Exploring the potential inadvertent effects of Gulf of Maine and Georges Bank area closures on cod life-history variation

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¹ Note: This is a draft final report and contains one completed manuscript outlining the life-history differences between red and normal cod, and one draft manuscript (an executive summary and completed figures) detailing the results of life-history comparisons for cod captured within and outside of major closed areas in the Gulf of Maine and Georges Bank. A completed final report containing both manuscripts in completed form, as well as an introductory section linking the two manuscripts, will be submitted to the NEC by October 31, 2010.

Closed Area Cod - DRAFT

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Exploring the life-history implications of colour variation in offshore Gulf of Maine, USA cod (*Gadus morhua*)

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Keywords: alternative life-history strategies, Atlantic cod (*Gadus morhua*), colour, ecosystem management, ecotypes, marine closures, partial migration, red cod.

Note: this manuscript has been published elsewhere:

Abstract: The evolution of alternative life-history strategies in fish has largely been overlooked by fisheries managers even though differences in the biology of life-history variants can have important implications for the scale and productivity of fisheries. Cod display strikingly variable colouration in the Gulf of Maine, and red and olive-coloured cod can be found in close sympatry. Here, we examined whether colour types from Cashes Ledge, a shallow, offshore (~ 100 km) feature, differ in key life-history traits including diet, depth distribution, growth and body morphologies. Red cod consumed significantly more crabs, lobsters, and demersal fish, whereas olive cod consumed more shrimp. Stable carbon isotope signatures ($\delta^{13}C$) varied significantly among colour types, but is thought to reflect baseline differences in $\delta^{13}C$ at Cashes Ledge (potentially useful for residency estimates). Red cod were confined to a small area of shallow water (< 20 m) and were significantly smaller at age than olive cod. Body shape was used to classify colour types correctly with 84% accuracy; red cod had shorter snout lengths, deeper bodies and more slender tails than olive cod. Collectively these results suggest that red cod are resident at Cashes Ledge and represent a distinct life-history strategy from olive cod.
1. Introduction

A variety of fish species have evolved alternative life-history strategies within and among populations that can be typified by differences in diet, growth, maturation, and movement patterns (Bernatchez et al., 1996; Kerr et al., 2009). For example, many salmonid populations exhibit partial migration whereby a portion of the population remains resident to the natal stream while another group migrates to the ocean (Jonsson and Jonsson 1993; Morinville and Rasmussen, 2003). These different life-history strategies likely represent tradeoffs between growth, foraging efficiency, survival and fecundity (Jonsson and Jonsson, 1993; Morinville and Rasmussen, 2003), and may impart species resiliency to long-term environmental fluctuations (Kaitala et al., 1993). In addition to life-history variation existing within populations, fish species have been known to develop into sympatric and sometimes reproductively isolated morphotypes or ecotypes (Bernatchez et al., 1996; Boughman et al., 2005). Similar to the case with partial migration, ecotypes in fish tend to differ in diet, morphology, movement and growth (e.g., limnetic versus littoral sticklebacks, Baker et al., 2005; and dwarf versus normal lake whitefish, Trudel et al., 2001).

Uninformed fisheries management strategies that fail to consider this level of life-history complexity can inadvertently alter the relative proportion of ecotypes and/or life-history variants (Thériault et al., 2008) and consequently, result in unintended perverse outcomes. For example, barriers to upstream migration in rivers and streams can remove the migrant form from anadromous salmonid populations, and consequently result in these populations being dominated by the smaller and less productive resident form (Morita et al., 2009). In another case, heavy fishing pressure, species introductions and habitat degradation led to the near extirpation of “coasters” (a migrant, lake-going form of brook trout, Salvelinus fontinalis) in Lake Superior; the resident and less productive stream-dwelling form is still widespread (Schreiner et al., 2004). A similar fate may have befallen Atlantic cod in many parts of the northwest Atlantic. For example, Sherwood et al. (unpublished) found evidence for partial migration in Newfoundland cod and argued that heavy fishing may have altered the balance of migrants and residents such that populations became dominated by nearshore residents following stock collapses in the late 1980’s. This shift may have severe consequences for reproductive capacity and
stock rebuilding potential. Overall, if different life-history strategies represent distinct units within a metapopulation (Levins, 1968; Hansson, 1991; McQuinn, 1997), then management activities that select for one metapopulation unit (i.e., the migrant) over the other may enhance the likelihood that it becomes locally extinct (Kell et al., 2009).

In the United States, there is some evidence for the existence of life-history variants of Atlantic cod in the Gulf of Maine. An acoustic tagging study of cod movement and habitat associations in Stellwagen Bank National Marine Sanctuary (western Gulf of Maine) has identified a variety of movement behaviors ranging from highly sedentary to transient (Lindholm et al., 2007). This finding may be similar to what Sherwood et al. (unpublished) describe as partial migration in Newfoundland cod. Furthermore, Wirgin et al. (2007) have identified genetically distinct cod spawning populations (spring and summer spawning cod) in Ipswich Bay (western Gulf of Maine) that appear to differ also in egg and larval dispersal capacity (J. Churchill, Woods Hole Oceanographic Institute, unpublished data). It is not known whether these cod differ with respect to other life-history parameters that are typical of ecotype variation in other species (e.g., resident versus migrant behavior).

In the Gulf of Maine, the offshore banks and ledges have been noted as important grounds for Atlantic cod (Vadas and Steneck, 1988; Witman and Sebens, 1992). Young-of-year cod are common in the kelp forests on the top of Cashes ledge (Steneck, 1997)(Figure 1). Older juveniles ranging between 30 and 40 cm are also typical in the kelp habitat, and adult cod up to 1 meter in length have also been captured as shallow as 20-30 m on Cashes Ledge (Steneck, 1997; Grabowski et al., unpublished data). In addition to the kelp forest on top of the ledge which provides critical habitat for young-of-year cod, Cashes Ledge exhibits low annual variation in temperature (i.e., between 5 – 8 °C; Vadas and Steneck, 1988) that is suitable for each major cod life-history phase.

Multiple research cruises to Cashes Ledge in the last few years (Grabowski and Sherwood) have revealed the coexistence at this location of what appears to be two very distinct life-history variants of cod (Figure 2): “red” cod (sometimes referred to as “rock” cod) and the more common “olive” cod (also known elsewhere as “white-bellies” or “offshore” cod; Wroblewski et al., 2005). Red cod have been noted at Cashes Ledge and other locations around the Gulf of Maine for generations by fishermen and by early
naturalists (Bigelow and Schroeder, 1953). However, there are no reports on the biological significance of colour variation in Gulf of Maine cod in the primary literature. Scientific studies on red cod have been conducted elsewhere (Gosse and Wroblewski, 2004; Wroblewski et al., 2005). However, in this case, the focus has been on a genetically isolated population (Ruzzante et al., 2000) in coastal Labrador (Gilbert Bay) that does not overlap in any major way with offshore and other nearshore populations (Green and Wroblewski, 2001). The red colour in this population is thought to derive from a diet rich in carotenoids (i.e., local food sources; Gosse and Wroblewski., 2004). Red colouration has also been observed in coastal Norwegian cod (Dannevig, 1953). The observation that red cod have been captured consistently side-by-side with olive cod at Cashes Ledge (Grabowski and Sherwood, unpublished data) demonstrates that this level of phenotypic colour variation can exist in close sympatry. However, the extent of ecological and life-history differences between red and olive cod in the Gulf of Maine is currently unclear. In particular, are differences driven by phenotypic plasticity to changing diets, as suggested by Gosse and Wroblewski (2004), or is red colour in cod from Cashes Ledge only one aspect of a very distinct life-history strategy or ecotype?

The objective of the present study was to explore the life-history implications of colour variation in Gulf of Maine cod. We hypothesized that red cod are resident on Cashes Ledge given that they are rarely encountered in surrounding deeper waters, and therefore, should display life-history characteristics associated with resident types in other species including a more benthic diet (i.e., from local sources; Morris and Green, 2002), smaller size-at-age (Gross 1987), and a more robust body morphology (Morinville and Rasmussen, 2008). Conversely, we hypothesized that olive cod on Cashes Ledge are transient, grow to larger sizes, consume a diet that is rich in forage fish, and have a more streamlined body shape. Finally, we explore the implications of the existence of these putative life-history variants for management of cod in the Gulf of Maine.

2. Methods
2.1. Study Site
Cashes Ledge is a north-south oriented seamount located in the centre of the Gulf of Maine that extends up to 6 m at low tide on Ammen Rock Pinnacle (42° 51.25' N, 68°
57.11' W; Figure 1). The only offshore kelp forest in the Gulf of Maine is located on Cashes Ledge, and 2-m long ribbons of *Laminaria laminaria* extend from the top of the ledge to ~30 m depth. However, the kelp forest begins to transition to pockets of *Agarum cribosum* at ~20 m depth, which extend slightly deeper than *Laminaria laminaria*. Large internal waves have been documented on Cashes Ledge that influence chlorophyll dynamics on the ledge and, consequently, benthic-pelagic coupling (Witman *et al.*, 1993).

Cashes Ledge has been recognized as a critical area where groundfish are extremely abundant due to the presence of essential fish habitat supporting multiple groundfish life stages. It was identified by Collins and Rathbun (1887) and by Rich (1929) as an isolated but productive fishing ground in the middle of the Gulf of Maine. More recent Cashes Ledge studies have recorded the highest population density of cod in the Gulf of Maine (Witman and Sebens, 1992; Steneck, 1997; Steneck and Carlton, 2001). On May 1, 2004, Cashes Ledge was closed on a year round basis to all bottom-tending mobile gear in order to protect the important habitats associated with it. Because of its ecological importance, Cashes Ledge has been and will continue to be an area subject to intensive management attention.

### 2.2. Sampling design

We collected cod on Cashes Ledge at depths of 10 to 75 m in summer 2007, summer and winter 2008, and spring 2009 via hook and line sampling aboard the F/V *Special J*. During each sampling trip, 3-4 rods were utilized to retrieve fish. Each 2 m cod rod was outfitted with 13.6 kg test nylon braided line and a 22.7-kg test monofilament leader with two 7/0 barbed snelled hooks, soft-shell clam bait (~5 grams per hook) on each hook to attract fish, and a 0.5 kg sinker weight. Each cod that was captured was measured (total length \[L_{\text{tot}}\]; cm), photographed for morphometric and colour analyses, the depth at which it was captured recorded (m), and returned to the laboratory on ice for further analyses. Each fish was then frozen until processed.

Cod were thawed in the laboratory just prior to being processed. Each fish was weighed prior to and after the removal of vital organs to obtain a total and gutted weight, respectively. The liver and gonads were also weighed individually, and stomachs were retained for stomach content analyses. Sagittal otoliths were removed in order to estimate the age of cod and analyse growth rates. A ~1 g tissue sample located directly
anterior to the first dorsal fin was obtained from each cod to conduct stable isotope analyses to examine whether the diet of red and olive cod differ.

2.3. Colour

Colour analysis was conducted using the images of cod collected at sea to compare whether cod can be classified quantitatively as red and olive cod. In order to standardize the cod colour analyses, we selected a circular region located directly posterior to the eye and anterior to the posterior margin of the operculum. The red to green ratio of this entire area was analysed using colour analysis software (Image Pro Express 6.0, Media Cybernetics Inc.) for each fish. The red to green ratio ($RGR = \frac{\text{mean intensity of red}}{\text{mean intensity of green pixels}}$) was selected because it is very insensitive to variability in light conditions. This ratio was then utilized to categorize all cod as either red ($RGR \geq 1.3$) or olive ($RGR < 1.2$) for all subsequent analyses described below.

2.4. Diet

Stomach content analyses were used to examine the diet composition of red vs. olive cod. For each cod, individual dietary items were identified to species (where possible), counted, measured (mm), excess water removed, and weighed (mg). Partial fullness index (PFI) of different prey was calculated for each cod to compare the relative importance of major prey groups for red vs. olive cod (Bowering and Lilly, 1992; Sherwood et al., 2007). Prey items were partitioned into the following prey groups, which collectively accounted for $>90\%$ of the diet composition by weight of cod sampled in this study: Benthos (polychaetes, amphipods, molluscs, brittlestars, echinoderms and other small crustaceans); shrimp (various species); crabs (various species); lobsters; demersal fish (haddock, sculpins, cunner, etc.); pelagic fish (herring, redfish, silver hake, pollock and blue whiting) and unidentified fish. PFI was calculated by dividing the total weight ($g$) of prey$_i$ in each cod by the length (cm $L_{tot}$) of that fish cubed, and multiplying this proportion by $10^4$.

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. Stable isotope ratios provide a time-averaged (over many weeks to months) depiction of diet (Sherwood & Rose, 2005). Each tissue sample was dried in a drying oven at 60 °C for
48 hr to constant weight, homogenized to a fine powder using a mortar and pestle, placed into 4 x 6 mm tin capsules, and weighed. Samples were then sent to the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, AZ) for analysis. Samplers were combusted in order to analyse the carbon and nitrogen stable isotope ratios of CO₂ and N₂, 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 (δ) in this study are defined as the parts per thousand deviations from the following standard materials: Pee Dee belemnite limestone for δ¹³C and N₂ in air for δ¹⁵N. We also corrected for the potential confounding effects of lipids on δ¹³C (Wada et al., 1987) by normalizing δ¹³C values to carbon to nitrogen ratios (McConnaughey and McRoy, 1979). Lipid-corrected δ¹³C values are henceforth denoted by δ¹³C'. Five percent of the samples were analysed in duplicate.

2.5. Growth
Ageing was conducted to compare the growth rates of red and olive cod. A sagittal otolith of each cod was cut in half and polished, and the number of annuli on each otolith was counted to estimate the age of each cod. Size-at-age curves (see section 2.7) were then created for both cod colour types by examining the relationship between cod age and total length (L₉₀).  

2.6. Morphometrics
Shape in fish is often associated with movement behavior. For example, ocean-going migrant brook trout are more streamlined than residents (Morinville and Rasmussen, 2008). Cod morphometrics was conducted using the images collected at sea to determine if the shapes of red and olive cod differ. Twelve homologous cod landmarks were carefully selected (Figure 3) to minimize the confounding effects of human-induced error on the results (Bookstein, 1990). Landmarks were identified and marked on each cod, and the distances between landmarks were calculated for each fish using a box-truss approach (Strauss and Bookstein, 1982; Cadrin 2000).
2.7. Statistical analyses

Mann-Whitney U tests were used to examine how colour type affects PFI for each of the seven prey groups. Separate two-way ANOVAs were used to test the effect of colour type and size class on carbon ($\delta^{13}$C') and nitrogen ($\delta^{15}$N) stable isotope ratios. Growth was modeled as a Von Bertalanffy growth function:

$$\text{VBGF}; L_t = L_{inf} (1 – e(-k(t-t_0)))$$  \hspace{1cm} (1)

where $L_t$ is length (cm) at age $t$, $L_{inf}$ is asymptotic length, $k$ is the Brody growth coefficient (yr$^{-1}$) and $t_0$ the x intercept. Von Bertalanffy growth functions (VGBF curves) were established for the following three groups: red, olive, and all cod. We tested for significant differences in VGBF curves of red and olive cod by an analysis of the residual sum of squares (ARSS; Chen et al., 1992). Two-way ANOVA was also used to determine if colour types significantly differed in size across multiple size classes. This was performed because of low confidence in VGBF parameters, likely due to contracted age ranges sampled (most fish were between 2 and 6 years old) and high size variability within ages (Kritzer et al. 2001). Because the interaction between colour type and size class was significant, separate t-tests were used for each size class to determine whether the size of red and olive cod significantly differed. The effect of depth on cod red to green ratios was analysed using one-way ANOVA. Significant results were examined using Tukey post hoc pairwise tests.

The box-truss approach resulted in 22 linear dimensions used to describe the shape of each cod (Figure 3). These linear dimensions were natural log transformed to normalize their distributions. Principle component analysis was then conducted on the natural log transformed values. The first principle component, which is an indicator of fish length (Cadrin 2000), was used to standardize for differences in fish size by regressing the first principle component against each log transformed box-truss dimension. Using the residuals of each regression, discriminant function analysis was then performed to determine the percentages of red and olive cod that could be categorized correctly (Solow, 1990). Finally, stepwise discriminant function analysis was used to reveal the top three box-truss dimensions that explain the highest proportion of the variance.
With respect to the potential confounding effects of spawning and stomach fullness on the box-truss measurements (particular body depth), no cod were in spawning condition. Furthermore, variations in stomach fullness were unlikely to have affected our results since Fulton’s condition factor (FCF = total weight (g) / length$^3$ (cm) × 100), which takes into account variations in gut fullness, was identical among colour types for the size range (30-60 cm) compared for morphometrics (mean ± 1 std FCF = 0.95 ± 0.09 and 0.96 ± 0.09 for olive and red cod, respectively).

3. Results

3.1 Colour

Red to green ratios (RGR values) were used to classify cod as red or olive (Figure 4). RGR values varied from 1.01 to 2.45. An abrupt cut-off in high RGR values occurred at about 68 cm. RGR values beyond this size were no higher than 1.2. As such, 1.2 was taken as the cut-off (high-end) values for olive cod. All cod with RGR values above 1.3 were considered to be red (this left a small buffer zone in between types). Cod from ~30-70 cm display the entire range of RGR values (Figure 4); therefore, colour development is not ontogenetic in cod within this size range.

3.2. Diet

Ontogenetic trends in diet of both colour types of cod were examined (Figure 5), and some differences in feeding habits were noted. First, a common pattern in diet ontogeny in cod (i.e., gradual transition from small prey (e.g., shrimp) to larger fish; Sherwood et al., 2007) was pronounced in olive cod and less so in red cod. Red cod appeared to target fish much earlier in their development. In addition, only red cod were observed to feed on lobsters, although these did not make up a very large proportion of the diet. Non-parametric tests (Mann-Whitney U test) revealed significant differences in PFI among colour types for shrimp (higher in olive cod; z = -3.7, $p < 0.0001$; Figure 6), crabs (higher in red cod; z = -2.3, $p < 0.05$), lobsters (higher in red cod; z = -4.0, $p < 0.0001$), and demersal fish (higher in red cod; z = -3.0, $p < 0.01$); sample sizes in all cases were 64 for red cod and 163 for olive cod. Overall, red cod appeared to target larger benthic and demersal prey at smaller sizes than olive cod.
Stable isotope analysis of muscle tissue from red and olive cod suggested that cod diets differ among colour types (Figure 7). There was a strong significant effect of colour type on both $\delta^{13}C'$ (ANOVA, $F_{1,134} = 46.5, p < 0.0001$) and $\delta^{15}N$ (ANOVA, $F_{1,134} = 14.9, p < 0.0001$). There was an effect of size on $\delta^{15}N$ ($F_{2,134} = 23.2, p < 0.0001$) but not on $\delta^{13}C'$. In addition, there was a significant interaction effect of size class × colour type on both $\delta^{13}C'$ ($F_{3,134} = 3.9, p < 0.05$) and $\delta^{15}N$ ($F_{3,134} = 5.0, p < 0.01$). Interestingly, $\delta^{13}C'$ values were more pelagic in red cod than in olive cod at all sizes. $\delta^{15}N$, on the other hand, was significantly higher in olive cod only for smaller sizes (< 50 cm).

3.3. Growth
Von Bertalanffy growth functions varied among colour types (Figure 8). Despite low confidence in VBGF parameter estimates (Table 1), growth curves were significantly different among colour types (ARSS, $F_{3,241} = 6.19, p < 0.001$); red cod attain smaller sizes than olive cod ($L_{\text{inf}}$ for red and olive cod: 92 and 143 cm, respectively, although there was extremely low confidence in these values). Given the low confidence in VBGF parameters, size-at-age was also compared among age classes. ANOVA revealed a significant effect of both age ($F_{8,261} = 21.8, p < 0.0001$) and colour type ($F_{1,261} = 7.8, p < 0.01$) on length. Significant differences in size among colour types were seen for age 2 ($t$-test, $p < 0.05$, $n = 58$) and age 4 cod ($t$-test, $p < 0.001$, $n = 71$). In both cases, mean size was lower in red cod.

3.4. Distribution
The distributions of red and olive cod on Cashes Ledge differed substantially (Figure 9a). ANOVA revealed a significant effect of depth on RGR values ($F_{2,53} = 18.0, p < 0.0001$). RGR values were significantly higher at the shallowest depth sampled (<20 m) than either of the two deeper depths (20-30 m and > 30 m), which indicated that red cod are apparently located largely on the top of Cashes Ledge (Ammen Rock). Additionally, red cod were very rare over larger scales in the central Gulf of Maine (Figure 9b); high RGR values were seen only in very close proximity to Ammen Rock.

3.5. Morphometrics
Discriminant function analysis of morphometric characters correctly classified cod back to their respective colour types 84% of the time (Figure 10). Red cod were classified
correctly at a slightly higher rate than olive cod (Table 2). Stepwise discriminant function analysis revealed that the following three dimensions were the three most important for discriminating between red and olive cod (Figure 3): (D8) from the anterior edge of the base of the pelvic fin to the anterior edge of the base of the second dorsal fin; (D1) from the tip of the snout to the center of the eye; and (D22) from the anterior end of the base of the third dorsal fin to the anterior end of the base of the second anal fin. Examination of these three dimensions revealed that the anterior end of red cod are more robust (i.e., D8: red > olive cod), red cod have shorter snouts (i.e., D1: red < olive cod), and the posterior portion of their bodies are slightly more slender than olive cod (i.e., D22: red < olive cod).

4. Discussion
The present study finds evidence for what is interpreted as significant life-history variation among colour types of Atlantic cod in the Gulf of Maine (Cashes Ledge). Gosse and Wroblewski (2004) concluded that red colour in a coastal population of cod in Labrador was due to a diet rich in carotenoids (e.g., benthic invertebrates) based on the observation that if cod switch diet to fish, they lose their red colour. Similarly, Bigelow and Schroeder (1953) suggested that colour variation in Gulf of Maine cod is no more than an expression of diet and habitat preferences which can vary over a cod’s lifetime. Results of this study indicate that, while colour expression in cod can be ephemeral under certain circumstances, the expression of red colour is likely associated with a very distinct life-history strategy. Differences in diet (Figures 5,6), habitat preferences (distribution around Ammen Rock, Figure 9a), growth (Figure 8) and body shape (Figure 10) are all consistent with the existence of alternate life-history strategies in cod (and possibly ecotype variation), as shown in other species of fish (Jonsson and Jonsson, 1993; Morinville and Rasmussen, 2003; Kerr et al., 2009; Bernatchez et al., 1996). It is unknown whether this life-history variation results from a conditional strategy (e.g., partial migration) or genetic differences.

Near the extreme end of life-history variation within fish species is ecotype differentiation (e.g., Boughman et al., 2005; Trudel et al., 2001). Ecotypes usually imply or arise from some level of genetic isolation (e.g., Bernatchez et al., 1996; Baker et al.,
In this sense, red cod from Gilbert Bay, Labrador, being genetically isolated from other coastal cod populations in Newfoundland and Labrador (Ruzzante et al., 2000), and also differing in growth (Gosse and Wroblewski, 2004) and diet (Morris and Green, 2002) may in fact be a distinct ecotype of Labrador cod. Genetic isolation has not been tested for red cod from Cashes ledge, or any other location in the Gulf of Maine, and therefore it may be too early to conclude that these cod represent a distinct (genetic) ecotype. The fact that they co-occur with olive cod on Cashes Ledge suggests that they may not be genetically distinct. On the other hand, significant genetic population structure has been observed for other groups of cod coexisting over similarly contracted scales in the Gulf of Maine. Most strikingly, cod from Ipswich Bay (western Gulf of Maine) are genetically differentiated based on timing of spawning (Wirgin et al., 2007). It is suspected, in this case, that early spawners (winter months) are more migratory, as a corollary to higher egg and larval dispersion in winter (J. Churchill, WHOI, unpublished manuscript) than in spring when late spawners spawn. Similarly, differences in egg characteristics (buoyancy) can be correlated with sub-population structure in cod (Stenevik et al., 2008). It is hypothesized here that potential differences in timing and location of spawning, and potentially egg buoyancy and other early life-history characteristics, may lead to genetic isolation in Cashes Ledge cod. Thus, even though red cod may coexist with olive cod at Cashes Ledge, there are mechanisms (oceanographic and biological) that could feasibly lead to genetic differentiation of colour types. This hypothesis requires further investigation.

The alternative hypothesis is that colour variation at Cashes Ledge, and possibly other locations in the Gulf of Maine, represents a conditional strategy (Repka and Gross, 1995) for cod. The best known example of the conditional strategy in fish is partial migration in anadromous salmonids (Jonsson and Jonsson, 1993; Morinville and Rasmussen, 2003; Thériault and Dodson, 2003). In many cases of partial migration, it is believed that adoption of one approach over the other (e.g., resident versus migrant) depends early in life on environmental conditions (e.g., food availability near the natal location, Nordeng 1983; Forseth et al., 1994) and/or physiological status (e.g., growth: Bohlin et al., 1996; Forseth et al., 1999). In some cases, variable migratory tactics within populations can be shown to be heritable (e.g., Zimmerman and Reeves, 2002), although
in most cases heritability remains unclear (Hendry et al., 2004). A number of different scenarios may result in a conditional strategy for cod in the Gulf of Maine. Perhaps one of the more likely is that red cod represent juveniles that are advected to the center of the Gulf of Maine as larvae. Cashes Ledge is likely the only suitable habitat for them to settle into for up to 100 km in every direction. This could create a unique set of circumstances for developing juveniles that may “decide” to adopt a resident strategy on Cashes Ledge. All other life-history differences from there on may be a function of this early choice. Alternatively, olive cod at Cashes Ledge may just be cod from other areas of the Gulf of Maine that migrate there to forage. Before any conclusions can be drawn about whether cod at Cashes Ledge are expressing a conditional strategy or represent genetically distinct ecotypes, a great deal more needs to be learned about their residency behaviour, spawning times, and population genetics.

Regarding residency, our results are consistent with red cod residing at Cashes Ledge. Resident fish among and within populations tend to have more robust body shapes (Morinville and Rasmussen 2008) and attain smaller sizes (Gross 1987) than migrant fish, which was shown to be the case for red versus olive cod at Cashes Ledge (Figures 10 and 8, respectively). Furthermore, we hypothesized that red cod would also have a more benthic diet, indicative of feeding on more locally-derived food sources (e.g., Gosse and Wroblewski, 2004). Diet did vary among red and olive cod. Specifically, olive cod displayed a typical ontogenetic progression in diet (Sherwood et al., 2007) from small invertebrates (like shrimp) to fish (Figure 5). Red cod, on the other hand, consumed higher proportions of demersal fish at smaller sizes as well as larger quantities of crabs. Only red cod were observed to feed on lobsters. The lack of shrimp in red cod diets was likely due to their isolation on top of Ammen Rock (Figure 9a). Shrimp (e.g., Pandalus borealis) are typically distributed over fine-grained bottom sediments at depth (Haynes and Wigley, 1969) (i.e., not on top of Ammen rock). Shrimp are an important diet stage in cod (Sherwood et al., 2007) and the absence of shrimp in the diet of red cod may be what drives them to feed on larger benthic invertebrates. This in turn, may explain their deeper bodies and shorter heads (Figure 10), which are possible adaptations to feeding on large prey.
Stable isotope signatures differed among cod types (Figure 7), however the sign of the difference was the opposite of what was expected. In particular, both $\delta^{13}C'$ and $\delta^{15}N$ were more depleted (lower) in red cod than olive cod. Given that diet results show no obvious focus of red cod on pelagic or lower trophic level prey, it is hypothesized that observed stable isotope differences represent distinct stable isotope ecology at Cashes Ledge (i.e., baseline variations). Specifically, Cashes Ledge is bottom habitat that may be continually and strongly coupled with the surrounding pelagic zone (Witman et al., 1993). All resident organisms on Cashes Ledge, including benthic invertebrates and demersal fish, may therefore have $\delta^{13}C'$ signatures that resemble typical values of pelagic consumers as opposed to the benthos (see Sherwood and Rose, 2005 for a discussion of what mediates differences in stable isotope signatures for fish and invertebrates inhabiting continental shelves). Therefore, distinct $\delta^{13}C'$ values in red cod may be more of an indication of residency at Cashes Ledge than differences in feeding. Natural gradients in $\delta^{13}C$ have been used elsewhere to infer residency and movement in fish (Rasmussen et al., 2009). A logical next step for addressing the question of cod residency at Cashes Ledge would be to acoustically tag individuals and track their movements via a fixed acoustic receiver array (e.g., Lindholm et al., 2007).

Distributions of red cod at Cashes Ledge (Figure 9a) and the paucity of red cod at sites distant from Ammen Rock (Figure 9b) are further suggestive of residency for this putative life-history type. In addition, the highly localized nature of red cod at Cashes Ledge may provide some insight into the mechanisms that maintain red colouration in cod. Gosse and Wroblewski (2004) showed in a feeding experiment that red cod lose their colour when they are deprived of a diet rich in carotenoids (i.e., benthic invertebrates). Similarly, red colour in cod from Norway was attributed (Fox and Vevers, 1960) to feeding primarily on shore crabs (Carcinus maenas). These results and observations would imply that whenever cod feed on crustacean rich diets they are more likely to express red colour (e.g., crabs and lobsters at Cashes Ledge, Figure 5). However, Sherwood et al., (2007) presented diet results for over 16,000 cod from various regions in Newfoundland and Labrador. Despite major differences in diet (from 80% by weight shrimp, Pandalus borealis, in offshore Labrador to mostly fish in southern Newfoundland), there were no differences in colour. All cod from this study displayed
the typical countershaded pattern (G. Sherwood, personal observation) shown in Gosse and Wroblewski (2004). These contrasting situations illustrate that while fish need to consume a diet rich in carotenoids in order to express colouration (e.g., Ahilan and Prince Jeyaseelan, 2001), they only do so under certain circumstances. In every case, including the present study, red cod inhabit shallow (mostly inshore water; this study may be the only example of red cod occurring up to 100 km offshore, owing to the uniqueness of Cashes Ledge). Why cod express colour in shallow water is currently unknown. We speculate that red colour in cod may impart a cryptic advantage for living in kelp forests. The top of Cashes Ledge is noted for the dense stands of Laminaria kelp, which extend from the surface to ~30 m. Furthermore, red cod are only found in kelp and other algal habitats in the Gulf of Maine. Alternatively or complementarily, red colouration may protect cod from ultraviolet light, which can affect fish in various ways including causing skin damage when fish are overexposed (Zagarese and Williamson, 2000). This should only be an issue for fish living in very shallow water; the fact that red cod at Cashes Ledge are found mostly within 20 m of the surface is consistent with this hypothesis.

Conclusions

Red cod at Cashes Ledge appear to contribute to a rich diversity of life-history variants being discovered in populations of Atlantic cod throughout their range (e.g., Lindholm et al., 2007; Wirgin et al., 2007; Sherwood et al., unpublished). Our results suggest that red cod are highly localized on the top of Cashes Ledge, whereas olive cod extend deeper and grow to larger sizes, which is typical of a more transient life history strategy. Therefore, the Cashes Ledge Closure Area may be protecting red cod because they are resident within the closure, but affording little protection to olive cod if they move in and out of the reserve. Because red cod grow more slowly, management initiatives that select for red cod and other resident cod that may not express colour (e.g. Lindholm et al., 2007 for resident cod on Stellwagen Bank) could exacerbate the problem of reduced total cod biomass available by slowing the rate of rebuilding in the Gulf of Maine (assuming resident fish are less productive). Furthermore, the maximum size of red cod was substantially smaller than that of olive cod, suggesting that red cod may achieve a maximum size that is well below the ‘whale cod’ that sustained cod fisheries for centuries prior to collapse (Collins and Rathburn, 1887; Rich, 1929; Bigelow and Schroeder,
1953). Fecundity is typically positively correlated with body size, suggesting that red cod are in fact less productive. A cod population that is dominated by slow-growing, small resident cod may be incapable of fully recovering to historic productivity levels in spite of efforts to reduce fishing pressure in the Gulf of Maine. Therefore, managers should carefully consider such perverse and unintended consequences for life-history variation within and among populations when implementing future management initiatives.
5. Acknowledgements
We thank Curt Brown, Julien Gaudette, Aaron Lyons, Adam Baukus, Nicole Stephens, Jessica Lueders-Dumont, Nicole Condon, Josh Emmerson, Marissa McMahan, Spencer Blair-Glantz, Erin Wilkinson, Pat Meyers, Laura Armstrong, Zach Whitener, Matt Moretti and Jane Johnson for assistance in the field and laboratory. We thank John Shusta (FV Special J) for collecting fish. Funding for this project was provided by the Northeast Consortium (NA06NMF4720095) and the National Science Foundation (OCE-01-22031).
6. References


Steneck, R.S. 1997. Fisheries-induced biological changes to the structure and function of the Gulf of Maine Ecosystem. Plenary Paper. pages 151 - 165 in Wallace, G.T., and


Table 1. Parameter estimates and standard error (SE) for Von Bertalanffy growth function curve fits. RSS is residual sum of squares.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Red cod</th>
<th>Olive cod</th>
<th>All cod</th>
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<td>RSS</td>
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<tr>
<td>$N$</td>
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Table 2. The number and percentage of correctly classified red and olive cod using discriminant function analysis after correcting for differences in size among fish.

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<th>Predicted red</th>
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<tr>
<td>Red</td>
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<td>49</td>
<td>84%</td>
</tr>
<tr>
<td>Total</td>
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**Figure 1.** Map of Gulf of Maine showing location of Cashes Ledge. Contours (increasing line thickness) are 25, 50, 100, 150, 275, 500, 1000, 2500, and 5000 meters.
**Figure 2.** Image of red and olive cod captured on same line at Cashes Ledge.
Figure 3. Schematic diagram of the box-truss network used to examine whether the morphology of red and olive cod differ. Twelve Landmarks and 22 linear dimensions (numbered) were selected to test for differences in the shape of colour types.
Figure 4. Red to green ratio (RGR) versus length for cod from Cashes Ledge. Dashed vertical line represents upper bound of high RGR values; horizontal dashed line represents maximum RGR value for what are considered olive cod. Cod with intermediate RGR values (1.2-1.3; $n = 34$) are not shown and were excluded from all analyses.
Figure 5. Mean partial fullness index (PFI) of various prey items in the diet of olive and red cod by 5 cm length interval. Prey categories are as follows: BEN, benthos; SHR, shrimp; CRA, crabs; LOB, lobster; DEM, demersal fish; PEL, pelagic fish; FIS, unidentified fish. Samples sizes are shown in parentheses.
Figure 6. Mean partial fullness index (PFI) by prey category and colour type. Asterisks represent significant differences among types (Mann-Whitney U test): *** $p < 0.0001$; ** $p < 0.01$; * $p < 0.05$. Prey categories are as follows: BEN, benthos; SHR, shrimp; CRA, crabs; LOB, lobster; DEM, demersal fish; PEL, pelagic fish; FIS, unidentified fish.
Figure 7. Mean (± 95% CI) δ¹³C' versus mean δ¹⁵N (± 95% CI) for red and olive cod by size class (cm).
Figure 8. Modeled growth (Von Bertalanffy growth function) for red and olive cod from Cashes Ledge.
Figure 9a. The distribution of red and olive cod captured on Cashes Ledge in angler surveys in 2007-2009. Circles denote the locations where fishing was conducted during surveys, and the shading of circles represents the mean RGR value of the catch (see legend). Note how high mean RGR values are largely confined to area above 30 m depth, an area about $2 \times 1$ km.
Figure 9b. Three-dimensional plot indicating spatial variation in RGR values in the vicinity of Cashes Ledge. Maximum distance between sampling sites is 77 km.
Figure 10. Discriminant function analysis of morphometric characters classified 84% red and olive cod correctly. Open circles signify red cod and closed circles are olive cod.
Exploring the effects of Gulf of Maine and Georges Bank area closures on cod life-history variation

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

Note: This manuscript is in preparation. Key figures and figure captions have been included here to highlight important results.
Abstract (draft): From 1994 to 1998, five major year-round closed areas were established in the Gulf of Maine (GOM) and on Georges Bank (GB) to promote recovery of groundfish species including Atlantic cod (*Gadus morhua*). In addition to curbing groundfish mortality, closed areas may also provide an added benefit of more suitable foraging opportunities in the absence of bottom-tending fishing gear. Here, we test the hypothesis that GOM and GB closed areas are having a net positive impact on cod growth and condition via increased feeding success. While growth was not significantly different among sites inside and outside of 4 major closed areas, cod did achieve higher ages and sizes inside compared to outside of closed areas; age and size distributions were much more complete inside closed areas. Mean stomach fullness tended to be higher in 3 out of the 4 closed areas compared to adjacent open areas, which may explain higher condition factor (Fulton’s) inside closed areas, particularly for larger cod, potentially accounting for why closed areas harbor more old/large cod. Finally, body shape was compared among cod from open and closed areas and found to be significantly more robust inside closed areas compared to outside where cod tended to have more streamlined body shapes. These morphometric results will be discussed in terms of a shift in life-history strategies towards more sedentary behavior which may be counterproductive to large-scale cod rebuilding. Overall, however, it may be concluded that closed areas are achieving the goal of providing good feeding grounds for cod at the same time as they are protecting large/old individuals.
Table 1. Von Bertalanffy growth function parameters for cod from various area/closure status combinations. RSS is residual sum of squares. Note that high $L_\infty$ values tend to occur outside of closed areas where the age structure is truncated (Figure 2). Hence, we are only catching the linear part of the growth curve in these cases.

<table>
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**Figure 1.** Map of Gulf of Maine and Georges Bank 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.
Figure 2. Age-frequency distributions and growth curves for cod sampled in and near (out) 4 major closed areas in the Gulf of Maine and Georges Bank. Von Bertalanffy growth function parameters for each growth curve is tabulated in Table 1.
Figure 3. Mean age of cod inside and outside of 4 major closed areas. Error bars represent standard error. Asterisks indicate significant difference among ‘in’ and ‘out’ ($p < 0.001$, student’s $t$-test); ‘ns’ means not significant. Overall, age was significantly related to area (ANOVA, $F_{3,618} = 32.6$, $p < 0.0001$) and status (i.e., ‘in’ vs. ‘out’; ANOVA, $F_{1,618} = 6.0$, $p < 0.05$) for all areas combined. The interaction term was not significant.
Figure 4. Mean length of cod inside and outside of 4 major closed areas. Error bars represent standard error. Asterisks indicate significant difference among ‘in’ and ‘out’ ($p < 0.0001$, student’s $t$-test); ‘ns’ means not significant. Overall, length was significantly related to area (ANOVA, $F_{3,635} = 61.8$, $p < 0.0001$) and status (i.e., ‘in’ vs. ‘out’; ANOVA, $F_{1,635} = 10.6$, $p < 0.001$) for all areas combined. The interaction term was also significant (ANOVA, $F_{3,635} = 8.6$, $p < 0.0001$).
Figure 5. Mean stomach fullness index (SFI = stomach weight (g) / length$^3$ (mm) x 10$^4$) for cod inside and outside of 4 major closed areas. SFI was significantly higher inside closed areas compared to adjacent (out) for CAI and CL (Kruskal-Wallis, $p < 0.05$) and for all areas pooled (Kruskal-Wallis, $p < 0.0001$).
Figure 6. Mean partial fullness index for various prey items (see legend) by 10 cm length interval for cod inside and outside of 4 major closed areas. Feeding appears to be more complete inside of closed areas compared to adjacent open areas for 3 out of 4 of the areas.
Figure 7. Mean partial fullness index of 8 most important prey groups for cod studied by area and closure status (i.e., ‘in’ vs. ‘out’). Asterisks represent significant difference between closure status within area (Kruskal-Wallis, p < 0.05). Over all areas, only 3 prey taxa mean PFI’s were significantly different among closure status (demersal fish, higher inside closed areas, p < 0.05; crabs, higher inside closed areas, p < 0.001; and benthos, lower inside closed areas, p <0.05). Error bars represent standard error. Comparisons were done for overlapping size classes (i.e., < 80 cm).
Figure 8. Stable carbon ($\delta^{13}$C) versus stable nitrogen ($\delta^{15}$N) signatures for cod from inside and outside of Cashes Ledge and Jeffrey’s Ledge. Error bars represent standard error. $\delta^{13}$C varies significantly among areas (lower at Cashes ledge; ANOVA, $F_{1,209} = 18.1, p < 0.0001$) and closure status (lower, more pelagic, inside closed areas; ANOVA, $F_{1,209} = 18.9, p < 0.0001$). Carbon results are consistent with higher fish and herring in the diet for CL but not for JL where higher herring occurs outside of closed area. $\delta^{15}$N varies significantly among areas (ANOVA, $F_{1,209} = 25.3, p < 0.0001$), however not among closure status. Stable isotope results for CAI and CAII will be included in final draft.
Figure 9. Fulton’s condition factor of cod inside and outside of 4 major closed areas by closure status. Condition is either lower for cod outside of closed areas or trending downwards compared to cod from inside closed areas, where condition is mostly trending upwards at larger sizes (except for JL). Higher condition in cod appears to coincide with higher feeding intensities regardless of closure status, however, mostly higher inside closed areas (Figure 6).
**Figure 10.** Discriminant function analysis of 13 body shape variables for red cod and cod captured inside, outside and near the edge of 5 major closed areas. Body shape of normal colored cod is significantly more robust (less streamlined) inside closed areas than outside. Note that this analysis is preliminary. The final report will contain a more complete morphometric analysis that uses box-truss measurements (see manuscript 1 methods and results).