A comparison of cod life-history parameters inside and outside of four year-round groundfish closed areas in New England, USA

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From 1994 to 2002, five major year-round closed areas were established in the Gulf of Maine and on Georges Bank to promote recovery of groundfish species, including Atlantic cod (Gadus morhua). Here, we present life-history data for cod sampled within and next to four of the five closed areas to test the hypothesis that closed areas benefit cod. We found a positive effect of closure status on cod age, length and growth for three of the four closed areas; contrary results for the fourth area (Jeffreys Ledge) may be due to recreational fishing pressure. Diet results were not consistent across closed areas, but for the two areas farthest from shore (Cashes Ledge and Closed Area II), cod tended to have higher gut fullness and higher trophic niche breadth (based on stable isotopes) inside vs. outside. Body shape analysis revealed a consistent effect of closure status on cod morphometry with cod inside closed areas exhibiting less streamlined bodies. We discuss this apparent selection for more sedentary cod with lower productivity potential but highlight the demographic result (i.e. higher age and greater size inside closed areas) as critical considerations for resource managers that are designing or altering the configuration and/or scale of closed areas to protect and rebuild demersal fish species.

Keywords: age, Atlantic cod, closed areas, diet, Georges Bank, growth, Gulf of Maine, life-history variation, morphometrics, stable isotope.

Introduction

Gulf of Maine (GOM) and Georges Bank (GB) cod (Gadus morhua) have been a mainstay for New England fishing communities for centuries with early European explorers and then settlers targeting this species for both food and export (Kurlansky, 1997). In fact, human exploitation of cod in this region predates the arrival of Europeans with archaeological evidence of indigenous peoples fishing cod going back millennia (Bourque et al., 2008). Over more recent times (i.e. the last few decades), New England cod have undergone major changes in both abundance and management. Following establishment of a US exclusive economic zone (EEZ) in 1976, cod landings were quite high, although apparently not as high as in the 1800s (Alexander et al., 2009). However, throughout the 1980s and into the 1990s, cod fishing mortality was excessive, as evidenced by a decline in the stock that clearly manifested by the mid-1990s, which led to stricter effort controls taking effect in the fishery. Among these input controls were limited days at sea, gear restrictions (e.g. minimum mesh size), and area closures.

Starting in 1994, five year-round closed areas were implemented on GB and in the GOM (Figure 1) to replace or augment a series of rolling closures which had been in effect in various forms since the 1970s (NEFMC, 2014). The year-round closures include Closed Areas I and II (CAI and CAII) on GB and the Nantucket Lightship Area (NLA) on Nantucket Shoals, which were established in their current form in 1994, the Western GOM Closure Area or Jeffrey’s Ledge (JL; also spans Stellwagen and Tillies Banks) which was added in 1998, and the Cashes Ledge Closed Area (CL) in the central GOM which was closed in 2002 (NEFMC, 2014). These closed areas are not off-limits to all fishing activities, as is the case for other marine protected areas (MPAs) around the world (e.g. Edgar et al., 2007). Rather, they were intended to protect benthic habitats and reduce groundfish mortality particularly for cod, haddock, Melanogranmus aeglefinus, and yellowtail flounder, Pleuronectes ferruginea. Certain commercial groundfishing technologies are excluded (i.e. primarily commercial bottom tending gear such as trawling and gillnetting), while other activities are...
allowed, either throughout the areas (e.g. recreational fishing) or in special access areas (e.g. scallop dredging and long-lining). As of 2015, the total amount of bottom currently off-limits to bottom-tending gear, year-round, in the GOM and on GB is about 22,000 km² (Murawski et al., 2005) or roughly the size of New Hampshire.

In 2010, the management of groundfish in the US northeast shifted from input controls to output controls, or quota management. At the time of this change, it was believed that New England cod stocks were rebuilding with overfishing no longer occurring (Mayo et al., 2009). In addition, since hard quotas were being imposed with built-in uncertainty buffers, the continued necessity of closed areas was questioned. Some stakeholders hold that closed areas, for the purpose of rebuilding groundfish in New England, have become obsolete. However, at the end of 2011, it became apparent that the size of the GOM cod stock had been overestimated by the 2008 assessment (NEFSC, 2012), and that rebuilding was no longer attainable in the near term. The situation is not much better for GB cod (NEFSC, 2013). As opposed to calls for maintaining the current closed areas during this period of crisis, there has been a growing pressure from the fishing industry to reopen areas closed to groundfishing. This may be to lessen the financial burden of a 78% reduction (effective 2013) in quota for GOM cod, but also because the process of reconfiguring closed areas for different purposes other than groundfish rebuilding (e.g. to protect benthic biodiversity) had already begun (NEFMC, 2014). More recently, an interim assessment for GOM cod determined that GOM cod spawning-stock biomass (SSB) is now at

Figure 1. Map of GOM and GB showing location of four major closed areas and general sampling areas. CAI, Closed Area I; CAII, Closed Area II; CL, Cashes Ledge; JL, Jeffrey’s Ledge. Bathymetry lines are 50 m contours. Ellipses show general area of sampling.
just 3–4% of the target level (Palmer, 2014), which has triggered a shutdown of the groundfish fishery in most of the GOM (effective November 2014). Over the backdrop of a deepening cod crisis in the GOM/GB region and an ongoing discussion at the New England Fishery Management Council level to alter the existing boundaries of the closed areas in this region, it is essential that all evidence for their impact on cod be considered.

There is no consensus among managers and industry members that closed areas have achieved the goal of reducing cod fishing mortality. However, there is some evidence that there have been ecological benefits that may translate into advantages for cod. For example, studies have shown that benthic communities are more diverse inside vs. outside closed areas (Collie et al., 1997; Fisher and Frank, 2002; Hermsen et al., 2003). This may provide more complete feeding opportunities for demersal fish like cod. Murawski et al. (2005) examined catch patterns next to closed areas for a variety of groundfish species and found that cod were the species most associated with closed areas (haddock was). However, this result may not represent all cod. Sherwood and Grabowski (2010) examined the life history of red cod at CL and concluded that this colour morphotype represents a highly sedentary form of cod that may reside entirely within the closed area, primarily at Ammen Rock. Similarly, Lindholm et al. (2007) studied residency behaviour of cod on Stellwagen Bank and found that a proportion of acoustically tagged individuals were highly and consistently associated with specific bottom features. More broadly, there is growing evidence throughout the North Atlantic that most cod stocks and populations are made up of resident and migratory components (Svedäng et al., 2007; Bergstad et al., 2008; Grabowski et al., 2011; LeBris et al., 2013). Thus, while there may not be evidence for cod using closed areas more than open areas as a whole in the GOM, there is a possibility that closed areas are favouring one type of life history (i.e. resident) over another (i.e. migrant), and that this difference has yet to be recognized.

The purpose of this study was to explore life-history parameters of cod inside and outside of four year-round closed areas, all of which are currently being considered for reconfiguration and/or reopening (NEFMC, 2014). Specifically, we hypothesized that cod growth, feeding success, condition and survival are higher inside of closed areas than outside. We also considered the possibility that closed areas may be promoting the recovery, or at the very least, persistence of individuals with more sedentary behaviour over those with migratory tendencies. We inferred migratory behaviour using body shape analysis (Sherwood and Grabowski, 2010; see Morphometrics section for further explanation).

Methods

Sampling

Cod were collected by rod and reel and longline from inside and next to four of the five year-round closed areas in the GOM and on GB (Figure 1). Cod from “inside” closed areas came mostly from areas well inside (>5 km), whereas cod from “outside” closed areas were captured at distances >5 km from closed areas. Immediately following capture, cod were measured (total length, \( L_{\text{tot}} \) nearest mm) and photographed for morphometric analysis and then stored on ice for transport back to the lab where they were kept frozen until they were dissected. Sampling occurred primarily from late spring to early autumn 2007–2009.

In the lab, cod were thawed and weighed (total weight, \( W_{\text{tot}} \) nearest g). The livers, stomachs, and gonads were removed and weighed (\( W_{\text{liv}} \), \( W_{\text{stom}} \), \( W_{\text{gon}} \) respectively, nearest g). All other viscera were removed and gutted weight was recorded (\( W_{\text{gut}} \), nearest g). Sagittal otoliths were removed for age and growth analyses, and sex was recorded. Age was determined from cracked and polished otoliths using an image analysis system. An ~1 g muscle tissue sample located directly anterior to the first dorsal fin was obtained from each cod for stable isotope analysis.

Stomach content and stable isotope analyses

For each cod, individual dietary items were identified to species (where possible), counted and measured (nearest mm), excess water was removed, and items were weighed (nearest mg). To simplify analyses and consider only general trends in feeding, prey items were partitioned into the following three broad prey groups: benthos (various species of polychaetes, amphipods, molluscs, brittlestars, echinoderms, shrimp, lobsters, and crabs), pelagic fish (Atlantic herring, Clupea harengus, redfish, Sebastes fasciatus, silver hake, Merluccius bilinearis, and pollock, Pollachius virens), and demersal fish (haddock, sculpins, Myoxocephalus sp., cusner, Tautogolabrus adspersus, and cod). Fish that were not identified to species were assumed to be pelagic fish. Partial fullness index (PFI) of the different prey groups was calculated for each cod to remove the influence of length on stomach fullness (Bowering and Lilly, 1992; Sherwood et al., 2007). PFI was calculated by dividing the total weight (g) of prey group \( i \) in each cod by the total length (\( L_{\text{tot}}, \text{cm} \)) of that fish cubed, and multiplying this proportion by 10\(^4\). Total fullness index (TFI) was calculated in a similar manner by substituting the weight of a prey group with the total weight of all prey in the stomach (g). Finally, feeding intensity (FI) was calculated as the percentage of cod within each area (both inside and outside) that had food in their stomachs (i.e. prey weight greater than zero).

Stable isotope ratios of carbon (\( \delta^{13}C \)) and nitrogen (\( \delta^{15}N \)) in fish muscle tissue are indicative of prey origin (pelagic vs. benthic) and trophic level, respectively, and provide a time-averaged depiction of diet (Sherwood and Rose, 2005). In previous studies, it was necessary to characterize the baseline for both \( \delta^{13}C \) and \( \delta^{15}N \) using primary consumer stable isotope values to infer diet origin and trophic level of higher consumers independent of baseline variations (e.g. Sherwood and Rose, 2005). Primary consumer stable isotope values were not available for this study. However, given that we were primarily interested in the variability of stable isotope signatures (see Results) and that we employed a paired design such that major baseline variation is less likely within a pairing (i.e. inside vs. outside a closed area), we are confident in the utility of our stable isotope results. Each muscle tissue sample was dried in a drying oven at 60°C for 48 h to constant weight, homogenized to a fine powder using a mortar and pestle, placed into 4 × 6 mm tin capsules, and weighed. Samples were then sent to the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, AZ, USA) for analysis. Samples were combusted to analyse the carbon and nitrogen stable isotope ratios of CO\(_2\) and N\(_2\), respectively, using an elemental analyser followed by gas chromatograph separation interfaced via continuous flow to an isotope ratio mass spectrometer. Stable carbon and nitrogen ratios (\( \delta \)) in this study are defined as the parts per thousand deviations from the following standard materials: Pee Dee belemnite limestone for \( \delta^{13}C \) and N\(_2\) in air for \( \delta^{15}N \). Ten per cent of the samples were analysed in duplicate; the average coefficient of variation for duplicates was 0.0097 for \( \delta^{13}C \) and 0.0135 for \( \delta^{15}N \).
Condition indices

Two indices of condition were considered: Fulton’s condition factor (FCF) and liver somatic index (LSI). FCF was calculated as $W_{\text{gut}} \times L_{\text{tot}}^{-3} \times 100$ and LSI as $W_{\text{gut}} \times W_{\text{org}}^{-1} \times 100$. FCF is primarily an indicator of protein reserves (i.e. muscle mass), whereas LSI indicates excess lipid stores in cod (Yaragina and Marshall, 2000). To remove any seasonal variability in these indices, we calculated seasonally adjusted values. For example (for FCF), $\text{FCF}_{\text{adj}} = \text{FCF} - \text{FCF}_{\text{avg}}$ where $\text{FCF}_{\text{avg}}$ is the average condition factor (all sizes and areas combined) by month. FCF varied significantly by month (analysis of variance (ANOVA), $F_{5,626} = 49.0$, $p < 0.0001$). The same calculation was performed for LSI, which also varied significantly by month (ANOVA, $F_{5,564} = 38.4$, $p < 0.0001$). Both FCF$_{\text{adj}}$ and LSI$_{\text{adj}}$ were significantly related to length: $\text{FCF}_{\text{adj}} = 0.029 - 0.00005 \times L$; $r^2 = 0.01$; $p < 0.05$; $\text{LSI}_{\text{adj}} = -1.73 + 0.003 \times L$; $r^2 = 0.07$; $p < 0.0001$. The relationship for FCF$_{\text{adj}}$ vs. length was deemed biologically insignificant given the low $r^2$ value and length coefficient. On the other hand, the relationship between LSI$_{\text{adj}}$ and length was strong enough to warrant correcting for length before comparing among areas and status. Thus, the residuals of this relationship were used for further testing. Gonadal somatic index was not considered since very few cod were in spawning condition.

Morphometrics

Body shape in fish is an indicator of swimming activity among species (Sherwood and Rose, 2005). Within populations, body shape may also vary according to migratory propensity such that more migrant individuals have more streamlined body shapes than more resident individuals (Morinville and Rasmussen, 2008; Sherwood and Grabowski, 2010). We used body shape analysis here to infer migrant vs. resident behaviour in cod. Cod morphometric analyses were conducted using the images collected at sea following the procedure outlined in Sherwood and Grabowski (2010). In short, 11 homologous cod landmarks were digitized and the distances between landmarks were calculated for each fish using a box-truss approach (Strauss and Bookstein, 1982; Cadrin, 2000). We purposely excluded a landmark at the anterior margin of the first anal fin to remove the possibility that variations in stomach fullness would affect body shape results. Each of the resultant 17 distances (Figure 5) was natural log-transformed to normalize distributions and principal component analysis was then conducted on those values. The first PC, which is an indicator of fish length (Cadrin, 2000), was used to standardize for differences in fish size by regressing it against each log-transformed box-truss dimension. Using the residuals of each regression, discriminant function analysis (DFA) was then performed to determine the percentages of cod that could be categorized correctly by status (Solow, 1990). Loading factors on the first discriminant function were also compared among the status by Student’s t-test. Red cod which are a highly resident form of cod found in shallow habitats including at CL (Sherwood and Grabowski, 2010) were excluded from all analyses.

Statistical analysis

Comparisons of life-history parameters were made within (inside vs. outside) and among the four major closed areas. Hereafter, different closed areas are referred to as “area” and inside vs. outside is referred to as “status”, both fixed variables. Age was compared among area and status using ANOVA, whereby the effect of both variables and their interaction on mean age was examined. A Mann–Whitney test was also used to test for differences in median age among status by area, and a chi-squared test was employed to examine proportions of older cod (>5 years old, arbitrary) captured inside vs. outside of closed areas for all areas combined. The variation in cod length among areas and status and their interaction was also examined by ANOVA and by Student’s t-test (within areas). Length–weight relationships (LWRs) were constructed using the formula: $\log W = a + b \times \log L$, where $a$ is the intercept and $b$ is the slope or scaling coefficient. Analysis of covariance (ANCOVA) with $\log W$ as the dependent variable, status as a fixed factor (coded “0” for inside and “1” for outside), $\log L$ as the covariate, and an interaction term between status and $\log L$ were used to assess the difference in slopes among status and within areas. von Bertalanffy growth function (VBGF) curves were generated for each area–status combination (Chen et al., 1992). Significant differences among these curves inside vs. outside for each area separately and for all areas combined were tested by the analysis of the residual sum of squares (ARSS, Chen et al., 1992). Differences in FI among status were examined using chi-squared tests (i.e. using the number of empty stomachs vs. number with food) for all areas combined and by area. Total fullness index (TFI) was compared among areas and status using ANOVA and by status using Student’s t-tests for each area separately. Only TFI values greater than zero were used. Before conducting these tests, TFI was cube-root transformed to reduce heteroscedacity. This analysis was repeated for each prey group using cube-root transformed PFI values. The relationship between prey size and predator size (i.e. cod length) was explored by ANCOVA for all areas combined and within each area with status as a fixed factor (coding as above) and length as the covariate; the interaction between length and status was also examined. Given the dependency on length, residual prey size values were calculated and compared among status by Student’s t-test for all areas combined and by area. Differences in the variance of stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) inside and outside of the closed areas for all areas combined were assessed using Levene’s test. There was a significant effect of length on $\delta^{15}N$ signatures ($r^2 = 0.34; p < 0.0001; N = 310$). Therefore, residual $\delta^{15}N$ values were compared among area and status by ANOVA and within area by Student’s t-test. The same analyses were performed for $\delta^{13}C$, which was not related to length. Finally, differences in FCF$_{\text{adj}}$ and residual LSI$_{\text{adj}}$ among areas and status were examined using ANOVA and within areas using Student’s t-test.

Results

Table 1 is a summary of all results across all closed areas and all life-history parameters. The table shows mean values ($\pm 1$ SE), sample sizes, trends for differences between life-history parameters inside vs. outside of closed areas (shading), as well as significant differences (asterisks) where they existed. The results shown in the table are further expanded below for each life-history parameter in the order that they appear.

Both area and status influenced cod age distributions (Figure 2a). Age varied significantly among areas (ANOVA: $F_{3,679} = 34.1$; $p < 0.0001$) and status (ANOVA: $F_{1,679} = 6.4$; $p < 0.05$) and the interaction between these two variables was marginally significant (ANOVA: $F_{3,679} = 2.3$; $p = 0.07$). Median age was consistently 1 year older for cod captured inside closed areas compared with outside for all areas, but this difference was significant for CAI only (Mann–Whitney test: $Z_{120} = 3.92; p < 0.0001$). Overall, more old cod (age >5 years) were captured in closed areas ($n =$
Table 1. Summary of results for 11 life-history variables in cod sampled inside and outside of four major closed areas.

<table>
<thead>
<tr>
<th>Life-history parameter</th>
<th>CAI</th>
<th>CAII</th>
<th>CL</th>
<th>JL</th>
<th>All</th>
<th>CAI</th>
<th>CAII</th>
<th>CL</th>
<th>JL</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean age (years)</td>
<td>2.87 (14.5, 54)**</td>
<td>4.63 (13.4, 118)</td>
<td>3.05 (0.09, 217)</td>
<td>2.76 (0.09, 131)</td>
<td>3.32 (0.07, 520)**</td>
<td>2.18 (0.07, 113)</td>
<td>4.18 (0.24, 22)</td>
<td>2.84 (0.12, 114)</td>
<td>3.07 (0.14, 67)**</td>
<td>2.75 (0.07, 316)</td>
</tr>
<tr>
<td>Mean length (mm)</td>
<td>607.1 (14.5, 54)**</td>
<td>692.9 (13.4, 118)</td>
<td>517.8 (7.8, 217)</td>
<td>473.1 (7.4, 131)</td>
<td>555.6 (6.2, 520)**</td>
<td>466.6 (8.7, 113)</td>
<td>690.2 (15.9, 22)</td>
<td>485.1 (9.4, 114)</td>
<td>520.0 (15.7, 67)**</td>
<td>500.2 (6.4, 316)</td>
</tr>
<tr>
<td>Scaling coefficient (b)</td>
<td>3.03 (0.06, 51)**</td>
<td>2.92 (0.04, 115)*</td>
<td>3.05 (0.04, 209)**</td>
<td>2.98 (0.08, 127)</td>
<td>2.92 (0.02, 505)</td>
<td>2.94 (0.06, 110)</td>
<td>2.74 (0.13, 21)</td>
<td>2.94 (0.06, 112)</td>
<td>3.38 (0.06, 65)</td>
<td>2.99 (0.03, 311)</td>
</tr>
<tr>
<td>Asymptotic length (mm)</td>
<td>742.0 (37.1, 44)**</td>
<td>896.8 (34.0, 110)*</td>
<td>705.6 (28.7, 161)**</td>
<td>665.7 (26.6, 109)</td>
<td>838.4 (25.7, 425)**</td>
<td>648.0 (78.4, 76)</td>
<td>753.2 (49.0, 21)</td>
<td>610.2 (29.6, 107)</td>
<td>767.8 (182.5, 52)**</td>
<td>806.7 (21.4, 256)</td>
</tr>
<tr>
<td>TFI (g cm⁻¹)</td>
<td>0.91 (0.03, 47)</td>
<td>0.94 (0.02, 102)</td>
<td>0.95 (0.02, 209)**</td>
<td>0.83 (0.02, 93)</td>
<td>0.91 (0.01, 397)*</td>
<td>0.87 (0.02, 93)</td>
<td>0.88 (0.05, 20)</td>
<td>0.86 (0.02, 92)</td>
<td>0.93 (0.03, 27)**</td>
<td>0.88 (0.01, 262)</td>
</tr>
<tr>
<td>Mean residual prey size (mm)²</td>
<td>−0.05 (0.03, 93)</td>
<td>−0.01 (0.02, 283)</td>
<td>−0.01 (0.03, 248)</td>
<td>0.02 (0.03, 186)</td>
<td>−0.01 (0.01, 80)</td>
<td>0.07 (0.04, 73)**</td>
<td>0.08 (0.06, 43)</td>
<td>0.01 (0.02, 193)</td>
<td>−0.02 (0.01, 270)</td>
<td>0.01 (0.01, 579)</td>
</tr>
<tr>
<td>Mean residual δ¹⁵N (%)</td>
<td>−0.36 (0.12, 18)</td>
<td>0.23 (0.11, 19)*</td>
<td>0.16 (0.06, 80)</td>
<td>−0.15 (0.04, 80)</td>
<td>−0.01 (0.04, 197)</td>
<td>0.01 (0.08, 16)**</td>
<td>−0.16 (0.11, 20)</td>
<td>0.08 (0.06, 42)</td>
<td>0.01 (0.07, 36)</td>
<td>0.01 (0.04, 114)</td>
</tr>
<tr>
<td>FL (‰)</td>
<td>66.7 (53)</td>
<td>86.4 (118)</td>
<td>77.8 (185)</td>
<td>71.5 (130)</td>
<td>79.2 (466)</td>
<td>83.7 (11)</td>
<td>90.9 (22)</td>
<td>80.0 (90)</td>
<td>86.6 (65)*</td>
<td>83.3 (288)</td>
</tr>
<tr>
<td>Mean body condition</td>
<td>−0.02 (0.01, 51)</td>
<td>0.00 (0.01, 117)</td>
<td>0.01 (0.01, 193)*</td>
<td>0.00 (0.01, 129)</td>
<td>0.00 (0.00, 490)</td>
<td>0.03 (0.01, 110)**</td>
<td>−0.02 (0.01, 21)</td>
<td>−0.01 (0.01, 89)</td>
<td>0.02 (0.01, 67)</td>
<td>0.01 (0.08, 288)</td>
</tr>
<tr>
<td>Mean liver condition</td>
<td>−1.38 (0.17, 50)</td>
<td>0.25 (0.08, 91)</td>
<td>−0.44 (0.15, 178)</td>
<td>0.32 (0.15, 121)</td>
<td>−0.19 (0.08, 440)</td>
<td>0.80 (0.13, 108)**</td>
<td>0.20 (0.13, 19)</td>
<td>−0.37 (0.17, 74)</td>
<td>−0.13 (0.20, 64)</td>
<td>0.20 (0.09, 265)**</td>
</tr>
<tr>
<td>Mean body shape</td>
<td>−0.32 (0.17, 41)</td>
<td>−0.02 (0.16, 57)</td>
<td>−1.07 (0.11, 45)</td>
<td>−0.10 (0.10, 61)</td>
<td>−0.33 (0.07, 204)</td>
<td>0.76 (0.16, 40)**</td>
<td>0.87 (0.19, 23)**</td>
<td>0.21 (0.13, 45)**</td>
<td>0.22 (0.12, 44)**</td>
<td>0.45 (0.08, 150)**</td>
</tr>
</tbody>
</table>

Standard error and sample size are indicated in parentheses. Significant results (in vs. out by area and all areas combined) are indicated by asterisks and in bold. Shaded cells indicate values that were greater for each comparison (significant or not).

aFrom LWR (logW = a + b logL).
bPower transformed (TFI²).cResiduals from log prey size (mm) vs. cod length (mm).
dResiduals from δ¹⁵N vs. cod length (mm).
ePercentage of stomachs with food present (significance test: chi-squared).
fSeasonally adjusted (see Methods).
gMean discriminant function 1 score from morphometric analysis; more positive values indicate more streamlined body form.

Significance levels: ***p < 0.0001; **p < 0.01; *p < 0.05.
47) compared with open areas (n = 5; chi-squared test: \( \chi^2_{2,60} = 18.8; p < 0.0001 \)) and this difference was most pronounced for CAI and CL (Figure 2). Length also varied significantly among areas (ANOVA: \( F_{3,679} = 66.1; p < 0.0001 \)) and status (ANOVA: \( F_{1,679} = 14.7; p < 0.0001 \)) and the interaction between these two terms was significant (ANOVA: \( F_{3,679} = 10.2; p < 0.0001 \)). In this case, the mean length was significantly higher inside than that outside for CAI (Student’s t-test: \( t_{230} = 6.9; p < 0.0001 \)) and CL (Student’s t-test: \( t_{268} = 2.6; p < 0.01 \)). Although not significant, the trend for the other two areas was higher mean length inside CAII and higher mean length outside JL. Figure 2b shows length distributions and medians.

LWRs were also affected by both area and closure status (Table 2). Scaling coefficient or \( b \) values (i.e. the slope from equation: \( W = a + b \times \log L \)) tended to be higher inside than those outside closed areas for CAI, CAII, and CL. However, \( b \) values were not significantly different among status within these three areas when the interaction between the effect of status and \( \log L \) was considered (ANOVA: \( p > 0.05 \)). For the area JL, \( b \) was significantly higher outside than that inside the closed area (ANOVA: \( p < 0.05 \)). Somewhat counterintuitively, the interaction term was also significant for all data combined (ANOVA: \( p < 0.05 \)) such that \( b \) values were higher outside than those inside closed areas. This result was likely driven by the significant interaction effect for JL only and the fact that the \( b \) value for outside JL was so high (Table 2).

Similar to the age distribution and LWR results, VBGF parameters varied with area and closure status (Table 3). \( L_w \) was higher for cod inside closed areas compared with outside for all areas except JL. There was no consistent trend in \( k \) values among cod from inside and outside of closed areas, although \( k \) values were generally higher in the GOM (JL and CL) compared with those on GB (CAI and CAII); the reverse was true for \( L_w \). VBGF curves were significantly different among cod captured inside vs. outside of closed areas for all areas combined and within areas for CAI, CL, and JL. The difference among curves was marginally significant for CAII (Table 3). Length at ages 3 and 5 was higher inside vs. outside for all comparisons except for JL (both ages) and CAII (age 3) (Table 3).

FI (i.e. per cent stomachs with food present) for all areas combined was marginally higher outside of closed areas than inside (chi-squared test: \( \chi^2_{2,60} = 3.52; p = 0.06 \)). This result was driven primarily by a significant difference in FI between inside and outside for CL (chi-squared test: \( \chi^2_{2,60} = 4.71; p < 0.05 \)). For the cod that had food in their stomachs, TFI (cube root transformed) was significantly higher inside than outside of closed areas (Student’s t-test: \( t_{535} = 0.01 \); all areas combined). Overall, TFI varied significantly among areas and closure status, and the interaction was significant (Table 4); within areas, TFI was significantly higher inside vs. outside for CL only (Student’s t-test: \( t_{192} = 4.16 \); \( p < 0.0001 \)), while the trend was similar for CAI and CAII, but not for JL. TFI was not significantly related to length.

PFI\textsubscript{benthos} varied significantly among areas and closure status, and the interaction was significant (Table 4, Figure 3). Within areas, PFI\textsubscript{benthos} was significantly higher inside for CL only (Student’s t-test: \( t_{192} = 4.90; p < 0.0001 \)); the trend was similar for CAI and CAII but not for JL (Figure 3). PFI\textsubscript{pelagic} did not vary significantly among areas and closure status (ANOVA), and PFI\textsubscript{demersal} varied only among closure status with higher values inside closed areas. In this case, PFI\textsubscript{demersal} was significantly higher inside for CAI only (Student’s t-test: \( t_{92} = 4.16; p < 0.05 \)). While PFI\textsubscript{demersal} values were universally quite low compared with benthos and pelagic fish, demersal fish were virtually absent from the diet of cod outside of closed areas. Thus, while FI was generally higher outside of closed areas, stomach fullness was generally lower inside of closed areas where there was a greater representation of demersal fish.

For all areas combined, as well as within most areas, the prey size was significantly related to cod length, status, and the interaction between length and status (ANOVA: see Table 5). In all cases where the interaction term was significant (i.e. \( p < 0.05 \) for CAI, CL and JL), the nature of the interaction was such that the slope of the prey size–cod size relationship was higher inside closed areas vs. outside. And although not significant, the slope of the prey size–cod size relationship was higher inside than outside CAII. None of the above results were affected by constraining the data to cod lengths < 80 cm.

### Table 2. LWRs (log \( W = a + b \times \log L \)) for cod captured inside and outside of 4 major closed areas as well as all areas combined.

<table>
<thead>
<tr>
<th>Area</th>
<th>Status</th>
<th>( a )</th>
<th>SE</th>
<th>( b )</th>
<th>SE</th>
<th>( R^2 )</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAI</td>
<td>In</td>
<td>-2.07</td>
<td>0.10</td>
<td>3.04</td>
<td>0.06</td>
<td>0.98</td>
<td>56</td>
</tr>
<tr>
<td>CAI</td>
<td>Out</td>
<td>-1.87</td>
<td>0.08</td>
<td>2.93</td>
<td>0.05</td>
<td>0.96</td>
<td>127</td>
</tr>
<tr>
<td>CAII</td>
<td>In</td>
<td>-1.89</td>
<td>0.06</td>
<td>2.92</td>
<td>0.03</td>
<td>0.98</td>
<td>122</td>
</tr>
<tr>
<td>CAII</td>
<td>Out</td>
<td>-1.58</td>
<td>0.24</td>
<td>2.74</td>
<td>0.13</td>
<td>0.96</td>
<td>21</td>
</tr>
<tr>
<td>CL</td>
<td>In</td>
<td>-1.92</td>
<td>0.05</td>
<td>2.96</td>
<td>0.03</td>
<td>0.96</td>
<td>401</td>
</tr>
<tr>
<td>CL</td>
<td>Out</td>
<td>-1.91</td>
<td>0.10</td>
<td>2.94</td>
<td>0.06</td>
<td>0.95</td>
<td>113</td>
</tr>
<tr>
<td>JL</td>
<td>In</td>
<td>-1.95</td>
<td>0.13</td>
<td>2.97</td>
<td>0.08</td>
<td>0.92</td>
<td>135</td>
</tr>
<tr>
<td>JL</td>
<td>Out</td>
<td>-2.57</td>
<td>0.09</td>
<td>3.34</td>
<td>0.05</td>
<td>0.98</td>
<td>76</td>
</tr>
<tr>
<td>All</td>
<td>In</td>
<td>-1.79</td>
<td>0.04</td>
<td>2.88</td>
<td>0.02</td>
<td>0.96</td>
<td>717</td>
</tr>
<tr>
<td>All</td>
<td>Out</td>
<td>-1.98</td>
<td>0.05</td>
<td>2.99</td>
<td>0.03</td>
<td>0.96</td>
<td>340</td>
</tr>
</tbody>
</table>
Table 3. VBGF parameters for cod from various area/status combinations.

<table>
<thead>
<tr>
<th>Area</th>
<th>Status</th>
<th>L∞ (cm)</th>
<th>SE</th>
<th>k</th>
<th>SE</th>
<th>r²</th>
<th>N</th>
<th>RSS</th>
<th>F</th>
<th>d.f. denom</th>
<th>p</th>
<th>L1 (cm)</th>
<th>L5 (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAI</td>
<td>In</td>
<td>742.0</td>
<td>37.1</td>
<td>0.67</td>
<td>0.16</td>
<td>0.79</td>
<td>44</td>
<td>120901</td>
<td>12.89</td>
<td>114</td>
<td>&lt;0.0001</td>
<td>642.6</td>
<td>716.0</td>
</tr>
<tr>
<td>CAI</td>
<td>Out</td>
<td>648.0</td>
<td>78.4</td>
<td>0.62</td>
<td>0.25</td>
<td>0.34</td>
<td>76</td>
<td>430558</td>
<td>0.58</td>
<td>120</td>
<td>0.05</td>
<td>547.1</td>
<td>618.8</td>
</tr>
<tr>
<td>CAI</td>
<td>All</td>
<td>784.5</td>
<td>66.3</td>
<td>0.47</td>
<td>0.12</td>
<td>0.58</td>
<td>120</td>
<td>738454</td>
<td></td>
<td></td>
<td></td>
<td>593.0</td>
<td>709.7</td>
</tr>
<tr>
<td>CAII</td>
<td>In</td>
<td>896.8</td>
<td>34.0</td>
<td>0.37</td>
<td>0.06</td>
<td>0.72</td>
<td>110</td>
<td>633519</td>
<td>2.29</td>
<td>125</td>
<td>0.0016</td>
<td>641.3</td>
<td>755.8</td>
</tr>
<tr>
<td>CAII</td>
<td>Out</td>
<td>753.2</td>
<td>49.0</td>
<td>0.68</td>
<td>0.50</td>
<td>0.41</td>
<td>21</td>
<td>61013</td>
<td></td>
<td></td>
<td></td>
<td>655.3</td>
<td>728.1</td>
</tr>
<tr>
<td>CAII</td>
<td>All</td>
<td>877.4</td>
<td>29.1</td>
<td>0.40</td>
<td>0.06</td>
<td>0.69</td>
<td>131</td>
<td>732669</td>
<td></td>
<td></td>
<td></td>
<td>613.1</td>
<td>758.7</td>
</tr>
<tr>
<td>CL</td>
<td>In</td>
<td>705.6</td>
<td>28.7</td>
<td>0.52</td>
<td>0.08</td>
<td>0.64</td>
<td>161</td>
<td>844138</td>
<td>5.24</td>
<td>262</td>
<td>0.0016</td>
<td>557.3</td>
<td>653.2</td>
</tr>
<tr>
<td>CL</td>
<td>Out</td>
<td>610.2</td>
<td>29.6</td>
<td>0.64</td>
<td>0.15</td>
<td>0.46</td>
<td>107</td>
<td>585879</td>
<td></td>
<td></td>
<td></td>
<td>520.7</td>
<td>585.3</td>
</tr>
<tr>
<td>CL</td>
<td>All</td>
<td>669.4</td>
<td>21.9</td>
<td>0.55</td>
<td>0.08</td>
<td>0.57</td>
<td>268</td>
<td>1515869</td>
<td></td>
<td></td>
<td></td>
<td>540.8</td>
<td>626.6</td>
</tr>
<tr>
<td>JL</td>
<td>In</td>
<td>565.7</td>
<td>26.6</td>
<td>0.72</td>
<td>0.20</td>
<td>0.34</td>
<td>109</td>
<td>479286</td>
<td>4.87</td>
<td>155</td>
<td>0.0029</td>
<td>500.5</td>
<td>550.2</td>
</tr>
<tr>
<td>JL</td>
<td>Out</td>
<td>767.8</td>
<td>182.5</td>
<td>0.38</td>
<td>0.31</td>
<td>0.57</td>
<td>52</td>
<td>345543</td>
<td></td>
<td></td>
<td></td>
<td>522.2</td>
<td>653.0</td>
</tr>
<tr>
<td>JL</td>
<td>All</td>
<td>626.2</td>
<td>36.1</td>
<td>0.56</td>
<td>0.15</td>
<td>0.41</td>
<td>161</td>
<td>902530</td>
<td></td>
<td></td>
<td></td>
<td>509.5</td>
<td>588.1</td>
</tr>
<tr>
<td>All</td>
<td>In</td>
<td>838.40</td>
<td>25.7</td>
<td>0.37</td>
<td>0.04</td>
<td>0.65</td>
<td>424</td>
<td>3298596</td>
<td>8.53</td>
<td>672</td>
<td>&lt;0.0001</td>
<td>562.1</td>
<td>706.6</td>
</tr>
<tr>
<td>All</td>
<td>Out</td>
<td>695.40</td>
<td>31.6</td>
<td>0.5</td>
<td>0.09</td>
<td>0.5</td>
<td>256</td>
<td>1762379</td>
<td></td>
<td></td>
<td></td>
<td>540.2</td>
<td>638.3</td>
</tr>
<tr>
<td>All</td>
<td>All</td>
<td>806.70</td>
<td>21.4</td>
<td>0.4</td>
<td>0.03</td>
<td>0.61</td>
<td>680</td>
<td>5253140</td>
<td></td>
<td></td>
<td></td>
<td>556.3</td>
<td>691.9</td>
</tr>
</tbody>
</table>

L∞ was constrained to zero. Also shown are results from analysis of residual sum of squares (ARSS) and estimated length at ages 3 (L3) and 5 (L5).

Table 4. ANOVA results for the effect of area, closure status and their interaction on TFI, PFI_benthos, PFIpelagic and PFI_demersal (all cube root transformed).

<table>
<thead>
<tr>
<th>Effect</th>
<th>TFI</th>
<th>PFI_benthos</th>
<th>PFIpelagic</th>
<th>PFI_demersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>F</td>
<td>p</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Status</td>
<td>3.56</td>
<td>&lt;0.05</td>
<td>3.37</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Area × Status</td>
<td>3.45</td>
<td>&lt;0.05</td>
<td>5.33</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

Denominator degrees of freedom in all cases was 525.

Cod from outside of closed areas (all areas combined) were observed to occupy a more limited trophic niche space than cod from inside closed areas. δ15N and δ13C values inside closed areas were significantly less variable than outside (Levene’s test: p < 0.05; Figure 4). Notably missing from outside of closed areas were variables that were higher inside closed areas were primarily considered, and between 77 and 87% of the time within areas; the average among areas was 81% (Table 6). We then explored the mean loading values from DFA for cod by area/status (Figure 5). Mean loading scores were consistently higher outside than those inside closed areas. Morphometric features that were higher outside included length measurements from the head region; cod outside closed areas had longer heads. On the other hand, variables that were higher inside closed areas were primarily from the middle region of the body indicating deeper bodies.

Discussion

The purpose of this study was to compare a range of life-history variables (Table 1) for cod inside and outside of closed areas in New England to provide evidence for or against the hypothesis that closed areas have a net positive effect on cod. In this sense, a positive effect can mean greater longevity (enhanced age structure), higher growth, better feeding opportunities or higher condition. We also considered the possibility that closed areas may be selecting for more sedentary life styles (via body shape analysis; sensu Sherwood and Grabowski, 2010), the first ever consideration, to our
knowledge, of what may be considered area-based-management-induced selection in cod. Closed areas had a fairly consistent effect on cod life history variation (Table 1), particularly on age and growth variables that were mostly enhanced inside closed areas. The following is a detailed discussion of each of the variables and how they responded to closure status in each of the closed areas as well as overall.

Closed areas generally contained older cod than that which were found in adjacent open areas. In fact, we found nearly 10 times more cod aged ≥5 years inside closed areas than that which were found outside. Additionally, the median age was consistently 1 year older inside closed areas than that which were found outside (four out of four comparisons). If we consider the per cent difference, the median age was 50% higher inside closed areas than that outside for three of the areas (3 vs. 2 years old; CAI, CL, JL) and 25% higher for CAII (5 vs. 4 years old). Finally, there were some spatial differences in closed area effects on age structure. The most complete age structures were seen at Closed Area II and CL (Figure 2), the two areas farthest from shore, and likely less vulnerable to non-restricted fishing activities (e.g. recreational fishing). In other words, allowing activities such as recreational fishing inside closed areas may erode some of the age benefits that might otherwise be fully realized if closed areas were completely closed to fishing.

The age benefit that we document here may be of great importance to the current management of cod in New England. The most recent GOM cod assessment indicates that this stock is at 3–4% of its

Table 5. ANCOVA results for the relationship between prey length and predator (cod) length for all areas combined and within areas.

<table>
<thead>
<tr>
<th>Area</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>b x c</th>
<th>r²</th>
<th>p</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAI</td>
<td>–69.6</td>
<td>0.21</td>
<td>64.6</td>
<td>–0.1</td>
<td>0.21</td>
<td>&lt;0.0001</td>
<td>166</td>
</tr>
<tr>
<td>CAII</td>
<td>–51.6</td>
<td>0.14</td>
<td>N.S.</td>
<td>N.S.</td>
<td>0.12</td>
<td>&lt;0.0001</td>
<td>326</td>
</tr>
<tr>
<td>CL</td>
<td>–67.9</td>
<td>0.20</td>
<td>40.6</td>
<td>–0.09</td>
<td>0.18</td>
<td>&lt;0.0001</td>
<td>441</td>
</tr>
<tr>
<td>JL</td>
<td>–19.8</td>
<td>0.12</td>
<td>42.6</td>
<td>–0.09</td>
<td>0.04</td>
<td>&lt;0.001</td>
<td>456</td>
</tr>
<tr>
<td>All</td>
<td>–33.8</td>
<td>0.13</td>
<td>44.0</td>
<td>–0.08</td>
<td>0.10</td>
<td>&lt;0.0001</td>
<td>1,389</td>
</tr>
</tbody>
</table>

Relationship is of the form \( l_{\text{prey}} = a + b \times l_{\text{cod}} + c \times \text{“status”} + d \times l_{\text{cod}} \times \text{“status”} \).
target biomass level (Palmer, 2014). Additionally, the assessment finds few fish over 5 years old and states that this truncation in the age structure may compromise future recruitment success of the stock (Palmer, 2014). There are many reasons why age truncation may impact recruitment and rebuilding potential. It is well known that fish populations that contain a wide range of ages and, in particular, large proportions of old females can be more resilient and productive (Secor, 2000; Berkeley et al., 2004; Ottersen et al., 2006; Fogarty and O'Brien, 2009; Secor et al., 2014). In cod, old/large females help to ensure higher egg number and egg/larval viability (Kjesbu et al., 1996, Marteinsdottir and Steinarsson, 1998; Trippel, 1998) and also tend to spawn more effectively (Hixon et al., 2014). Specifically, older/larger females may release batches over many weeks during a spawning season, thus making it more likely for at least some of their eggs to encounter favourable conditions (i.e. sensu the match/mismatch hypothesis; Cushing, 1990), whereas younger/smaller and inexperienced females may spawn only one batch and potentially at the wrong time for egg survival (Trippel, 1998; Wright and Trippel, 2009).

There are currently no measures in place explicitly to ensure the survival of old/large females in the GOM/GB region or in any other fished cod population in the North Atlantic. Gear restrictions (e.g. minimum mesh sizes) and minimum size limits can protect young fish, but there is little that can be done to avoid capturing the largest individuals; to the contrary, these are often the most sought after. Harvest slots (taking only medium sized fish), as is successfully used in many recreational fisheries (Gwinn et al., 2013), would be virtually impossible to implement in what is primarily a trawl fishery for cod, although this may be an effective management option for the recreational cod fishery. Perhaps the only way to ensure survival of old/large females is through area management, of which closed areas are an integral part, along with rolling (spawning) closures (Berkeley et al., 2004). Our study indicates that closed areas, in their current configuration, may be crucial in buffering against further degradation in the age structure of GOM and GB cod, a process that would almost certainly lead to delays in rebuilding.

In general, our results suggest that the age/length/growth variables appeared to respond most consistently to closure status (Table 1). Of the 16 possible comparisons (four variables × four closed areas), 12 were significantly different among samples of cod captured inside vs. outside of closed areas. The pattern of response to closed area status was opposite for JL cod compared
with cod from the other three areas, which all responded consistently. In particular, mean age, mean length, scaling coefficient \((b)\), and asymptotic length were all higher (significantly or not) inside closed areas vs. outside for CAI, CAII, and CL, whereas the opposite was true for JL. These results suggest that cod inside those closed areas excluding JL (possibly because of higher recreational fishing effort inside JL) may experience lower mortality leading to higher age and length as well as higher growth resulting in enhanced \(b\) values and asymptotic lengths.

Cod diet and trophic relationships responded less consistently to closure status than age and growth variables. Although responses varied, the general trend was for higher stomach fullness (CAI, CAII, CL), smaller prey size (CAI, CAII, CL), higher \(\delta^{15}N\) or trophic position (CAII, CL) and lower FI (CAII, CL) inside vs. outside closed areas. Lower FI is often related to higher prey size (e.g. Albery Arrington et al., 2002) which is consistent with our \(\delta^{15}N\) results (Madigan et al., 2012), but not the prey size findings. Nonetheless, these results are consistent with cod inside closed areas having access to a broader range of feeding opportunities. This finding is further bolstered by the stable isotope results (Figure 4), which indicated that cod inside closed areas occupied broader trophic niches than those outside. Growing fish, including cod, with access to a diverse prey base, including large prey like other fish, tend to be more efficient than fish with access to more simplified (i.e. low diversity) prey bases; this can translate into higher condition and growth (Sherwood et al., 2002, 2007). Thus, our results revealing more diverse feeding opportunities inside closed areas may explain why we also observed higher growth inside.

Our morphometric analyses indicated that the reclassification rate was quite high (81% on average). Furthermore, there was a consistent functional aspect to the differences in body shape between cod captured inside and outside of closed areas. Specifically, cod from inside closed areas tended to have deeper bodies and shorter heads compared with cod from outside closed areas that had longer heads and narrower bodies (Figure 5). Sherwood and Grabowski (2010) compared body shape between red (a highly resident morphotype) and normal cod (assumed to be more migratory) and found similar differences in that the red cod had shorter heads and deeper bodies than the normal cod. We interpret the body shape results here as an indication of differences in migratory behaviour. Cod inside closed areas have body shapes more consistent with sedentary behaviours, whereas cod outside closed areas are more fusiform, as would be expected of a more migratory life-history strategy.

Our finding that body shape differed inside vs. outside of closed areas expands upon previous work on fisheries-induced selection for specific traits. Specifically, Olsen et al. (2004) showed that years of industrialized fishing resulted in maturation at younger ages and smaller sizes in northern cod (Newfoundland; NAFO Divisions 2J3KL). Fudge and Rose (2008) demonstrated that this change in maturity corresponded to an increase in fecundity at earlier ages. Meanwhile, Sinclair et al. found that cod fishing in the Gulf of St Lawrence favoured fast growth in the 1970s and then slow growth in the late 1980s and 1990s. Perhaps, these changes in reproductive endpoints and growth rates also coincided with changes in migratory propensity towards more resident/benthic lifestyles (GDS, unpublished). These examples related the effects of selective fishery removals on specific cod traits. In this paper, we document what may be the first known instance of an effect of spatial management on a cod life history trait—migration.

It is unclear whether this effect of closed areas on body shape, and presumably migration, is negatively or positively affecting the productivity of the stock. Robichaud and Rose (2004) reviewed migratory behaviour in 174 cod groups throughout the North Atlantic and found that maximum historical biomass was highest for migratory groups. Whether selection for more sedentary cod in closed areas will result in lower productivity in New England cod stocks requires further investigation.

Collectively, our results suggest that closed areas are demographically and ecologically beneficial to cod in the GOM and on GB. However, due to practical constraints, we sampled in relatively confined areas within and around the closed areas (Figure 1). Thus, it is currently unknown whether the benefits we demonstrate are widespread throughout closed areas or restricted to key habitats (e.g. Ammen Rock in CL or a habitat closure in the northern corner of CAII). The spatial extent of closed areas necessary to sustain cod has been considered previously. For northern cod, model simulations suggest that the early 1990’s stock collapse in Newfoundland might have been prevented by prior establishment of closed areas encompassing 80% of the fished area (Guénette et al., 2000). This estimate, which would prove highly impractical to implement, reflects the highly migratory nature of the northern cod before stock collapse (Rose, 1993). Following collapse, migratory pathways and behaviour was highly disrupted (Rose, 2003; Wrobleswki et al., 2005). In this case, Guénette et al. (2000) estimated that closing 20% of fishable bottom would be required to promote stock recovery. This estimate is more in line with the amount of bottom currently covered by year-round closed areas in the GOM and on GB/Nantucket Shoals (~17%; NEFMC, 2014, estimated from Map 52, pg 166). Given the mostly resident nature of GOM cod (Lindholm et al., 2007; Howell et al., 2008; Sherwood and Grabowski, 2010), this amount may be sufficient for the region.

While our results demonstrated that the closed areas on GB and in the GOM benefit cod, these closed areas have been found to have ecological benefits for other species. For instance, sea scallop biomass increased 14-fold within the closed areas on GB and southern New England from 1994 to 1998 immediately after their inception (Murawski et al., 2000). These authors also noted that closed areas are an effective management tool to improve yield per recruit by reducing mortality on sublegal individuals, thereby reducing growth overfishing. Given that sea scallops are far less mobile than Atlantic cod, it is not surprising that the closed area benefits for scallops were far more noticeable. In general, for more mobile species, effective management of exploitation outside of closed areas will be just as critical as the closed areas themselves (Murawski et al., 2000). The combination of reduced fishing effort coupled with closed areas protecting spawning aggregations of haddock could explain the 10-fold increase in the GB haddock stock between 1995 and 2005 (Brodzka et al., 2008). Collectively, these studies suggest that closed areas can contribute to the recovery of fishery species, even for mobile species like cod.

Closed areas have been used globally as an ecosystem management tool to rebuild fisheries in temperate marine ecosystems. Several global syntheses of no-take reserves have found greater biomass, density, species richness, and size of organisms within them compared with adjacent open areas (Côté et al., 2001; Gell and Roberts, 2003; Halpern and Warner, 2003; Lester et al., 2009). Some have suggested that closed area effects are more idiosyncratic and are dependent on factors such as their location, size, and age (Jennings, 2006; Côté et al., 2001; Kaiser, 2005; Clauzet et al., 2008; Edgar et al., 2014). While Lester et al. (2009) found that even small reserves can result in significant benefits irrespective of location, with temperate reef reserves equalising or outperforming...
tropical reef reserves, larger and older reserves generally result in greater positive effects on species biomass and abundance (Halpern and Warner, 2003; Claudet et al., 2010; White et al., 2011; Edgar et al., 2014). In our study system, it is unclear whether reserve size scales with benefits for cod and other species.

The efficacy of closed areas for rebuilding fishery species is likely tightly coupled with their life histories. For instance, as species disperse over greater distances either as larvae or through adult movement, the likelihood of reserves having local benefits on biomass decreases (Pelc et al., 2009; Claudet et al., 2010; White et al., 2011). Given that cod have long-lived larvae that are potentially broadly dispersed and are highly mobile as adults, it is somewhat surprising that we found older cod inside the reserves than out. This effect could be a function of the relatively large size of the closures in the GOM and GB, which collectively close over 22,000 km² to commercial fishing for groundfish. Our findings also speak to the importance of investigating more subtle population responses such as growth and age distributions in addition to focusing on effects of closures on the biomass and abundance of key species.

Future studies should be designed to examine the relationship between the spatial scale of closures and their effects on the population dynamics and productivity of cod and other species more closely. Furthermore, focusing on the benefits and costs (e.g. displacement of fishing effort to other areas or species) of closed areas to fish populations needs to be weighed against those of other species and ecosystem management tools such as reducing effort and modifying gear to avoid overfished species. The outcome of this research could help inform decisions regarding changes to closed area boundaries. The New England Fisheries Management Council (NEFMC) has completed an amendment process to either modify or maintain New England closed areas (as of summer 2015). The council has recommended status quo protections remain in place for CL and only minor reduction in the size of JL. Major changes have been proposed for GB closed areas including reduction in CAII, opening of CAI and addition of new closed areas. However, as of final submission of this article these recommendations were not yet made rules by NOAA Fisheries.

It is unknown to what extent any changes in closed area boundaries or size may erode the benefits that may have taken some years to accumulate. Russ and Alcala (2004) showed that closed area benefits for predatory fish (biomass) may take 15–40 years to manifest. Unfortunately, since we do not know the required size of New England closed areas for promoting cod age structure, any reductions in their scale, through the current amendment process or future actions, should be viewed as a risk that may impede rebuilding efforts, and should be carefully weighed against the potential benefits to resource users.

Conclusions

This study demonstrates a net positive effect of New England closed areas on cod biology. Age was consistently higher inside closed areas and this finding alone may be enough to herald the benefit of closed areas for promoting cod stock sustainability and recovery given the well-recognized advantage of maintaining older spawners in fished populations (Hixon et al., 2014; Secor et al., 2014). Closed areas also appear to be selecting for more sedentary body types in cod which suggests that they may be less effective for conserving individuals with more migratory propensities. A shift in life-history strategy towards more resident lifestyles may entail a loss in productivity (sensu Robichaud and Rose, 2004). Additionally, the potential for closed areas to create pockets of high density may make these aggregations more prone to environmental disturbances and catastrophes (McGilliard et al., 2011). However, these effects are less certain. What is certain is that New England cod stocks are in a state of crisis (Palmer, 2014). Management should be concerned not only with rebuilding SSB but also with conserving components of the existing SSB that contribute to disproportionately higher reproductive output (i.e. old fish). Perhaps, the only way to do this is through closed area management. Any alterations to the existing closed areas in the GOM and on GB should be considered carefully in light of what might further be lost (demographically) from already highly degraded cod stocks.

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References


