



## Contribution to the Symposium: ‘Gadoid Fisheries: The Ecology of Management and Rebuilding’ Original Article

# Consequences of a mismatch between biological and management units on our perception of Atlantic cod off New England

Lisa A. Kerr<sup>1\*</sup>, Steven X. Cadrin<sup>2</sup>, and Adrienne I. Kovach<sup>3</sup>

<sup>1</sup>Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA

<sup>2</sup>School for Marine Science and Technology, University of Massachusetts Dartmouth, 200 Mill Road, Suite 325, Fairhaven, MA 02719, USA

<sup>3</sup>Department of Natural Resources and the Environment, University of New Hampshire, 46 College Road, Durham, NH 03824, USA

\*Corresponding author: tel: +1 207 228 1639; fax: +1 207 773 8672; e-mail: [lkerr@gmri.org](mailto:lkerr@gmri.org)

Kerr, L. A., Cadrin, S. X., and Kovach, A. I. Consequences of a mismatch between biological and management units on our perception of Atlantic cod off New England. – ICES Journal of Marine Science, 71: 1366–1381.

Received 15 January 2014; revised 27 May 2014; accepted 28 May 2014; advance access publication 6 July 2014.

A mismatch between the scale of fishery management units and biological population structure can potentially result in a misperception of the productivity and sustainable yield of fish stocks. We used simulation modelling as a tool to compare the perception of productivity, stability, and sustainability of Atlantic cod (*Gadus morhua*) off New England from an operating model based on the current US management units to a model that more closely reflects the biological complexity of the resource. Two age-structured models were compared: (i) the management unit model, wherein cod were grouped based on the current spatially defined US management areas (Gulf of Maine and Georges Bank), and (ii) the biological unit model, consisting of three genetically defined population components (northern spring spawning, southern winter/spring spawning, and eastern Georges Bank spring-spawning groups). Overall, the regional productivity and maximum sustainable yield of the biological unit model was lower compared with the management unit model. The biological unit model also provided insights on the distribution of productivity in the region, with southern and northern spawning groups being the dominant contributors to the regional spawning–stock biomass and yield and the eastern Georges Bank spawning group being the minority contributor at low to intermediate levels of fishing mortality. The comparison of models revealed that the perception of Atlantic cod derived from the management unit model was of a resource that is more resilient to fishing mortality and not as susceptible to “collapse” as indicated by the biological unit model. For Atlantic cod, one of the main risks of ignoring population structure appears the potential for overexploitation of segments of the population. Consideration of population structure of cod changed our perception of the magnitude and distribution of productivity in the region, suggesting that expectations of sustainable yield of cod in US waters should be reconsidered.

**Keywords:** Atlantic cod, biocomplexity, simulation modelling, stock structure.

## Introduction

Inconsistencies between the scale of biological population structure and the fishery management units of fish species are increasingly recognized, with more research investments for understanding stock structure and advances in stock identification techniques (Reiss *et al.*, 2009). Management units composed of multiple biological populations can be difficult to assess with accuracy. Lumping populations into stock units can result in misperceptions of the magnitude and distribution of productivity and conceal declines of more vulnerable populations (Frank and Brickman, 2000; Sterner, 2007; Kell *et al.*, 2009; Ying *et al.*, 2011). Conversely, management units that are only a portion of a self-sustaining

population can present problems with accurate understanding of stock dynamics and detecting linkages between stock dynamics and the environment (Frisk *et al.*, 2008).

Furthermore, implementing sustainable fishery management can be challenging when the scale of management action does not match the scale of biological processes (Begg *et al.*, 1999a). For example, managing a “mixed stock” consisting of populations that differ in their productivity and dynamics as a single stock can result in underfishing more productive stocks and overfishing less productive stocks (Ricker, 1958). In extreme cases, failure to consider complex population structure in fishery management may result in a loss of unique spawning components (Stephenson,

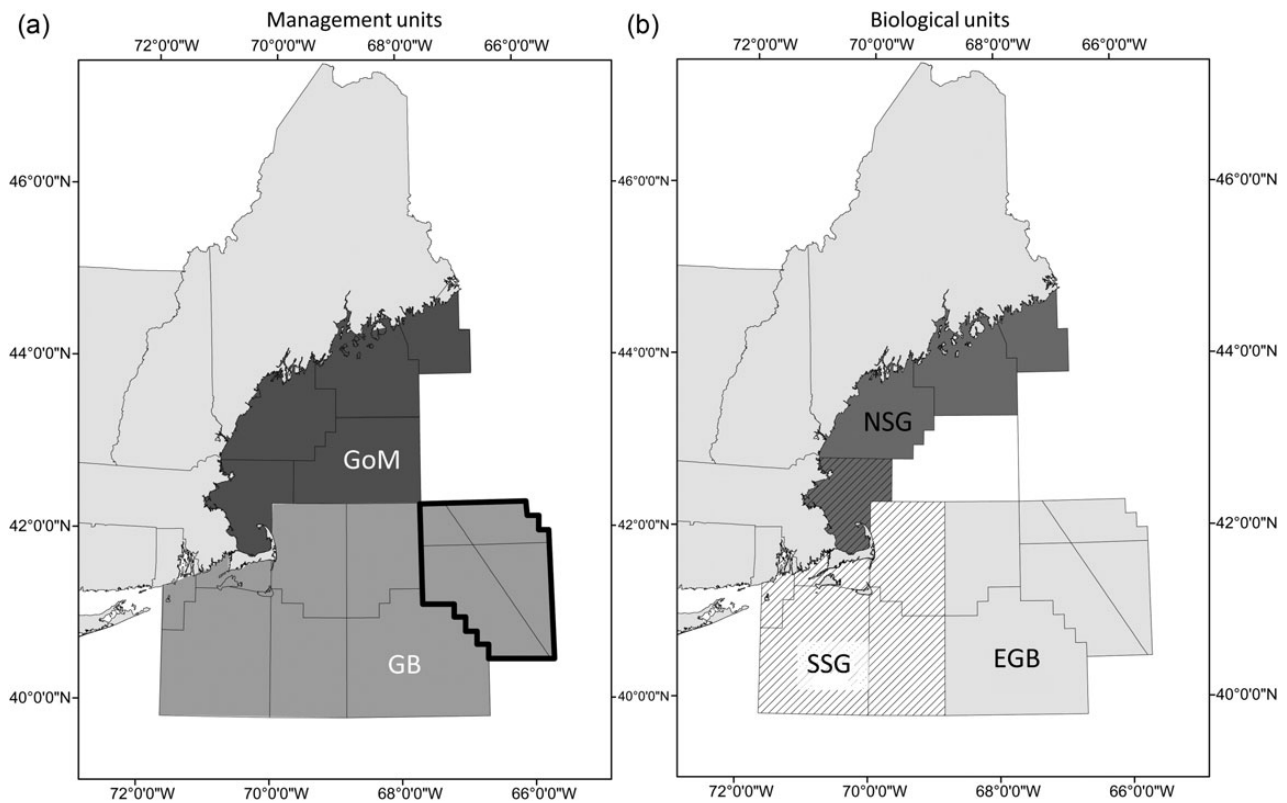
1999; Smedbol and Stephenson, 2001). The loss of historical spawning components has been documented for many commercially important fish stocks, including Atlantic salmon (*Salmo salar*; Parrish *et al.*, 1998), Atlantic herring (*Clupea harengus*; Stephenson, 1997), and Atlantic cod (*Gadus morhua*; Ames, 2004). Unique spawning components can exhibit unique responses to the environment (aka response diversity), and this response diversity has been integrally linked to some species' persistence (Hilborn *et al.*, 2003; Kerr *et al.*, 2010a, b). Preserving the response diversity of spawning components has been demonstrated to contribute to the sustainability and persistence of regional fish populations, such as sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay Alaska (Hilborn *et al.*, 2003). Mismatches between the population structure of a fishery resource and spatial designation of management units can potentially prevent accurate assessment of population productivity and dynamics and undermine the effectiveness of management action.

Consideration of stock biocomplexity may require reevaluation of the spatial and temporal scale of fishery management units or additional management tools to protect unique populations (e.g. spawning closures). Accounting for complex population structure will place greater demands on our monitoring, assessment, and management processes (Stephenson, 1999; Frank and Brickman, 2001). However, the "precautionary approach" to fishery management (i) dictates that we err on the side of caution when there is uncertainty regarding the consequences of exploitation of a resource and (ii) justifies conservation of population components within a stock (Hammer and Zimmermann, 2005). Recognition of biological complexity and implementation of management at the appropriate spatial or temporal scale will likely enhance the sustainability of the resource and, in some cases, may increase the long-term yield from the fishery. In situations of a known mismatch between population structure and designation of management units for a species, it is imperative that we examine potential ecological and fishery impacts of ignoring biological complexity in management. Simulation modelling is a useful framework in which to evaluate the consequences of aggregating data across multiple populations into a stock unit or explicitly considering underlying complex population structure (Frank and Brickman, 2000; Sterner, 2007; Kell *et al.*, 2009; Kerr *et al.*, 2010a, b; Kerr and Goethel, 2014).

A mismatch between biological population structure and spatially defined stock units has been suggested for cod in Canadian waters (Sterner, 2007) and off the Atlantic coast of the United States (Kovach *et al.*, 2010). Several studies have explored how the perception of cod stocks may change when underlying complex population structure is considered or when regarded as a unit stock using simulation modelling (Frank and Brickman, 2000; Fu and Fanning, 2004; Sterner, 2007; Reich and DeAlteris, 2009; Kerr *et al.*, 2010a). Simulation modelling by Frank and Brickman (2000) revealed that aggregation of data across substocks of Atlantic cod can mask underlying dynamics and prevent detection of depletion of substocks to critical levels. Owing to the loss of substock richness that can occur under the assumption of a single unit stock, relaxation of fishing pressure will not necessarily result in the expected level of stock recovery (Frank and Brickman, 2000). Frank and Brickman (2000) hypothesized that this may be why, despite implementation of fishing moratoria for Canadian cod stocks, many collapsed stocks have failed to recover. Further, simulation modelling by Sterner (2007) also suggested that local extirpations may explain the phenomenon of stock collapse and slow recovery of Canadian cod fisheries. Sterner (2007) found that failure to identify

substock diversity can lead to overestimation of the growth and harvest potential of a stock, and management based on this information can lead to extirpation of local populations with high catchability. Fu and Fanning (2004) used simulation modelling to explore the impact of lumping or splitting inshore and offshore substocks of Atlantic cod off eastern Nova Scotia. Simulations indicated that separate management prevented substock collapse, whereas combined management tended to result in overfishing the more vulnerable stock. Reich and DeAlteris (2009) used simulation modelling to explore the theoretical consequences of ignoring historical fine-scale structuring of Atlantic cod in the Gulf of Maine on estimates of spawning-stock biomass (SSB), yield, and recruitment. Simulations revealed that grouping spawning aggregations into one stock could lead to overestimation of SSB, recruitment, and yield of the cod resource (Reich and DeAlteris, 2009). Kerr *et al.* (2010a) developed empirically based simulation models to explore the consequences of considering Atlantic cod within the Gulf of Maine to be a single unit or three spawning groups (Massachusetts Bay, Ipswich Bay, coastal Maine). In this case, consideration of Gulf of Maine cod as a single unit stock led to underestimation of the productivity and potential yield of the system. Given the current overfished status of Atlantic cod in US waters (NEFSC, 2013), it is relevant to broadly consider the appropriateness of the management unit structure for cod in US waters and whether refinement of this structure might engender improved fishery management.

Since 1972, Atlantic cod in the US waters of the Northwest Atlantic have been assessed and managed as two unit stocks: (i) Gulf of Maine, and (ii) Georges Bank. The Gulf of Maine stock management area includes inshore waters off the coasts of Massachusetts, New Hampshire, and Maine and offshore waters in the central Gulf of Maine (Figure 1a). The Georges Bank stock management area includes southern New England and eastern Georges Bank waters, and the transboundary US/Canadian management area (Figure 1a). Fish within these management units are considered to be a single unit with one shared fate (i.e. the "unit stock" concept; Cadrin and Secor, 2009). However, the synthesis of information from multiple stock identification methods, including genetic, tagging, and growth analyses, applied to Atlantic cod in US waters has revealed a new paradigm of cod population structure (Begg *et al.*, 1999b; Wirgen *et al.*, 2007; Tallack, 2009a; Kovach *et al.*, 2010; Annala, 2012; Zemeckis *et al.*, 2014a). Based on microsatellite and single-nucleotide polymorphism markers, Kovach *et al.* (2010) identified three major groups that were genetically differentiated with some ongoing gene flow: (i) northern spring-spawning complex, which spawns in coastal Gulf of Maine waters from Massachusetts Bay to Bigelow Bight (and historically along the coast of Maine) in spring; (ii) southern winter/spring-spawning complex, which spawns within the inshore Gulf of Maine in winter and at different offshore locations and seasons within the Gulf of Maine and southern New England waters; and (iii) a population that spawns on northeast Georges Bank in late winter/early spring (Figure 1b). The identification of significant genetic variation among temporally and spatially defined spawning groups of cod challenges the appropriateness and effectiveness of the current spatially defined management units of Atlantic cod in US waters. Under the current spatially defined stock units, more than one spawning population is included in a management unit. The Gulf of Maine stock unit includes the northern spawning group and a portion of the southern spawning group, and the Georges Bank stock unit includes the eastern Georges Bank and a portion of the southern spawning group (Figure 1a and b).



**Figure 1.** Map of the current spatially defined US management areas (a), including the Gulf of Maine (GoM) and Georges Bank (GB) management units (NEFSC, 2012). Statistical areas are outlined within stock boundaries. The eastern portion of Georges Bank (outlined in bold) is managed jointly by the United States and Canada as a transboundary resource. Map of statistical areas from which data were drawn to represent biological units (b), including the northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups. There is spatial overlap, but seasonal separation in spawning time of the northern and southern spawning groups. Thus, data from the overlap area for these groups were drawn from different seasons (spring vs. autumn) representative of the groups' spawning time.

The goal of our study was to contrast the newly emerged paradigm of Atlantic cod population structure in US waters with a view of the resource based on the current management unit structure. We specifically contrasted the perception of productivity, stability, and sustainability of Atlantic cod in the Northwest Atlantic from a population model (also termed an “operating” model in the context of simulation) based on the current US management units to a model that more closely reflects the biological complexity of the resource revealed in recent genetics and tagging studies (Wirgin *et al.*, 2007; Tallack, 2009a; Kovach *et al.*, 2010). We hypothesized that a model that more accurately characterizes spawning groups and their connectivity would revise our expectations of the productivity, stability, and sustainability of the regional cod resource.

## Methods

### Model framework and data sources

The Atlantic cod resource off New England was modelled using an age-structured framework for age 1–9+ fish, where 9+ is a group containing all fish age 9 and older. Two operating models were conceived as a means of testing our hypothesis. Models were written in the R statistical programming environment (R Development Core Team, 2012). In one model, termed the “management unit” model, cod were defined according to the current US management areas: (i) Gulf of Maine, and (ii) Georges Bank (Figure 1a). This

operating model was designed to reflect the perception of Atlantic cod stock structure and demography (stock–recruit parameters, vital rates, and recruitment indices) under the current stock boundary paradigm. Parameters were derived from the 2012 stock assessments of Gulf of Maine and Georges Bank cod conducted by the Northeast Fisheries Science Center (NEFSC; (Tables 1 and 2, Figure 2).

The alternative operating model, termed the “biological unit” model, was structured to reflect the new paradigm of Atlantic cod population structure off New England informed by genetic, tagging, and growth analyses (Begg *et al.*, 1999b; Wirgin *et al.*, 2007; Tallack, 2009a; Kovach *et al.*, 2010). This model consisted of three population components: (i) northern spawning group, (ii) southern spawning group, and (iii) eastern Georges Bank spawning group (Figure 1b). Sources of data used to parameterize the biological unit model included fish collections made in the NEFSC stratified random bottom trawl survey (1982–2012) and Massachusetts Department of Marine Fisheries (MDMF) inshore bottom trawl survey (2000–2008, Table 1). These surveys include information on cod catch in number and weight per tow and fish length. Age and maturity stage are available for a subsample of fish from these trawl surveys. The data used to estimate vital rates, recruitment indices, and recruitment variability of each spawning group were selected using GIS software (ArcGIS, Version 9.3) according to the spatial and the temporal domains described in Table 1.

**Table 1.** Summary of the data and data sources used to estimate vital rates and recruitment indices for management and biological units.

<b>Model</b>	<b>Components</b>	<b>Vital rates</b>	<b>Recruitment estimates and indices</b>
Management unit model	Gulf of Maine stock unit Georges Bank stock unit	NEFSC stock assessment (NEFSC, 2012)	NEFSC stock assessment (NEFSC, 2012)
Biological unit model			
Northern spawning group	Massachusetts Bay spring-spawning component Ipswich Bay spring-spawning component	NEFSC and MDMF spring trawl survey observations in statistical area 514 (2008–2012)	NEFSC spring trawl survey observations in statistical areas 511, 512, 513, 514 (1982–2012)
Southern spawning group	Coastal Maine spring-spawning component Ipswich Bay winter-spawning component Massachusetts Bay winter-spawning component Jeffery's Ledge winter-spawning component Stellwagen Bank winter/spring-spawning component Nantucket Shoals winter/spring-spawning component Cox Ledge winter/spring-spawning component	NEFSC spring trawl survey observations in statistical areas 511, 512, 513 (2008–2012) NEFSC autumn trawl survey observations in statistical area 514 (2008–2012) NEFSC and MDMF spring trawl survey observations in statistical areas 521, 526, 537, 538 (2008–2012)	NEFSC spring trawl survey observations in statistical areas 521, 526, 537, 538 (1982–2012)
Eastern Georges Bank spawning group	Eastern Georges Bank spring-spawning component	NEFSC spring trawl survey observations in statistical areas 522, 525, 551, 552, 561, 562 (2008–2012)	NEFSC spring trawl survey observations in statistical areas 522, 525, 551, 552, 561, 562 (1982–2012)

See Figure 1 to view spatial structure of model.

**Table 2.** Input parameters for age-structured simulation models of Atlantic cod in US waters; parameters of the management unit model (Gulf of Maine (GoM) and Georges Bank (GB) management units) were informed by the most recent stock assessment (NEFSC, 2012) and parameters of the biological unit model [northern spawning (NSG), southern spawning (SSG), and eastern Georges Bank (EGB) spawning groups] were independently estimated.

Parameter type	Parameter	Parameter definition	Biological unit model			Management unit model	
			NSG	SSG	EGB	GoM	GB
Mortality	$M$	Natural mortality	0.2	0.2	0.2	0.2	0.2
	$F$	Fishing mortality	0–1	0–1	0–1	0–1	0–1
Stock–recruit model	$\alpha$	Recruits per spawner at low stock size	0.35	1.2	0.14	0.7	0.38
	$\beta$	Density-dependent parameter	1.40E–05	2.82E–05	1.47E–05	2.98E–05	7.07E–06
	$R_{max}$	Maximum expected recruitment	9 316 829	15 601 140	3 629 466	8 643 095	19 904 340
	$S_{max}(t)$	Stock size that produces maximum recruitment	71 484	35 458	68 158	33 581	141 519
von Bertalanffy growth model	$L_{\infty}$	Asymptote (cm)	131.15	110.98	86.55		
	$k$ (year <sup>-1</sup> )	Rate at which the growth model approaches the asymptote	0.12	0.17	0.29		
	$a_0$	Length-at-age 0	–0.35	–0.65	–0.33		
Length–weight relationship (kg)	$a$	Length–weight parameter	4.05E–06	3.95E–06	1.19E–05		
	$b$	Length–weight parameter	3.21	3.24	2.93		
Maturity–length relationship	$A$	Maturity ogive parameter	–5.06	–4.03	–5.61		
	$B$	Maturity ogive parameter	1.65	1.80	2.52		

The data sources (NEFSC and MDMF trawl surveys) that informed life history parameters of management and biological unit models were the same. However, by design, there were differences in the area from which data were drawn to estimate parameters (Figure 1a and b). The timing and location of the selected data encompassed known spawning locations and timing for these populations, ensuring a high likelihood that the fish sampled were representative of the respective populations instead of a “mixed stock”. The spatial extent of spawning groups was delineated in accordance with information from several studies examining cod stock structure (Begg et al., 1999b; O’Brien et al., 2005; Tallack, 2009b; Kovach et al., 2010). The only difference in the spatial domain from which data were selected for the two models was that statistical area 515 (central Gulf of Maine) was excluded from the characterization of biological units and is included in the Gulf of Maine management unit. We hypothesized that statistical area 515 is likely to be an area of spatial overlap of populations or may even include a small resident population (Cashes Ledge; Sherwood and Grabowski, 2010). It must be emphasized that differences in the spatial extent of the management and biological unit models do not directly impact estimates of regional productivity; this point is described in more detail below.

**Management unit model**

Recruitment ( $R_{i,t}$ ), the abundance of age 1 fish in stock  $i$  at time  $t$  was calculated using a Ricker stock–recruit relationship:

$$R_{i,t} = \alpha_i S_{i,t} e^{-\beta_i S_i} e^{\varepsilon_i}, \tag{1}$$

where  $\alpha_i$  is the recruits per spawner at low stock size (slope of curve near the origin),  $\beta_i$  the density-dependent parameter, and  $S_i$  the SSB of stock  $i$ . The modelling of the error term ( $\varepsilon_i$ ) is described in detail below. Ricker stock–recruit models were fit to estimates of recruitment and SSB from the most recent stock assessments for the Gulf of Maine and Georges Bank cod management units (NEFSC, 2012) using a maximum likelihood approach. The Ricker model was chosen over a Beverton–Holt model based on model selection using the Akaike information criterion (AIC).

The parameters of the Ricker curve can also be expressed in terms of the curve’s maximum point at  $R_{max}$ , the maximum expected recruitment, and  $S_{max}$ , the spawner biomass when recruitment reaches its maximum (Quinn and Deriso, 1999). The peak for stock units was estimated using:

$$(R_{max_i}, S_{max_i}) = \left( \frac{\alpha_i}{\beta_i e^1}, \frac{1}{\beta_i} \right). \tag{2}$$

The sum of  $R_{max_i}$  and  $S_{max_i}$  estimates of Gulf of Maine and Georges Bank management units were used to characterize the expected productivity of Atlantic cod at the regional scale ( $R_{max_R}$  and  $S_{max_R}$ ) for both management and biological unit models (described in further detail below).

Abundance-at-age for ages 2–8 was calculated:

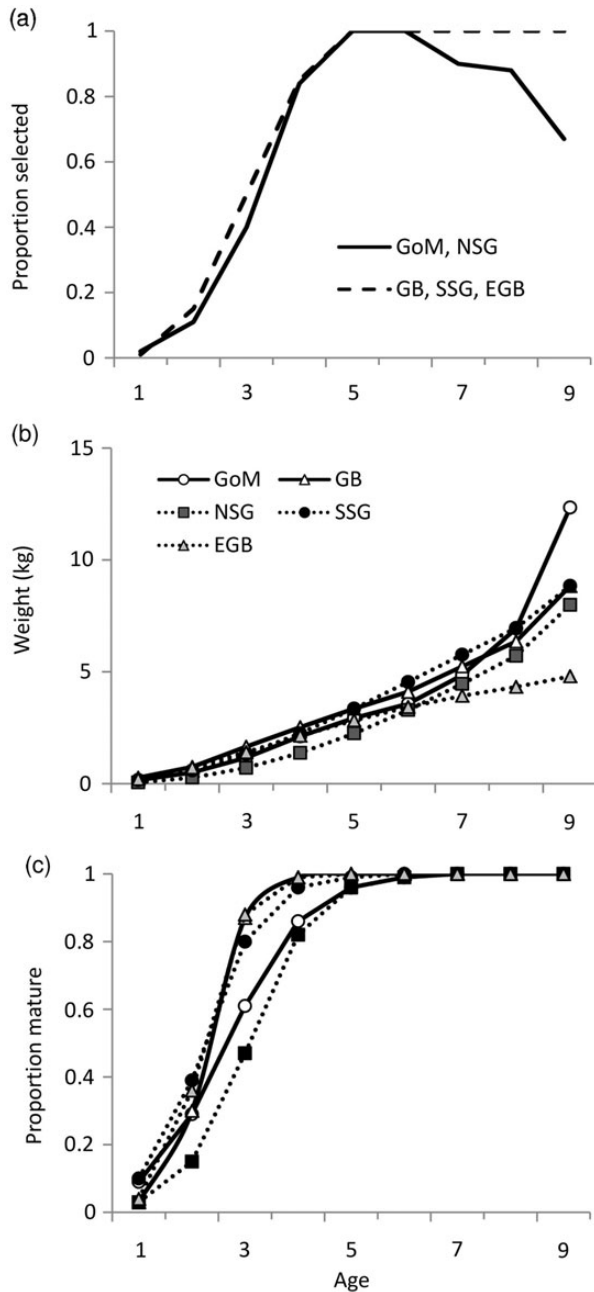
$$N_{i,a,t} = N_{i,a-1,t-1} e^{-[M+F(S_{i,a-1})]}, \tag{3}$$

where  $N_{i,a,t}$  is the age-specific abundance of stock  $i$  at time  $t$ ,  $M$  the natural mortality,  $F$  the fishing mortality, and  $s_{i,a}$  the age-specific selectivity into the fishery for stock  $i$ . Information on natural mortality and age-specific selectivity into the fishery was taken directly from the 2012 stock assessment for the Gulf of Maine and Georges Bank stocks (NEFSC, 2012, Table 2). Abundance of age 9+ fish was calculated as:

$$N_{i,a,t} = N_{i,a-1,t-1} e^{-[M+F(S_{i,a-1})]} + N_{i,a,t-1} e^{-[M+F(S_{i,a})]}. \tag{4}$$

SSB at time  $t$  was calculated as a function of the number of fish at age, weight-at-age, and maturity-at-age of Atlantic cod in each stock  $i$  [The calculation of number of fish at age was adjusted for the fraction of total annual mortality ( $t_i$ ) experienced by stock  $i$  from the start of the calendar year to the assumed time of spawning. The assumed spawning date for the Georges Bank stock is 1 January and is 1 April for the Gulf of Maine stock (NEFSC, 2012)]:

$$S_{i,t} = \sum_{a=1}^{a=9+} N_{i,a,t} e^{-[M+F(S_{i,a})]t_i} W_{i,a} P_{i,a}, \tag{5}$$



**Figure 2.** Age-specific recruitment to the fishery (a), weight (b), and maturity (c) data for management [Gulf of Maine (GoM) and Georges Bank (GB)] and biological units [northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups] of Atlantic cod off New England.

where  $W_{i,a}$  is the average spawning weight (t) of an age  $a$  fish and  $P_{i,a}$  the average proportion of age  $a$  fish that are mature in stock  $i$ .

Yield ( $Y_{i,t}$ ) was calculated as:

$$Y_{i,t} = \sum_{a=1}^{a=9+} N_{i,a,t} \frac{F s_{i,a}}{F s_{i,a} + M} [1 - e^{-(F s_{i,a} + M)}] W_{i,a}, \quad (6)$$

$W_{i,a}$  was consistently used in the calculation of yield across models, although the various fisheries do not entirely take place at spawning

time. Catch weights are available for management units, but we do not have information to inform catch weight of the spawning groups. Using stock weights may pose a consistent and small bias, although a comparison between spawning–stock weight and catch weight of cod for GoM and GB stock units showed negligible differences (NEFSC, 2012).

**Biological unit model**

Recruitment or abundance-at-age 1 ( $R_{i,t}$ ) was calculated using a Ricker stock–recruit relationship for each spawning group  $i$  [Equation (1)]. The sum of  $R_{\max,i}$  and  $S_{\max,i}$  values for Gulf of Maine and Georges Bank management units was to constrain the total expected regional recruitment ( $R_{\max,R}$ ) and associated spawner biomass ( $S_{\max,R}$ ) for the biological units model. The regional values were apportioned to individual biological units ( $i$ ) based on the relative magnitude of indices of recruitment ( $I$ , mean number age 1 fish per tow) and SSB ( $J$ , average stock biomass in kg per tow) for each spawning group  $i$ .

$$r_{\max,i} = \frac{I_i}{\sum I_i} R_{\max,R} \quad s_{\max,i} = \frac{J_i}{\sum J_i} S_{\max,R}. \quad (7)$$

SSB and recruitment indices for each spawning group were developed based on catch per unit effort (cpue) of fish in the NEFSC trawl survey (1982–2011). Using an age–length key specific to each spawning group, length frequency data from survey data representative of each spawning group were converted into age frequency, and the number of age 1 fish per tow (cpue) was calculated and averaged for each year. Ricker stock–recruit parameters ( $\alpha_i, \beta_i$ ) were calculated from  $r_{\max,i}$  and  $s_{\max,i}$  estimates for each spawning group using Equation (2) (Table 2).

For each spawning group ( $i$ ), abundance-at-age for ages 2–8 was calculated by

$$N_{i,a,t} = (N_{i,a-1,t-1} \tau_{i,i} + N_{j,a-1,t-1} \tau_{j,i} + N_{k,a-1,t-1} \tau_{k,i}) e^{-[M+F(s_{i,a-1})]}, \quad (8)$$

where  $N_{i,a,t}$  is age-specific abundance of fish of the spawning group of interest,  $N_j$  and  $N_k$  represent spawning groups connected to  $N_i$  through straying, and  $\tau$  the proportional transfer of fish between (or retained within) spawning groups (e.g.  $\tau_{i,i}$  describes the proportion of fish remaining within spawning group  $i$  and  $\tau_{i,j}$  describes the proportion of fish that move from spawning group  $i$  to  $j$ ). Natural mortality ( $M$ ) was assumed to be 0.2, identical with the management unit model. Age-specific selectivity into the fishery ( $s_{i,a}$ ) from the most recent stock assessment for the Gulf of Maine management unit was assumed to be representative for the northern spawning group, and values for the Georges Bank management unit were assumed to be representative for the southern and eastern Georges Bank spawning groups (NEFSC, 2012, Table 2). Abundance-at-age for the age 9+ group was calculated by:

$$N_{i,a,t} = (N_{i,a-1,t-1} \tau_{i,i} + N_{j,a-1,t-1} \tau_{j,i} + N_{k,a-1,t-1} \tau_{k,i}) e^{-[M+F(s_{i,a-1})]} + (N_{i,a,t-1} \tau_{i,i} + N_{j,a,t-1} \tau_{j,i} + N_{k,a,t-1} \tau_{k,i}) e^{-[M+F(s_a)]}. \quad (9)$$

SSB for each spawning group was calculated as a function of the number of fish at age at the time of spawning, weight-at-age, and maturity-at-age of Atlantic cod in each spawning group [Equation

(5)]. The fraction of total annual mortality that occurs from 1 January to the time of spawning ( $t_i$ ) was calculated for each biological unit based on an assigned spawning date informed by peak spawning times for these groups. Time of spawning was assumed to be 1 June for the northern spring-spawning group (based on documented peak spawning during April–July), 1 February for the southern spawning group (based on documented spawning during October–May), and 1 March for the eastern Georges Bank spawning group (based on documented peak spawning during December–May; see review by Zemeckis *et al.*, 2014b, for details on spawning times).

Age-specific weight and proportion mature were estimated for each spawning group using survey data specific to the geographic region and time of spawning for each component of the spawning complex (Tables 1 and 2, Figure 2). Length–weight relationships were used to estimate weight-at-age ( $W_{i,a}$ ) of Atlantic cod:

$$W_{i,a} = a_i L_{i,a}^{b_i}, \tag{10}$$

where  $L_{i,a}$  is the length-at-age,  $a_i$  a proportionality constant, and  $b_i$  the exponent for spawning group  $i$ . Length-at-age for spawning group  $i$  was estimated from the von Bertalanffy growth model:

$$L_{i,a_i} = L_{\text{inf}_i} [1 - e^{-k_i(a-a_{0i})}], \tag{11}$$

where  $L_{\text{inf}_i}$  is the asymptotic size,  $k_i$  defines the rate at which the curve approaches the asymptote, and  $a_{0i}$  the hypothetical age at which the size of the fish is zero. The proportion of fish mature at age ( $P_{i,a}$ ) was determined by fitting a logistic regression to information on the sexual stage of fish collected at the time of capture (Table 2). Fish were classified as I (immature), and sexually mature fish were grouped into five categories: D (developing), R (ripe), U (ripe and running), S (spent), and T (resting; O’Brien *et al.*, 1993). Parameter estimation for biological units was conducted using a maximum likelihood approach to fit data to models.

### Connectivity

#### Management unit model

No connectivity was assumed between management units. This assumption conforms to the current management unit structure for Atlantic cod in US waters which does not account for connectivity between stock units.

#### Biological unit model

In the biological unit model, connectivity between spawning groups was estimated as an annual straying rate based on genetic data (Kovach *et al.*, 2010). The global  $F_{ST}$  value for the neutral genetic markers and estimates of the effective population size of each spawning group were used to approximate the proportion of individuals that stray and remain resident in their natal population. The proportion of migrants exchanged between populations ( $m_i$ ) was estimated following Slatkin (1985):

$$m_i = \frac{(1/F_{ST_i}) - 1}{4N_{e_i}}, \tag{12}$$

where  $N_{e_i}$  is the effective population size, and  $F_{ST_i}$  is a measure of population differentiation for spawning group  $i$  (Wright, 1951).  $N_{e_i}$  was estimated for the three spawning groups based on the neutral genetic markers only using the linkage disequilibrium method in the program LDNe (Waples and Do, 2008). Assuming exchange rates were equal between pairs of spawning groups, we

calculated the proportion of immigrants to ( $I$ ) and emigrants from ( $E$ ) to each spawning group as:

$$\tau_{i,j} = \frac{m_i}{2}, \tag{13}$$

and the proportion of fish that remain resident ( $\tau_{i,i}$ ) within each spawning group as:

$$\tau_{i,i} = 1 - \frac{m_i}{2}. \tag{14}$$

Together, the proportion of fish that remain resident and proportion of fish that move in each spawning group is equal to 1.

### Environmental variability

#### Management unit model

Coefficient of variation (CV) of the annual average number of age 1 recruits per tow from the spring NEFSC survey (1982–2011) was calculated for each management unit (Table 3). Recruitment variability was modelled as a lognormal random variate, such that the mean was zero and the standard deviation approximated as the CV of age 1 recruits for the management unit. There was no correlation in recruitment variability between management units (i.e. they are assumed to be independent units).

#### Biological unit model

Recruitment variability of each biological unit was modelled as a correlated lognormal variate with a mean equal to zero and the standard deviation approximated as the CV of age 1 recruits. The correlation of age 1 recruits between spawning groups was also calculated (Table 3). The annual average number of age 1 recruits per tow from the spatial domain associated with each biological unit (Table 1) from the spring NEFSC survey (1982–2011) was used as an index of recruitment (NEFSC, 2012).

**Table 3.** Coefficient of variation (on diagonal) of recruitment indices and correlation between recruitment indices (on subdiagonal) for Gulf of Maine (GoM) and Georges Bank (GB) management units and the northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups of Atlantic cod in US waters.

Management units	GoM	GB		
GoM	1.44	0.00		
GB	0.00	1.02		
Biological units	NSG	SSG	EGB	
NSG	0.55	–	–	
SSG	0.42	0.61	–	
EGB	0.06	0.31	0.95	

**Table 4.** Estimated proportion ( $\tau$ ) of fish that remain within (on diagonal) and migrate between (on subdiagonal) the northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups of Atlantic cod in US waters.

Biological units	NSG	SSG	EGB	
NSG	0.94	0.03	0.03	
SSG	0.03	0.85	0.12	
EGB	0.03	0.12	0.85	

## Simulations

In both models, we used simulation to evaluate the response of regional productivity, stability, and sustainable yield to changes in fishing pressure. Fishing mortality was held constant within a simulated scenario and increased incrementally across scenarios ranging from  $F = 0$  to 1.0. Stochasticity was introduced to the models as recruitment variability. The simulations were based on historical productivity, but we did not attempt to reproduce productivity in each historical year. A series of 500 stochastic model runs, each conducted over a 150-year period, were performed for each model simulation (only the last 100 years were used in analyses to allow simulations to approach a dynamic equilibrium). The mean productivity (SSB), stability ( $CV_{SSB}$ ), and maximum sustainable yield (MSY) were calculated for each management and biological unit and summed across the two stock units in the management unit model and the three spawning groups in the biological unit model. Additionally, biomass ( $B_{collapse}$ ) and fishing mortality ( $F_{collapse}$ ) reference points associated with “collapse” were calculated for biological and management units. A stock or biological unit was considered to be “collapsed” when the mean SSB was <10% of the mean SSB of the unfished stock.

## Sensitivity analyses

In addition to stochastic simulations, the productivity and sustainable yield of the biological unit and management unit models were also calculated without environmental variability across fishing mortality rates (i.e. models were deterministic). Simulations of the biological unit model were also run without connectivity across fishing mortality rates to evaluate the effect of connectivity on simulated results.

## Results

### Life history parameters

The estimated weight-at-age of cod was most similar between the Georges Bank management unit and the southern spawning group (Figure 2b). Weight-at-age of the Gulf of Maine management unit was also similar to these units, except heavier weight-at-age estimated for age 9+ fish (Figure 2b). The northern spawning group exhibited the lowest weight-at-age across younger age classes, whereas the eastern Georges Bank group exhibited the lowest weight-at-age for older age classes (ages >7). The proportion of fish mature at age was similar among the Georges Bank management unit and southern and eastern Georges Bank spawning groups (Figure 2c). Maturity-at-age of cod was estimated to be similar between the Gulf of Maine management unit and the northern spawning group, but the northern spawning group exhibited a lower proportion of fish mature at young ages (ages ≤3).

Stock–recruit relationships differed among the management and biological units (Table 2, Figure 3a); however, at the regional scale, the number of recruits was similar on average (Figure 3b). Between the two management units, maximum recruitment ( $R_{max_i}$ ) was highest, and the slope of the curve near the origin ( $\alpha_i$ ) was lowest in the Georges Bank management unit model (Table 2, Figure 3a). Among the three biological units, the eastern Georges Bank biological unit had the lowest  $r_{max_i}$  and slope, and the northern spawning complex had the highest values. The CV in recruitment indices was estimated to be higher in both management units compared with the biological units. Among biological units, the eastern Georges Bank unit had the highest CV in recruitment followed by the southern and northern spawning groups (Table 3). The

correlation in recruitment indices was highest between the northern and southern spawning groups, and lowest between the northern and eastern Georges Bank spawning groups (Table 3). Estimated straying rates were highest between the eastern Georges Bank and southern spawning groups (12%), with similar straying rates (3%) estimated between northern and southern spawning groups and northern and eastern Georges Bank spawning groups (Table 4). Estimated straying rates were similar in magnitude to inferences from tagging observations (Tallack, 2009a).

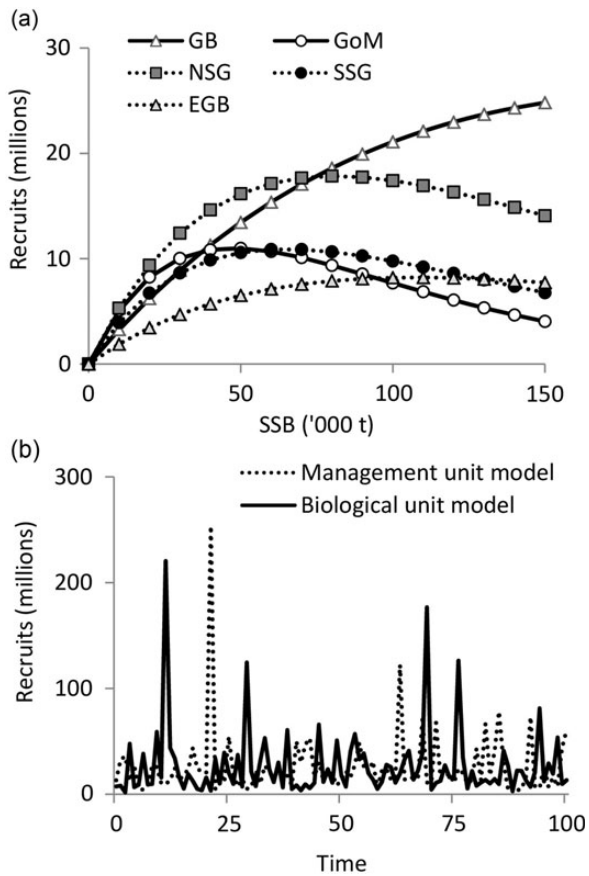
### Differences in the perception of the cod resource

Long-term expectations of SSB from the management unit model indicated that the Atlantic cod resource was greater in SSB than from the biological unit model across levels of fishing mortality (Figure 4a). The expected regional productivity of cod from the management unit model ranged from 661 373 t in the absence of fishing mortality to 35 005 t at the highest fishing mortality rate ( $F = 1.0$ ; Figure 4a). Expected productivity of Atlantic cod from the biological unit model ranged from 498 084 t in the absence of fishing mortality to 2 t at the greatest level of simulated fishing mortality ( $F = 1.0$ ; Figure 4a). Simulation of both the management unit and biological unit models became increasingly unstable with increasing fishing pressure (Figure 4b). The  $CV_{SSB}$  of the aggregate management and biological unit models was lower than that of the individual stocks or spawning groups across fishing mortality rates (Figures 4b, 5b, and 6b). The biological unit model was more stable (i.e. lower  $CV_{SSB}$ ) than the management unit model at low-to-intermediate levels of fishing mortality and less stable at the highest fishing mortality rates (Figure 4b). The estimated MSY of the biological unit model was considerably lower than that of the management unit model (Table 5, Figure 4c). The expected regional yield estimated from the management unit model peaked at 69 073 t at  $F_{msy} = 0.4$ , whereas the biological unit model peaked at 45 213 t at  $F_{msy} = 0.3$  (Table 5, Figure 4c). At the regional scale, the biological unit reached a “collapsed” state at lower fishing mortalities compared with the management unit model (Table 5).

In the management unit model, the Georges Bank stock was the dominant component of regional productivity across most levels of fishing mortality ( $F = 0–0.8$ ), comprising between 60 and 74% of the SSB (Figure 5a). The  $CV_{SSB}$  increased with increasing fishing mortality for both stock units, with the mean values ranging from 0.26 ( $F = 0$ ) to 0.97 ( $F = 1.0$ ) for the Georges Bank stock and 0.40 ( $F = 0$ ) to 0.95 ( $F = 1.0$ ) for the Gulf of Maine stock (Figure 5b). MSY was 69 073 t for the combined management units and 48 511 t ( $F_{msy} = 0.3$ ) and 21 767 t ( $F_{msy} = 0.4$ ) for the Georges Bank and Gulf of Maine stocks, respectively (Figure 5c). As fishing mortality increased, the proportional contribution of the Georges Bank stock to regional yield decreased and the contribution of the Gulf of Maine stock increased. The Gulf of Maine and Georges Bank management units “collapsed” at the highest levels of fishing mortality ( $F = 1.0$  and 0.9, respectively; Table 5).

In the biological unit model, the southern spawning group comprised between 38 and 61% of the regional SSB across fishing mortality scenarios (Figure 6a). The northern spawning group contributed between 6 and 36% of the regional SSB, with the highest relative contribution at the lowest  $F$  (Figure 6a). The eastern Georges Bank spawning group consistently contributed between 27 and 33% of the regional SSB (Figure 6a). Across fishing mortality scenarios, the spawning groups exhibited similar patterns in increasing  $CV_{SSB}$  with increasing levels of fishing mortality, with a marked increase in instability at high  $F$ -values ( $F \geq 0.8$ ,



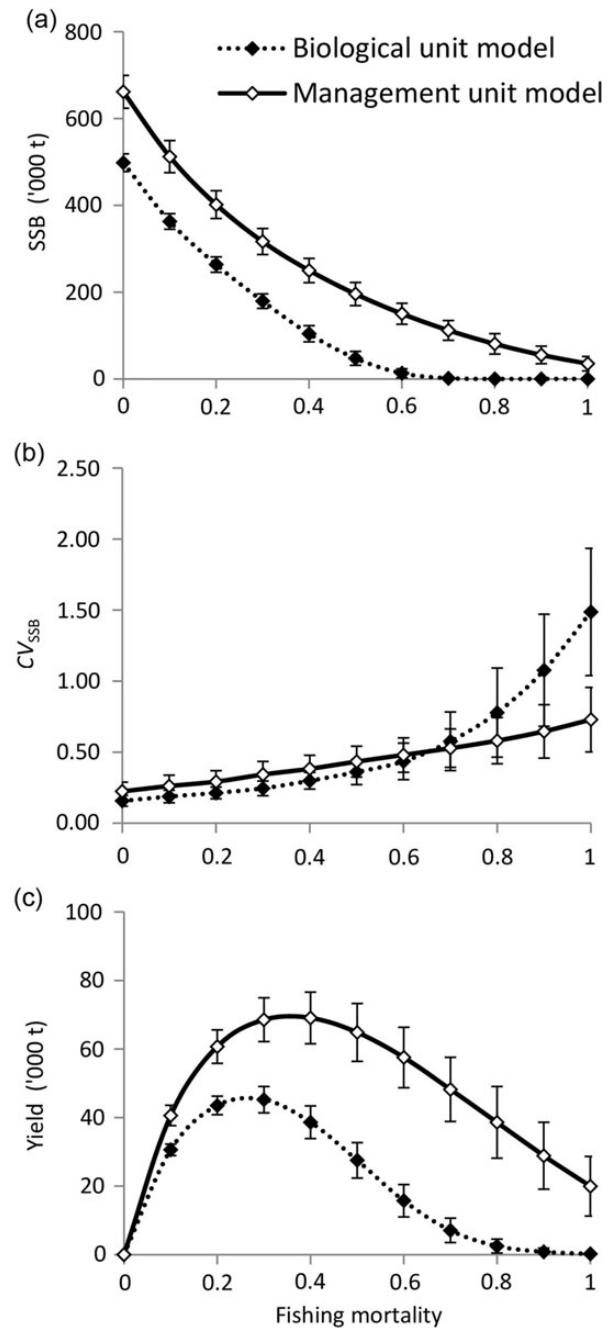


**Figure 3.** Stock–recruit relationships (a) for management [Gulf of Maine (GoM) and Georges Bank (GB)] and biological units [northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups] of Atlantic cod off New England. Number of age 1 recruits (b) simulated in the  $F = 0$  scenario for the biological and management unit models of Atlantic cod off New England.

Figure 6b). The southern and northern spawning groups were the dominant contributors to the regional yield, and the eastern Georges Bank spawning group was the minority contributor to regional yield at low-to-intermediate levels of fishing mortality (Figure 6c). At higher levels of fishing mortality ( $F > 0.5$ ), northern and eastern Georges Bank spawning groups were minority contributors to regional yield compared with the southern spawning group. The MSY of northern and southern spawning groups was similar: 16 133 and 16 865 t ( $F_{msy} = 0.3$ ), respectively, whereas the MSY of eastern Georges Bank group was lower (MSY = 12 216 t,  $F_{msy} = 0.3$ ). The biological units “collapsed” at intermediate levels of fishing mortality ( $F = 0.5–0.6$ , Table 5).

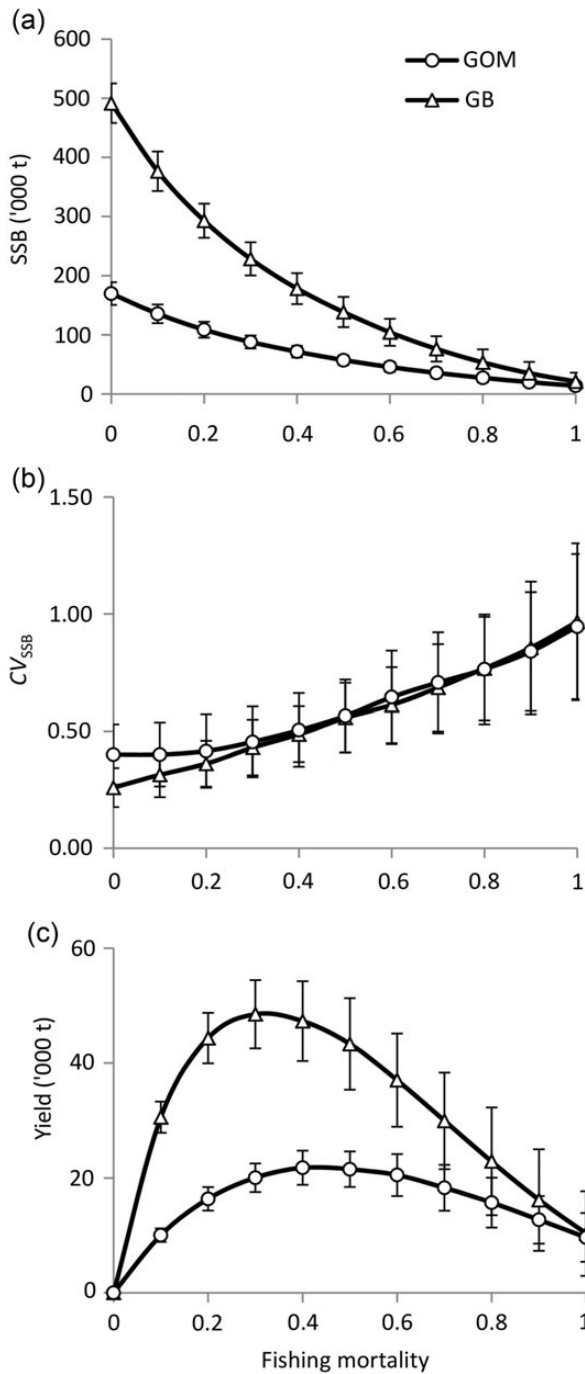
### Role of connectivity

Since the prior simulation scenario assumed no connectivity between management units, we will only discuss results for the biological unit model with and without connectivity. Simulation results of the biological unit model without connectivity revealed that this model system exhibited greater SSB at high levels of fishing mortality than the biological unit model with connectivity (Figure 7a). In the absence of connectivity, the eastern Georges Bank spawning group was less resilient to increasing levels of exploitation and “collapsed” at a lower level of fishing mortality ( $F = 0.4$ ), whereas the northern and southern spawning groups were generally more productive



**Figure 4.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of the biological and management unit models of Atlantic cod off New England across fishing mortality scenarios.

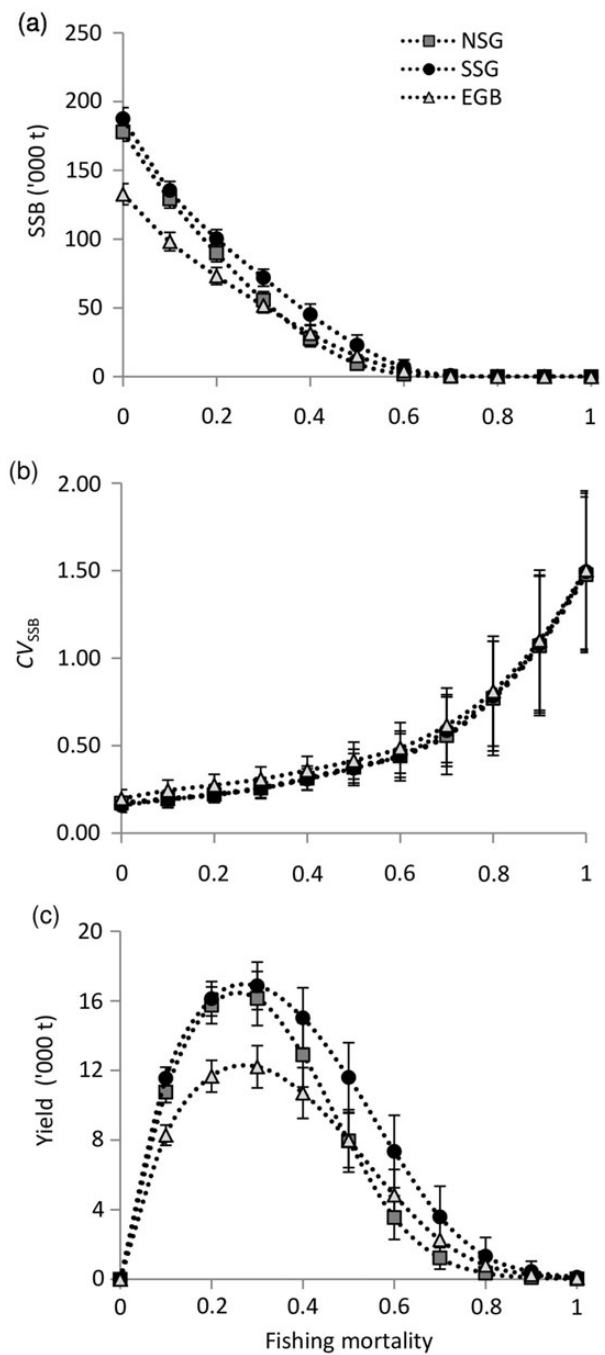
across levels of fishing mortality and more resilient to higher fishing mortality (Table 5, Figure 8a). Stability at the regional scale was higher in the absence of connectivity (Figure 7b). Stability at the local population scale was lower for the northern and eastern Georges Bank spawning groups, but was higher for the southern spawning group (Figure 8b). The difference in yield between the biological unit model with and without connectivity mirrored the trends in productivity at the local scale, with higher MSY for the northern and southern spawning groups and lower MSY for the eastern Georges Bank spawning group (Table 5, Figure 8c).



**Figure 5.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of the Gulf of Maine (GoM) and Georges Bank (GB) management units of Atlantic cod off New England across fishing mortality scenarios.

**Role of stochasticity**

At the regional scale, deterministic management and biological unit models exhibited considerably lower SSB and sustainable yield across most fishing mortality rates compared with the stochastic versions of these models (Table 5, Figure 9a and c). Similar to the stochastic model, the southern spawning group was slightly more productive than the northern spawning group, and the eastern Georges Bank group was the least productive when environmental



**Figure 6.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of the biological units [northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups] of Atlantic cod off New England across fishing mortality scenarios.

stochasticity was removed from the model (Table 5). In the management unit model, the Georges Bank management unit was more productive than the Gulf of Maine at low-to-intermediate levels of exploitation, but less productive at the highest levels of exploitation ( $F > 0.8$ ). In the absence of stochasticity, management unit models became unstable (did not converge to a stable equilibrium) at higher fishing mortality rates (Figure 9b), and biological unit models became unstable at  $F = 0.6$ . Thus, the management unit and

**Table 5.** Summary of estimated unfished biomass and biomass and fishing mortality metrics associated with MSY and collapse of northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups and Georges Bank (GB) and Gulf of Maine (GoM) management units.

Simulation scenario	Unit	Unfished biomass (t)	$B_{msy}$ (t)	MSY (t)	$F_{msy}$	$B_{collapse}$ (t)	$F_{collapse}$
Stochastic	Management unit total	661 373	249 709	69 073	0.4	66 137	0.9
	GoM	169 814	71 606	21 767	0.4	16 981	1.0
	GB	491 559	228 535	48 511	0.3	49 156	0.9
	Biological unit total	498 084	179 277	45 213	0.3	49 808	0.6
	NSG	177 859	55 640	16 133	0.3	17 786	0.5
	SSG	187 542	71 955	16 865	0.3	18 754	0.6
	EGB	132 683	51 682	12 216	0.3	13 268	0.6
No connectivity	Biological unit total	663 268	496 384	41 389	0.2	66 327	0.5
	NSG	191 344	103 193	18 783	0.3	19 134	0.5
	SSG	159 105	75 035	16 928	0.3	15 911	0.8
	EGB	145 935	53 611	8 439	0.2	14 594	0.4
No stochasticity	Management unit total	500 910	192 818	41 776	0.3	50 091	0.6
	GoM	120 518	54 023	12 280	0.3	12 052	0.7
	GB	380 392	138 795	29 712	0.2	38 039	0.6
	Biological unit total	408 004	193 213	31 808	0.2	40 800	0.5
	NSG	152 289	69 030	12 002	0.2	15 229	0.5
	SSG	153 502	74 719	11 902	0.2	15 350	0.5
	EGB	102 212	49 464	11 902	0.2	10 221	0.5

biological units “collapsed” at lower fishing mortality rates compared with models with stochasticity (Table 5, Figure 9a).

## Discussion

The results of our model simulations indicate differences in the perception of productivity, stability, and potential yield of the regional cod stock in US waters of the Northwest Atlantic depending whether one views the resource through the lens of the current management unit boundaries or the underlying biological population structure. Based on simulations with varying levels of fishing pressure applied, we found that the biological unit model portrayed a less productive resource at the regional scale compared with the management unit model. Additionally, a lower sustainable yield was expected when the stock was modelled from a biological perspective. Management and biological unit models exhibited similar levels of stability across low-to-intermediate fishing mortalities; however, the biological unit model was much less stable relative to the management unit model at high levels of  $F$ . The perception of Atlantic cod derived from the management unit model is of a resource that is more resilient to fishing mortality and not as susceptible to “collapse” as indicated by the biological unit model. The overall lower productivity and yield of the biological unit model compared with the management unit model is supported by prior theoretical modelling of Gulf of Maine cod (a cell-based spatial model without connectivity), which revealed that ignoring complex population structure within a stock unit can lead to overestimation of SSB and yield (Reich and DeAlteris, 2009).

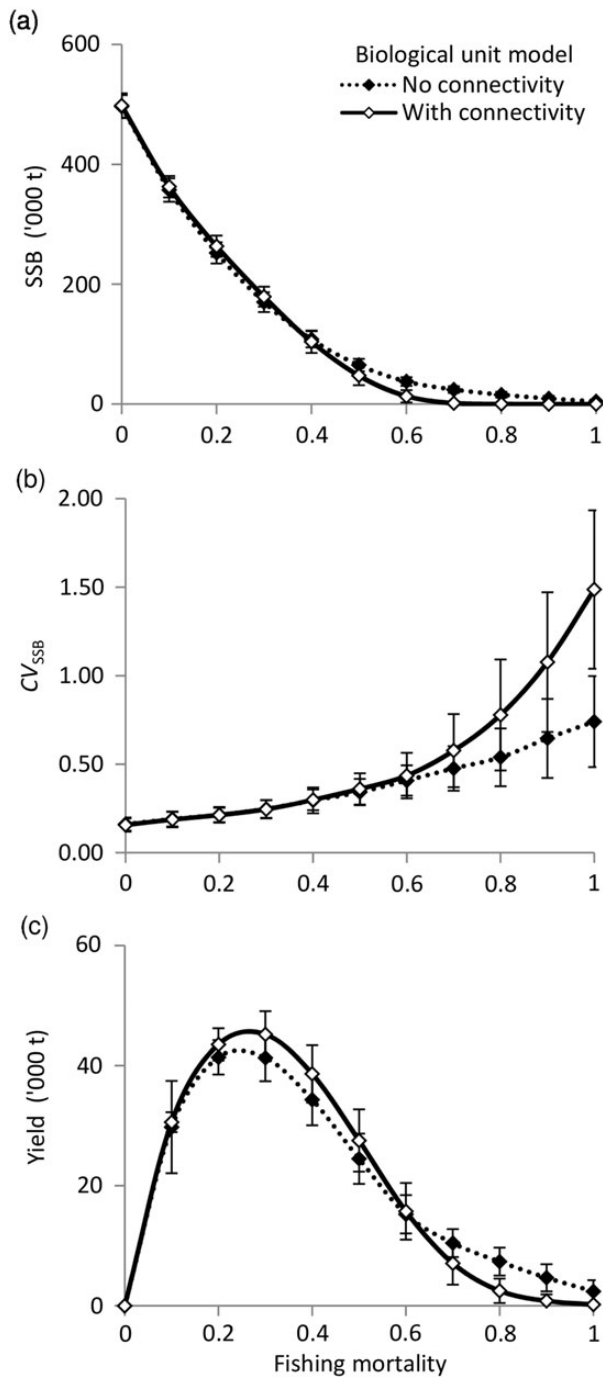
Management of fisheries according to spatially explicit designations that are not aligned with the population structure of a fish stock may have unintended consequences at the local and regional population scale (Reiss et al., 2009). Most importantly, an inaccurate assessment of population productivity will result in misleading management advice (e.g. calculation of total allowable catch, TAC). Our simulations indicate that the management unit model presents an overly optimistic perception of the resource’s SSB, the stability of this biomass, and potential sustainable harvest from the region. At the local scale, the MSY of the Gulf of Maine management unit (MSY = 21 767 t) is slightly higher than the biological

unit with which it has the most spatial overlap (northern spawning group MSY = 16 133 t). Of more concern is the large difference in estimated sustainable yield for the management and biological units in the Georges Bank region. Although not of identical spatial scale, the predicted MSY for the Georges Bank management unit (MSY = 48 511 t) is nearly four-fold the MSY of the eastern Georges Bank biological unit alone (MSY = 12 216 t) and is more than 1.6-fold the sum of the MSY of the eastern Georges Bank and the southern spawning groups (MSY = 29 081 t). Thus, for Atlantic cod, one of the main risks of ignoring population structure is a potential for overfishing segments of the population.

Overfishing can result in reduced biomass of a spawning group and, in extreme cases, can lead to local extirpation and loss of diversity within the regional population. On ecological time-scales, the loss of diversity of spawning groups can result in less stable regional population dynamics (i.e. higher probability of collapse), and on evolutionary time-scales, it can limit the ability of a species to adapt to changing environmental conditions (Smedbol and Stephenson, 2001; Reiss et al., 2009). The need to preserve the diversity of cod spawning groups is supported by recent genetic data indicating that most of the genetic differentiation occurred at selected loci, demonstrating ecological adaptation to environmental selection pressures (Kovach et al., 2010). Adaptive differences between spawning groups suggest that each is likely to respond uniquely to changes in the environment, and this type of response diversity has been linked with population persistence (Kerr et al., 2010a, b; Secor et al., 2009).

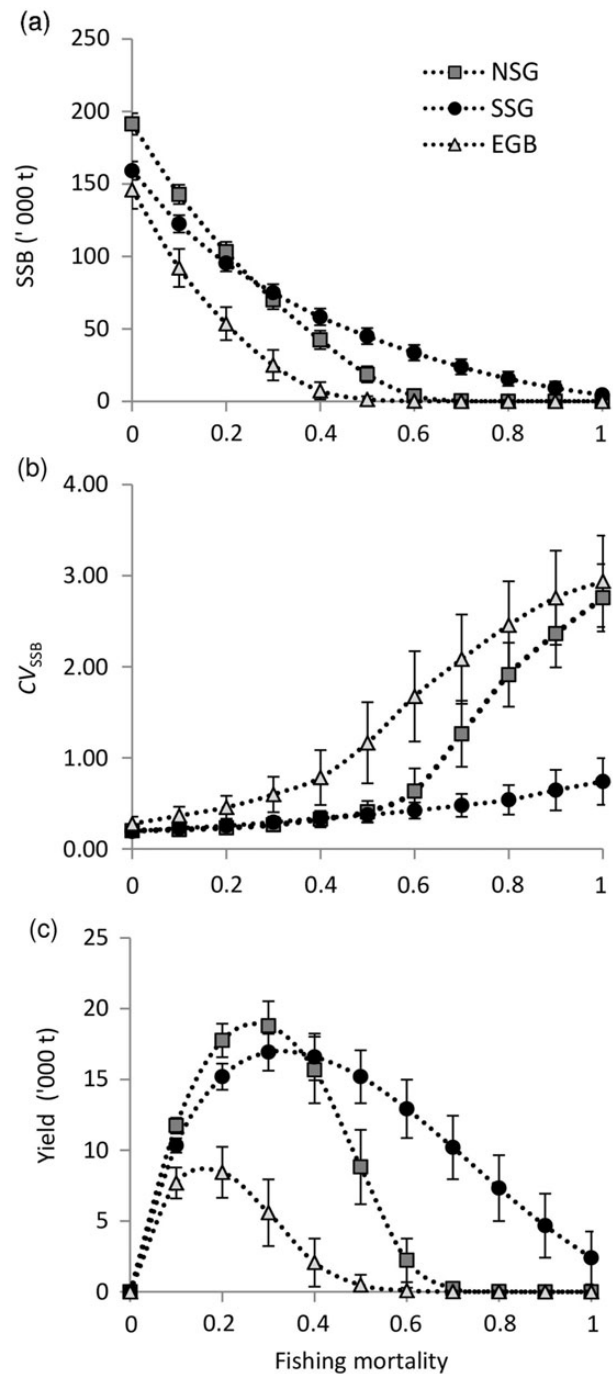
## Methodological considerations

Biological and management unit models were designed to be similar in structure to maximize the comparability between the management unit and biological unit operating models. The main difference was that the management unit model was informed by data collected at the scale of the current stock boundaries and in accordance with the “unit stock” assumption (i.e. no connectivity), while the biological unit model was designed to more closely reflect the biological complexity of the resource. The biological unit model was specified as the most accurate characterization of the unique vital rates and recruitment dynamics of discrete spawning groups



**Figure 7.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of the biological unit model simulated with and without connectivity of Atlantic cod off New England across fishing mortality scenarios.

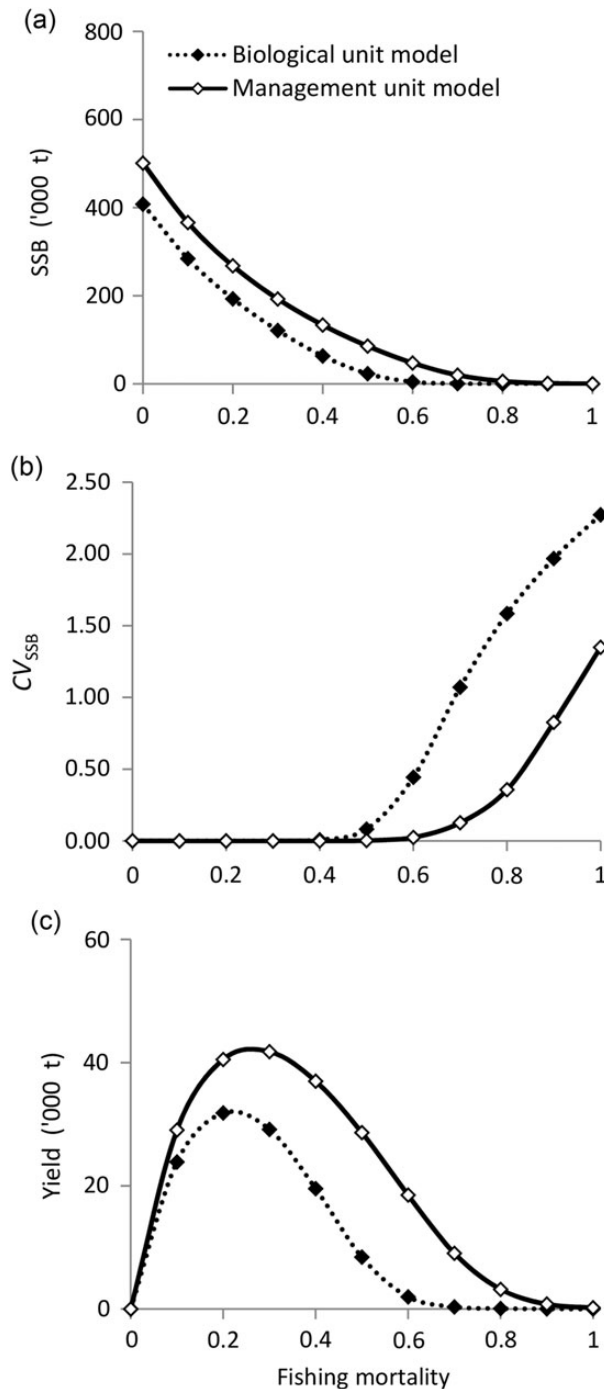
within the region, whereas the management unit model includes vital rates and dynamics that are derived from a mixture of spawning populations. Our results assume that the selected survey data are representative of the resource for the biological unit model simulations. Standardizing the scale of stock–recruit relationships between the biological and management unit models ensured that the differences identified between models are driven by the unique demographics and dynamics of spawning groups



**Figure 8.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of the biological units of Atlantic cod [northern (NSG), southern (SSG), and eastern Georges Bank (EGB) spawning groups] off New England simulated without connectivity across fishing mortality scenarios.

and are not an artefact of scaling recruitment. It must be emphasized that the goal of this analysis was not to estimate absolute values of SSB and sustainable yield from these models, but rather to assess the relative differences in long-term expectations between the management unit and biological unit models.

Differences in the perception of cod in the region were driven by differences in the spatial scale on which we characterize life history parameters and indices of recruitment and biomass for management



**Figure 9.** SSB (a), variability in SSB ( $CV_{SSB}$ ) (b), and yield (c) of biological and management unit models of Atlantic cod off New England simulated without stochasticity across fishing mortality scenarios.

and biological units (Figure 1a and b). We hypothesize that the parameters estimated for biological units, such as age–weight relationships and proportion mature-at-age, more accurately characterize these populations, compared with stock units that include multiple spawning populations in the estimation of these values. Differences in stock–recruit relationships between management and biological units contributed to the overall differences between models; they reflected the different perception of the relative biomass and

abundance of recruits when one views the resource through these different lenses. Management unit stock–recruit relationships suggest that the Georges Bank stock unit has a higher carrying capacity for recruits (high  $R_{max}$ ), yet lower resilience (slope at low stock size) to overfishing compared with the Gulf of Maine unit (Figure 2d). Among biological units, the northern spawning group is estimated to have the highest carrying capacity for recruits and highest resilience at low stock size, and the eastern Georges Bank is estimated to have the lowest values.

Deterministic model results revealed the perception that regional cod productivity and yield is lower, in both management unit and biological unit models, when environmental variability is not included in the model. The inclusion of environmental variability in the model drove variability in recruitment success and ultimately increased productivity across most scenarios. Thus, stochasticity in the model simulated an effect akin to the storage effect. The storage effect describes a phenomenon whereby “spawning stock biomass accumulates each year so that when early survival conditions are favourable, stored egg production can result in explosive population growth” (Secor, 2007). Age structure in the management and biological units buffered the effect of periods of poor simulated recruitment and contributed to the formation of strong year classes when conditions for survival were simulated to be good.

Additional factors contributing to the difference between models included the presence of connectivity in the biological unit model. The results of the stochastic simulations of the biological unit model without connectivity are consistent with past findings (Kerr et al., 2010a) that show connectivity between local populations decreases productivity and yield at the regional scale as well as in dominant populations and increases productivity in subordinate populations. The inclusion of connectivity in the system had the effect of dampening variation within individual populations (northern and eastern Georges Bank spawning group) and increasing the population’s resilience to fishing pressure. These results are consistent with the expectation of greater stability and sustainability of resources that have greater biocomplexity (Hilborn et al., 2003).

This study included data on cod in US waters as well as the eastern portion of Georges Bank, an area jointly managed between the US and Canada as a transboundary resource (Figure 1a). Although we restricted our modelling to cod in these regions, genetic and tagging evidence suggests that there is some connectivity between US and Canadian cod stocks (Hunt et al., 1999). Tagging efforts have revealed some movement between cod populations in US and Canadian waters between eastern Georges Bank and Browns Bank (Ruzzante et al., 1998; Hunt et al., 1999; Lage et al., 2004; Tallack, 2011), between the Bay of Fundy and both Georges Bank (Ruzzante et al., 1998; Tallack, 2011), and the Gulf of Maine (Hunt et al., 1999). However, observed movements may represent spatial overlap rather than population connectivity. Genetic analysis by Ruzzante et al. (1998) identified differences among cod from the Bay of Fundy, Georges Bank, Browns Bank, and Banquereau/Western Banks, suggesting three distinct population units: (i) Georges Bank, (ii) western Scotian Shelf (Browns Bank and Bay of Fundy), and (iii) eastern Scotian Shelf (Banquereau and Western Bank). Lage et al. (2004) found differentiation of Georges and Browns Bank cod from Nantucket Shoals, but no difference between Georges and Browns Bank, in apparent contrast to the findings of Ruzzante et al. (1998). Differences in the results of these studies may stem from differences in sampling sizes and spawning condition of sampled fish. Further genetic analysis is needed to resolve the level of connectivity between US and Canadian spawning

populations of cod. The influence of this connectivity on our modelled results would depend on the level of immigration and emigration of individual populations. There is the potential for immigrants from Canadian populations to enhance the biomass and stability of minority populations (e.g. eastern Georges Bank spawning group); however, the apparent productivity of more dominant populations (e.g. northern spawning group) may be lower if emigration occurs to Canadian populations.

### Considerations for management

Currently, the US fishery management system assesses and sets harvest limits for Atlantic cod based on a two-stock management construct. However, we know that fishing effort is not uniformly applied across stock areas. Records of commercial landings of Atlantic cod indicate that the distribution of fishing effort appears aligned with the temporal and spatial distribution of what we estimated to be the most productive biological spawning groups: the northern and southern spawning complexes. Stock assessments indicate that the highest fraction of annual commercial landings occurred in the inshore regions of the western Gulf of Maine within the Gulf of Maine stock (1994–2011) and in southern New England waters directly east of Cape Cod within the Georges Bank stock unit (NEFSC, 2013; M. Palmer, pers. comm.). Aligning the scale of assessment and management of Atlantic cod in the Northwest Atlantic with the behaviour of fish and the fishing fleet is likely to make the goal of sustainable fishing practices easier to attain (Lorenzen *et al.*, 2010). Changing the way we assess and manage fish stocks to better incorporate biological population structure may seem an insurmountable task in the face of an already complex process, characterized by a high degree of uncertainty. However, the potential costs of not incorporating population structure into our management schemes, stock declines, and failure of fisheries must be weighed against implementing a new approach to assessment and management of fishery resources. Simulation modelling has shown that the combined impact of heterogeneity in the distribution of fish and fishery removals can lead to overestimation of SSB and underestimation of fishing mortality when the stock unit is misspecified (Guan *et al.*, 2013).

Through this study, we developed an operating model to represent the newly emerged paradigm of cod population structure. Our objective was to show the different expectations of the resource when underlying complex population structure is considered or when regarded as a unit stock. In future work, the operating model could be used to generate typical fishery and survey data for stock assessment and fishery management through management strategy evaluation (MSE). Developing an operating model that characterizes the biological complexity of the system is a non-trivial first step in MSE and will enable simulation of realistic population dynamics as well as typical sampling error associated with fishery data. The next stage in an MSE of Atlantic cod should involve a broader group of scientists, managers, fishing industry members, and other stakeholders to evaluate alternative management procedures.

The results of simulation modelling suggest the need to re-evaluate the current spatially defined management units of Atlantic cod in US waters. Maintenance of the biocomplexity of cod in the region should be a management objective because it has been identified as a critical feature contributing to the persistence of fish resources (Hilborn *et al.*, 2003; Kerr *et al.*, 2010a, b). The estimated lower productivity and sustainable yield of the eastern Georges Bank spawning group compared with the northern

and southern spawning groups implies that this group should be assessed and managed as a separate stock. Assessing and conserving the sympatric northern and southern spawning components of cod in the Gulf of Maine independently may not be practical because of the spatial overlap of the northern and southern spawning groups. Furthermore, similar estimated productivity levels suggest that these spawning groups could be assessed and managed together. Monitoring of both the northern and southern spawning groups would be necessary to ensure maintenance of biocomplexity, and a conservative harvest approach would be needed to account for the apparent lower productivity of the northern spawning group. In theory, targeting spawning groups during the spawning period could enable fishing on distinct groups and avoid mixed composition of the catch. However, evidence indicates that the impact of fishing Atlantic cod while on spawning grounds goes beyond the removal of biomass and can disrupt the spawning behaviour of cod, which has been suggested as a cause of poor recruitment (Dean *et al.*, 2012). Further research on the spawning ecology, movement, and habitat utilization of cod in the Northwest Atlantic will enhance our ability to set harvest restrictions tailored to the life history of each spawning group.

Increasingly, research on stock structure reveals examples for which fishery management units are not aligned with the biological stock structure (Reiss *et al.*, 2009). Despite recognition of such mismatches, there has been little accounting for this in management to date (Lorenzen *et al.*, 2010). In some cases, such as in the Northwest Atlantic where sufficient data exist, management units may be redefined to reflect population structure using the current time-series of monitoring data. However, in other instances, population structure may be too complex or data may be limited, and management units will have to represent a simplification of the underlying genetic structure with a precautionary approach taken to conserve smaller, less stable populations. Simulation modelling can help us weigh the implications of a mismatch between biological population structure and management units on stock assessment and management (ICES, 2011; Kerr and Goethel, 2014).

### Acknowledgements

Support for this research was provided by the Massachusetts Marine Fisheries Institute and Gulf of Maine Research Institute. We acknowledge the contribution of research by SMASST cod tagging/genetic collaborators (including D. Martins, J. Loehrke, S. Tallack, D. Zemeckis, M. Dean, M. Armstrong, B. Hoffman, I. Wirgin, D. L. Berlinsky, and T. Breton) that contributed to the delineation of cod spawning complexes and funding of tagging and genetics research through the Northeast Consortium. This research was presented at the “Stock Structure of Atlantic Cod in the Gulf of Maine Region” workshop held 12–14 June 2012 (Portsmouth, NH, USA), and participants offered valuable feedback. This work would not have been possible without the data collected by the Massachusetts Division of Marine Fisheries and the NOAA Northeast Fisheries Science Center.

### References

- Ames, E. P. 2004. Atlantic cod stock structure in the Gulf of Maine. *Fisheries*, 29: 10–28.
- Annala, J. H. 2012. Final Report of the Workshop on Stock Structure of Atlantic cod in the Gulf of Maine Region. 12–14 June 2012, Portsmouth, NH. 24 pp.

- Begg, G. A., Friedland, K. D., and Pearce, J. B. 1999a. Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research*, 43: 1–8.
- Begg, G. A., Hare, J. A., and Sheehan, D. D. 1999b. The role of life history parameters as indicators of stock structure. *Fisheries Research*, 43: 141–163.
- 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, The Netherlands.
- Dean, M. J., Hoffman, W. S., and Armstrong, M. P. 2012. Disruption of an Atlantic cod spawning aggregation resulting from the opening of a directed gill-net fishery. *North American Journal of Fisheries Management*, 32: 124–134.
- Frank, K. T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 513–517.
- Frank, K. T., and Brickman, D. 2001. Contemporary management issues confronting fisheries science. *Journal of Sea Research*, 45: 173–187.
- Frisk, M. G., Miller, T. J., Martell, S. J. D., and Sosebee, K. 2008. New hypothesis helps explain elasmobranch “outburst” on Georges Bank in the 1980s. *Ecological Applications*, 18: 234–245.
- Fu, C., and Fanning, L. P. 2004. Spatial considerations in the management of Atlantic cod off Nova Scotia, Canada. *North American Journal of Fisheries Management*, 24: 775–784.
- Guan, W., Cao, J., Chen, Y., and Cieri, M. 2013. Impacts of population and fishery spatial structures on fishery stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1178–1189.
- Hammer, C., and Zimmermann, C. 2005. The role of stock identification in formulating fishery management advice. *In* Stock Identification Methods: Applications in Fishery Science, pp. 631–658. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. Waldman. Elsevier Academic Press, Burlington, MA.
- Hilborn, R., Quinn, T. P., Schindler, D. E., and Rogers, D. E. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Science of the United States of America*, 100: 6564–6568.
- Hunt, J. J., Stobo, W. T., and Almeida, F. 1999. Movement of Atlantic cod, *Gadus morhua*, tagged in the Gulf of Maine area. *Fishery Bulletin US*, 97: 842–860.
- ICES. 2011. Report of the Workshop on the Implications of Stock Structure, 5–7 April 2011. ICES Headquarters, Copenhagen. ICES Document CM 2011/SSGSUE: 03. 53 pp.
- 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. 2010a. Simulation modelling as a tool for examining the consequences of spatial structure and connectivity to local and regional population dynamics. *ICES Journal of Marine Science*, 67: 1631–1639.
- Kerr, L. A., Cadrin, S. X., and Secor, D. H. 2010b. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications*, 20: 497–507.
- Kerr, L. A., and Goethel, D. R. 2014. Simulation modeling as a tool for synthesis of stock identification information. *In* Stock Identification Methods, 2nd edn, pp. 501–533. Ed. by S. Cadrin, L. Kerr, and S. Mariani. Elsevier, Waltham, MA. 566 pp.
- Kovach, A. I., Breton, T. S., Berlinsky, D. L., Maceda, L., and Wirgin, I. 2010. Fine-scale spatial and temporal genetic structure of Atlantic cod off the Atlantic coast of the USA. *Marine Ecology Progress Series*, 410: 177–195.
- Lage, C., Kuhn, K., and Kornfield, I. 2004. Genetic differentiation among Atlantic cod (*Gadus morhua*) from Browns Bank, Georges Bank, and Nantucket Shoals. *Fishery Bulletin US*, 102: 289–297.
- Lorenzen, K., Steneck, R. S., Warner, R. R., Parma, A. M., Coleman, F. C., and Leber, K. M. 2010. The spatial dimensions of fisheries: putting it all in place. *Bulletin of Marine Science*, 86: 169–177.
- Northeast Fisheries Science Center (NEFSC). 2012. 53rd Northeast Regional Stock Assessment Workshop (53rd SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 12-05. 559 pp.
- Northeast Fisheries Science Center (NEFSC). 2013. 55th Northeast Regional Stock Assessment Workshop (55th SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 13-11. 845 pp.
- O’Brien, L., Burnett, J., and Mayo, R. K. 1993. Maturation of nineteen species of finfish off the northeastern coast of the United States, 1985–1990. NOAA Technical Report NMFS 113.
- O’Brien, L., Lough, R. G., Mayo, R. K., and Hunt, J. J. 2005. Gulf of Maine and Georges Bank (NAFO Subareas 5 and 6). *In* Spawning and Life History Information for North Atlantic Cod Stocks, pp. 95–104. Ed. by K. Brander. ICES Cooperative Research Report, 274. 152 pp.
- Parrish, D. L., Behnke, R. J., Gephaard, S. R., McCormick, S. D., and Reeves, G. H. 1998. Why aren’t there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55(Suppl. 1): 281–287.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York. 542 pp.
- R Development Core Team. 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- 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.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- 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., Taggart, C. T., and Cook, D. 1998. A nuclear DNA basis for shelf-and bank scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. *Molecular Ecology*, 7: 1663–1680.
- Secor, D. H. 2007. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research*, 57: 91–103.
- Secor, D. H., Kerr, L. A., and Cadrin, S. X. 2009. Connectivity effects on productivity, stability, and response diversity in an Atlantic herring metapopulation. *ICES Journal of Marine Science*, 66: 1726–1732.
- Sherwood, G. D., and Grabowski, J. H. 2010. Exploring the life-history implications of colour variation in offshore Gulf of Maine cod (*Gadus morhua*). *ICES Journal of Marine Science*, 67: 1640–1649.
- Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology, Evolution and Systematics*, 16: 393–430.
- Smedbol, R. K., and Stephenson, R. 2001. The importance of managing within-species diversity in cod and herring fisheries of the northwestern Atlantic. *Journal of Fish Biology*, 59(Suppl. A): 109–128.
- Stephenson, R. L. 1997. Successes and failures in the management of Atlantic herring fisheries: do we know why some have collapsed and others survived? *In* Developing and Sustaining World Fisheries Resources: the State of Science and Management. Proceedings of the Second World Fisheries Congress, pp. 49–54. Ed. by D. A. Hancock, D. C. Smith, A. Grand, and J. P. Buemer. CSIRO, Australia.
- Stephenson, R. L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research*, 43: 247–249.
- Sterner, T. 2007. Unobserved diversity, depletion and irreversibility: the importance of subpopulations for management of cod stocks. *Ecological Economics*, 61: 566–574.

- Tallack, S. 2009a. Proceedings from a workshop to identify future research priorities for cod tagging in the Gulf of Maine. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 09-09.
- Tallack, S. 2009b. Regional growth estimates of Atlantic cod *Gadus morhua*: applications of the maximum likelihood GROTAG model to tagging data in the Gulf of Maine (USA/Canada) region. *Fisheries Research*, 99: 137–150.
- Tallack, S. M. L. 2011. Stock identification applications of conventional tagging data for Atlantic cod in the Gulf of Maine. *In Proceedings from the 2nd International Symposium on Advances in Fish Tagging and Marking Techniques*, pp. 1–15. Ed. by J. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. Mesa, and Q. Phelps. American Fisheries Society Symposium 76. 560 pp.
- Waples, R. S., and Do, C. 2008. LDNE: a program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Resources*, 8: 753–756.
- Wirgin, I., Kovach, A. I., Maceda, L., Roy, N. K., Waldman, J., and Berlinsky, D. L. 2007. Stock identification of Atlantic cod in U.S. waters using microsatellite and single nucleotide polymorphism DNA analysis. *Transactions of the American Fisheries Society*, 136: 375–391.
- Wright, S. 1951. The genetical structure of populations. *Annals of Eugenics*, 15: 323–354.
- Ying, Y., Chen, Y., Lin, L., and Gao, T. 2011. Risks of ignoring fish population spatial structure in fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 2101–2120.
- Zemeckis, D. R., Dean, M. J., and Cadrin, S. X. 2014b. Spawning dynamics and associated management implications for Atlantic cod (*Gadus morhua*). *North American Journal of Fisheries Management*, 34: 424–442.
- Zemeckis, D. R., Martins, D., Kerr, L. A., and Cadrin, S. X. 2014a. Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. *ICES Journal of Marine Science*, 71: 1490–1506.

Handling editor: Emory Anderson