed by Massachusetts Bay, and coastal Maine the least productive (Figure 4). The more productive substocks (Ipswich Bay and Massachusetts Bay) were able to sustain greater fishing mortality ($F_{MSY} = 0.3$), compared with the coastal Maine substock ($F_{MSY} = 0.2$; Figure 4). The Ipswich Bay population was less stable than the Massachusetts Bay and coastal Maine substocks (Figure 4). Therefore, although the Ipswich Bay substock was more productive than the Massachusetts Bay substock, the lower stability of the former substock resulted in an equivalent sustainable exploitation rate. Achieving the maximum yield from the substock model relied on spatially explicit differences in fishing effort within the Gulf of Maine.

Overall, the single-stock model considers the stock to be one unit with equal vital rates and complete synchrony in recruitment dynamics. This simplified view of Gulf of Maine cod leads us to underestimate the productivity and potential yield of the system. Spatial differences in productivity and stability impact the sustainability of fishing effort, and suggest that spatial management of fishing pressure could both increase the yield of the fishery and better protect the Gulf of Maine Atlantic cod stock from overexploitation.

Discussion
Simulation models can serve as a tool to integrate information gained from multiple approaches to investigating population
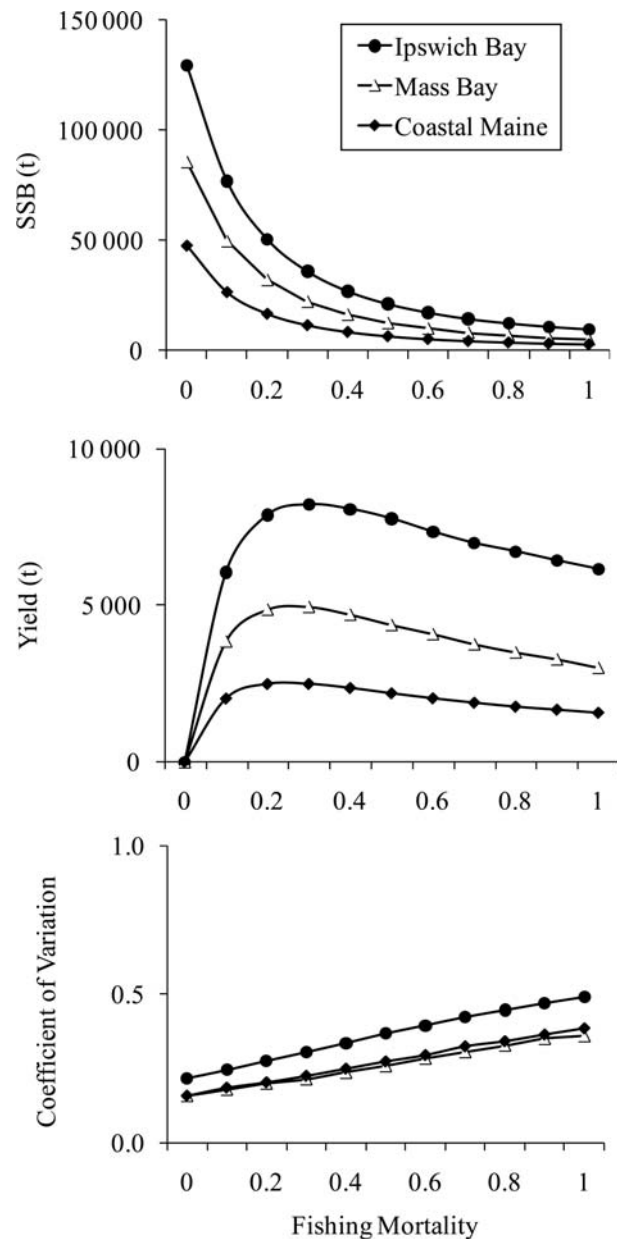

Figure 4. Spawning-stock biomass, yield, and *CV*s for the substocks (Coastal Maine, Ipswich Bay, Massachusetts Bay) of Gulf of Maine Atlantic cod across fishing mortality scenarios.

structure, e.g. genetics, electronic tagging, otolith chemistry, larval dispersal, and life history traits (Cadrin *et al.*, 2005), and permit the testing of hypotheses. The generalized model framework is adaptable to incorporation of a wide variety of different levels of organization, demographics, and dynamics. Additionally, the approach is amenable to consideration of a diversity of questions relevant to our understanding of spatial structure and connectivity, and to conservation and management goals. The case studies described illustrate the diversity of applications as well as the commonalities in dynamics that emerge across systems.

Using simulation modelling to examine three systems of fish populations, we gained a better understanding of the consequences of connectivity between, and structure within, local and regional populations to productivity, stability, resilience to

perturbation, and sustainability with respect to fishing. The relative abundance and extent of independent response to the environment of components were important determinants of system dynamics. Abundant stable components and asynchronous responses of components reduced the variance within the systems. Components with high productivity largely determined the resilience of systems and their ability to sustain fishing pressure. The form, as well as the magnitude, of connectivity between local populations impacted metapopulation dynamics. Increased connectivity between components through straying increased the synchrony of responses to environmental forcing, resulting in the decreased productivity and stability of systems. In contrast, an increased connectivity between components through entrainment decreased the synchrony of responses to environmental forcing, resulting in an increased system stability. This general model framework is easily altered to accommodate system biocomplexity (Hilborn *et al.*, 2003, Ruzzante *et al.*, 2006), making the approach useful for many hypothesis tests that would not be possible in field or laboratory settings.

Spatial modelling can be particularly useful in determining the appropriate spatial scale of management and conservation. Although MSE was not the focus of our study, these simulation frameworks could provide the operating models for MSE and would be a useful extension of the models. Employing a large-scale management strategy when significant spatial variability in productivity exists between local populations can be costly, resulting in potential loss of yield and localized population depletion (Tuckey *et al.*, 2007). In an extreme situation, overfishing of relatively unproductive populations can lead to extirpation (Ricker, 1958), and overfishing of productive populations (also known as source populations) can lead to widespread declines throughout a metapopulation (Kritzer and Sale, 2004). Failure to recognize these features of populations can jeopardize the realization of rebuilding expectations, because rebuilding capacity may be linked to structure within and connectivity between populations (Reich and DeAlteris, 2009). Similar to the results of our Atlantic cod simulation, the analysis by Wilberg *et al.* (2008) of source–sink dynamics of yellow perch (*Perca flavescens*) revealed differences in optimal harvest strategies attributable to spatial differences in the productivity and growth patterns of yellow perch among areas. Hence, we emphasize the importance of documenting spatial differences in vital rates, recruitment dynamics, and connectivity of populations with respect to the distribution of fishing effort and the management of a fishery. The results of these simulations are expected to reflect the systems of inference, because they are based on observed vital rates (growth, maturity, mortality, and recruitment), as well as information on connectivity (from natural or artificial tags) and the extent of reproductive isolation (from genetics). For example, our Gulf of Maine cod simulations conform more to the observed productivity of the resource than the more hypothetical simulations specified by Reich and DeAlteris (2009). Therefore, because of the realism incorporated in these models, their future modification to examine harvest policy performance will be less heuristic and more relevant to management.

Conservation efforts made at an inappropriate spatial scale can be ineffective and potentially lead to continued overfishing of unique subpopulations. Additionally, understanding how spatial scales affect population-level processes is particularly relevant to the designation of marine-protected areas (MPAs). Therefore, simulation modelling can increase our understanding of the dynamics of fish populations and inform better spatial fisheries management, the development of MPAs, habitat restoration, and conservation, by synthesizing the available field information and testing hypotheses for processes that are difficult to observe directly.

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References

Andrews, J. M., Gurney, W. S. C., Heath, M. R., Gallego, A., O'Brien, C. M., Darby, C., and Tyldesley, G. 2006. Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1027–1048.

Barrowman, N. J., and Myers, R. A. 2000. Still more spawner–recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic. Sciences, 57: 665–676.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fisheries Investigations London Series 2. 19. UK Ministry of Agriculture and Fisheries, London. 536 pp.

Breton, T. 2008. Spawning stock identification of Atlantic cod (*Gadus morhua*) in US waters using Pan I and microsatellite genetic markers. MSc thesis, University of New Hampshire. 75 pp.

Butterworth, D. S., and Punt, A. E. 1999. Experiences in the evaluation and implementation of management procedures. ICES Journal of Marine Science, 56: 985–998.

Cadrin, S. X., Friedland, K. D., and Waldman, J. (Eds) 2005. Stock Identification Methods: Applications in Fishery Science. Elsevier Academic Press, Burlington, MA. 719 pp.

Cadrin, S. X., and Secor, D. H. 2009. Accounting for spatial population structure in stock assessment: past, present and future. *In* The Future of Fishery Science in North America, pp. 405–425. Ed. by R. J. Beamish, and B. J. Rothschild. Springer, Dordrecht. 736 pp.

Corten, A. 2002. The role of "conservatism" in herring migrations. Reviews in Fish Biology and Fisheries, 11: 339–361.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, New York. 313 pp.

Heath, M. R., Kunzlik, P. A., Gallego, A., Holmes, S. J., and Wright, P. J. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod – the dynamic consequences of natal fidelity. Fisheries Research, 93: 92–116.

Hilborn, R., Quinn, T. P., Schindler, D. E., and Rogers, D. E. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the USA, 100: 6564–6568.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 20: 1–228.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fisheries Science, 41: 53–70.

Howell, W. H., Morin, M., Rennels, N., and Goethel, D. 2008. Residency of adult Atlantic cod (*Gadus morhua*) in the western Gulf of Maine. Fisheries Research, 91: 123–132.

ICES. 2008. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG), 11–19 March 2008. ICES Document CM 2008/ACOM: 02. 601 pp.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries, 3: 348–365.

Kell, L. T., Dickey-Collas, M., Hintzen, N. T., Nash, R. D. M., Pilling, G. M., and Roel, B. A. 2009. Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring. ICES Journal of Marine Science, 66: 1776–1783.

Kerr, L. A., Cadrin, S. X., and Secor, D. H. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecological Applications, 20: 497–507.

Kritzer, J. P., and Sale, P. F. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries, 5: 131–140.

Mansueti, R. J. 1961. Movements, reproduction, and mortality of the white perch, *Roccus americanus*, in the Patuxent Estuary, Maryland. Chesapeake Science, 2: 142–205.

McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries, 7: 297–329.

Peck, S. L. 2004. Simulation as experiment: a philosophical reassessment for biological modeling. Trends in Ecology and Evolution, 19: 530–534.

Porch, C. E., Turner, S. C., and Powers, J. E. 2000. Virtual population analyses of Atlantic bluefin tuna with alternative models of transatlantic migration: 1970–1997. ICCAT SCRS/00/98, Madrid, Spain. 23 pp.

Reich, D. A., and Dealteris, J. T. 2009. A simulation study of the effects of spatially complex population structure for Gulf of Maine Atlantic cod. North American Journal of Fisheries Management, 29: 116–126.

Ricker, W. E. 1958. Maximum sustainable yields from fluctuating environments and mixed stocks. Journal of the Fisheries Research Board of Canada, 15: 991–1006.

Ruzzante, D. E., Mariani, S., Bekkevold, D., André, C., Mosegaard, H., Clausen, L. A., Dahlgren, T. G., *et al.* 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. Proceedings of the Royal Society of London, B – Biological Sciences, 273: 1459–1464.

Secor, D. H., and Kerr, L. A. 2009. Lexicon of life cycle diversity in diadromous and other fishes. *In* Challenges for Diadromous Fishes in a Dynamic Global Environment, pp. 537–556. Ed. by A. J. Haro, K.

L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, *et al.* American Fisheries Society Symposium, 69. 943 pp.

Secor, D. H., Kerr, L. A., and Cadrin, S. X. 2009. Connectivity effects on productivity, stability, and persistence in a herring metapopulation model. ICES Journal of Marine Science, 66: 1726–1732.

Sinclair, M. 1988. Marine populations. An essay on population regulation and speciation. Washington Sea Grant Program, Seattle. 252 pp.

Smith, S. J., Hunt, J. J., and Rivard, D. (Eds) 1993. Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences, 120. 442 pp.

Tallack, S. (Compiling Ed.) 2009. Proceedings from a workshop to identify future research priorities for cod tagging in the Gulf of Maine, 12 February 2009. US Department of Commerce, Northeast Fisheries Science Center Reference Document 09–09. 76 pp. (Available from National Marine Fisheries Service, Woods Hole, MA, or online at http://www.nefsc.noaa.gov/nefsc/publications/).

Tuckey, T., Yochum, N., Hoenig, J., Lucy, J., and Cimino, J. 2007. Evaluating localized vs. large-scale management: the example of tautog in Virginia. Fisheries, 32: 21–28.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics, 20: 171–197.

Wilberg, M. J., Irwin, B. J., Jones, M. L., and Bence, J. R. 2008. Effects of source-sink dynamics on harvest policy performance for yellow perch in southern Lake Michigan. Fisheries Research, 94: 282–289.

Wirgin, I., Kovach, A. I., Maceda, L., Roy, N. K., Waldman, J., and Berlinsky, D. L. 2007. Stock identification of Atlantic cod in US waters using microsatellite and single nucleotide polymorphism DNA analysis. Transactions of the American Fisheries Society, 136: 375–391.

Working Group on Re-Evaluation of Biological Reference Points for New England Groundfish. 2002. Re-evaluation of biological reference points for New England groundfish. Northeast Fisheries Science Center. Reference Document 02–04. 395 pp.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics, 15: 323–354.