

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

Graham D. Sherwood and Jonathan H. Grabowski

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The evolution of alternative life-history strategies in fish has largely been overlooked by fisheries managers, although 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, with red- and olive-coloured cod found in close sympatry. Colour types from Cashes Ledge, a shallow, offshore (~100 km) feature, are examined to see whether they differ in key life-history traits including diet, depth distribution, growth, and body morphology. Red cod consumed significantly more crabs, lobsters, and demersal fish, whereas olive cod consumed more shrimp. Stable carbon isotope signatures ($\delta^{13}\text{C}$) varied significantly among colour types, but are thought to reflect baseline differences in $\delta^{13}\text{C}$ at Cashes Ledge (potentially useful for residence 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 snouts, deeper bodies, and more slender tails than olive cod. Collectively, the results suggest that red cod are resident at Cashes Ledge and represent a life-history strategy distinct from olive cod.

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

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G. D. Sherwood and J. H. Grabowski: Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA. Correspondence to G. D. Sherwood: tel: +1 207 2281644; fax: +1 207 7726855; e-mail: gsherwood@gmri.org.

Introduction

Several 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, whereas another group migrates to the ocean (Jonsson and Jonsson 1993; Morinville and Rasmussen, 2003). These different life-history strategies likely represent trade-offs between growth, foraging efficiency, survival, and fecundity (Jonsson and Jonsson, 1993; Morinville and Rasmussen, 2003) and may impart species resilience to long-term environmental fluctuations (Kaitala *et al.*, 1993). In addition to life-history variation within populations, some fish species have developed 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 vs. littoral sticklebacks (Baker *et al.*, 2005) and dwarf vs. 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 can 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 those populations being dominated by the smaller, 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 (*Gadus morhua*) in many parts of the Northwest Atlantic. For example, evidence has been found for partial migration in Newfoundland cod, perhaps indicative of heavy fishing altering the balance of migrants and residents such that populations became dominated by nearshore residents following stock collapses in the late 1980s (GDS, pers. obs.). This shift may have severe consequences for reproductive capacity and stock rebuilding. 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 another may make it more likely that the migrant 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) identified a variety of movement behaviours ranging from highly sedentary to transient (Lindholm *et al.*, 2007). This finding may be similar to what was described as partial migration

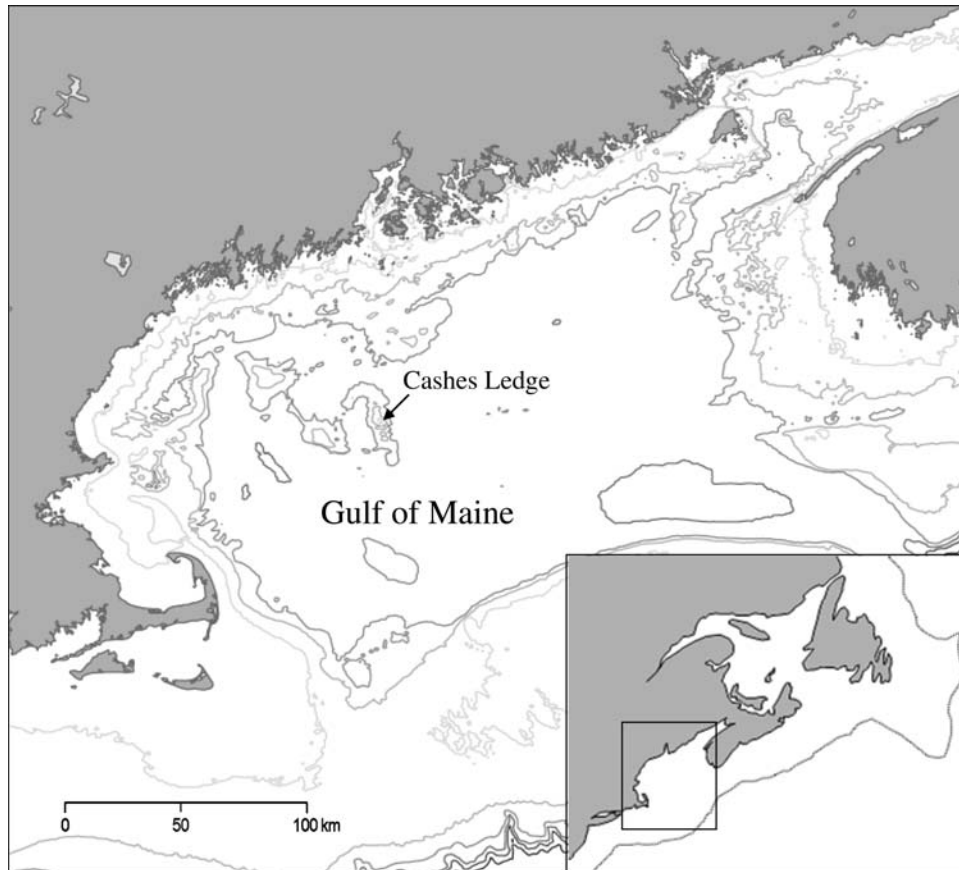


Figure 1. Map of the Gulf of Maine showing the location of Cashes Ledge. Contours (increasing line thickness) are 25, 50, 100, 150, 275, 500, 1000, 2500, and 5000 m.

in Newfoundland cod (GDS, pers. obs.). Moreover, *Wirgin et al.* (2007) identified genetically distinct cod spawning populations (spring and summer spawning) in Ipswich Bay (western Gulf of Maine) that appear to differ also in the dispersal capacity of eggs and larvae (J. Churchill, Woods Hole Oceanographic Institution, unpublished data). It is not known, however, whether these cod differ with respect to other life-history parameters that are typical of ecotype variation in other species, e.g. resident vs. migrant behaviour.

In the Gulf of Maine, the offshore banks and ledges are 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 of 30–40 cm are also typical in the kelp habitat, and adult cod up to 1 m long have also been captured as shallow as 20–30 m on Cashes Ledge (*Witman and Sebens, 1992; Steneck, 1997; JHG, unpublished data*). In addition to the kelp forest on the top of the ledge that provides crucial habitat for young-of-year cod, Cashes Ledge has little annual variation in temperature (5–8°C; *Vadas and Steneck, 1988*), which renders it suitable for each major life-history phase of cod.

Multiple research cruises to Cashes Ledge in the past few years by both authors have revealed the coexistence there of what appears to be two 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



Figure 2. A red and an olive cod captured on the same line at Cashes Ledge.

noted at Cashes Ledge and other locations around the Gulf of Maine for generations by fishers and 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, 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 near-shore populations (*Green and Wroblewski, 2001*). The red colour in the population is thought to derive from a local diet

rich in carotenoids (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 at the same time as olive cod at Cashes Ledge (JHG and GDS, 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. Specifically, are the differences driven by phenotypic plasticity to changing diets, as suggested by Gosse and Wroblewski (2004), or is the red colour of cod at Cashes Ledge only one aspect of a 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 water, so they 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, it could be that olive cod on Cashes Ledge are transient, grow larger, consume a diet rich in forage fish, and have a more streamlined body shape. Finally, we explored the implications of the existence of these putative life-history variants for cod management in the Gulf of Maine.

Methods

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

Cashes Ledge has been recognized as a critical area where groundfish are abundant owing 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 centre of the Gulf of Maine. More recent Cashes Ledge studies have recorded the highest population density of cod anywhere in the Gulf of Maine (Witman and Sebens, 1992; Steneck, 1997; Steneck and Carlton, 2001). On 1 May 2004, Cashes Ledge was closed year-round to all bottom-tending mobile gear to protect its important habitats. Because of its ecological importance, however, Cashes Ledge has been and will continue to be an area of keen management attention.

Sampling design

We collected cod on Cashes Ledge at depths of 10–75 m in summer 2007, summer and winter 2008, and spring 2009 via hook-and-line sampling aboard the FV “Special J”. During each sampling trip, 3–4 rods were utilized to retrieve fish. Each 2 m 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 g per hook) on each hook to attract fish, and a 0.5-kg sinker. Each cod captured was measured [total length (L_{tot}), cm], photographed for morphometry and

colour, the depth of capture recorded (m), and returned to the laboratory on ice for further analysis. Each fish was then frozen until processed.

Cod were thawed in the laboratory just before being processed. Each was weighed before 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 to determine the age of the cod and to evaluate 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 assess possible differences in the diet of red and olive cod.

Colour

Colour analysis was conducted using the images of cod collected at sea to compare whether cod can be classified quantitatively as red or olive. 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 (RGR) of this entire area was analysed using colour analysis software (Image Pro Express 6.0, Media Cybernetics Inc.) for each fish. The RGR (the mean intensity of red divided by the mean intensity of green pixels) was selected because it is insensitive to variability in light conditions. The ratio was then utilized to categorize all cod as either red (RGR \geq 1.3) or olive (RGR $<$ 1.2) for all subsequent analyses.

Diet

Stomach contents were used to compare the diet of red and olive cod. For each cod, individual diet items were identified to species (where possible), counted, measured (mm), the excess water removed, and weighed (mg). Partial fullness index (PFI) of the different prey was calculated for each cod to compare the relative importance of major prey groups for red and olive cod (Bowering and Lilly, 1992; Sherwood *et al.*, 2007). Prey items were partitioned into the following groups, which collectively accounted for >90% of the diet by weight of cod sampled in this study: benthos (polychaetes, amphipods, molluscs, brittlestars, echinoderms, and other small crustaceans); shrimps (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. The PFI was calculated by dividing the total weight (g) of prey_{*i*} in each cod by the length (L_{tot} ; cm) of that fish cubed and multiplying this proportion by 10^4 .

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) 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 and Rose, 2005). Each 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 the 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 parts per thousand deviations from the following standard materials: Pee Dee

belemnite limestone for $\delta^{13}\text{C}$, and N_2 in air for $\delta^{15}\text{N}$. We also corrected for the potential confounding effects of lipids on $\delta^{13}\text{C}$ (Wada *et al.*, 1987) by normalizing $\delta^{13}\text{C}$ values to carbon-to-nitrogen ratios (McConnaughey and McRoy, 1979). Lipid-corrected $\delta^{13}\text{C}$ values are from now on denoted by $\delta^{13}\text{C}'$. Just 5% of the samples were analysed in duplicate.

Growth and morphometrics

Age determination was conducted to compare the growth rates of red and olive cod. A sagittal otolith of each cod was cut into two through the centre and polished, and the number of annuli on each otolith was counted to estimate the age. Size-at-age curves (see below) were then created for both cod colour types by examining the relationship between cod age and total length (L_{tot}).

Shape in fish is often associated with movement behaviour. For example, ocean-going migrant brook trout are more streamlined than residents (Morinville and Rasmussen, 2008). Cod morphometrics were inspected on the images collected at sea to determine whether the shapes of red and olive cod differ. In total, 12 homologous landmarks of cod were 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).

Statistical analyses

Mann–Whitney U -tests were used to examine how colour type influences the 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 ($\delta^{13}\text{C}'$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios. Growth was modelled as a von Bertalanffy growth function (VBGF), $L_t = L_{\text{inf}}(1 - e^{-k(t - t_0)})$, where L_t is length (cm) at age t , L_{inf} the asymptotic length, k the Brody growth coefficient (year^{-1}), and t_0 the x -intercept. VBGF curves were established for the following three groups: red, olive, and all cod. We tested for significant differences in VBGF curves of red and olive cod by analysing the residual sum of squares (ARSS; Chen *et al.*, 1992). Two-way ANOVA was also used to determine whether colour types differed significantly in size across multiple size classes. This was performed because of low confidence in VBGF parameters, likely because of the curtailed age ranges sampled (most fish were between 2 and 6 years old) and great size variability within ages (Kritzer *et al.*, 2001). As 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 differed significantly. The effect of depth on cod RGRs was

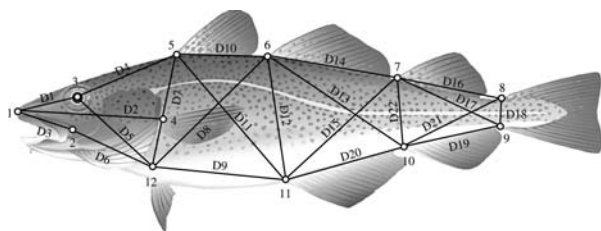


Figure 3. Schematic diagram of the box-truss network used to examine differences in the morphology of red and olive cod. In all, 12 landmarks and 22 linear dimensions (numbered) were selected to test for differences in the shape of colour types.

analysed using one-way ANOVA. Significant results were evaluated with the 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. 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 red and olive cod that could be categorized correctly (Solow, 1990). Finally, stepwise DFA was used to reveal the top three box-truss dimensions that explained the greatest proportion of the variance.

With respect to the potential confounding effects of spawning and stomach fullness on box-truss measurements (particularly body depth), no cod were in spawning condition. Moreover, variations in stomach fullness were unlikely to have affected our results because Fulton's condition factor [$\text{FCF} = \text{total weight (g)} / \text{length}^{-3} \text{ (cm)} \times 100$], 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 s.d.; $\text{FCF} = 0.95 \pm 0.09$ and 0.96 ± 0.09 for olive and red cod, respectively).

Results

Colour

The values of RGR were used to classify cod as red or olive (Figure 4); they varied from 1.01 to 2.45. An abrupt cut-off in high values of RGR was found at ~ 68 cm body length. Values of RGR for fish longer than this were ≤ 1.2 . Therefore, 1.2 was taken as the cut-off (high-end) value for olive cod, and all cod with RGR values ≥ 1.3 were considered to be red (this left a small buffer zone in between types). Cod from ~ 30 to 70 cm display the entire range of RGR values (Figure 4), so colour development is not ontogenetic in cod within this size range.

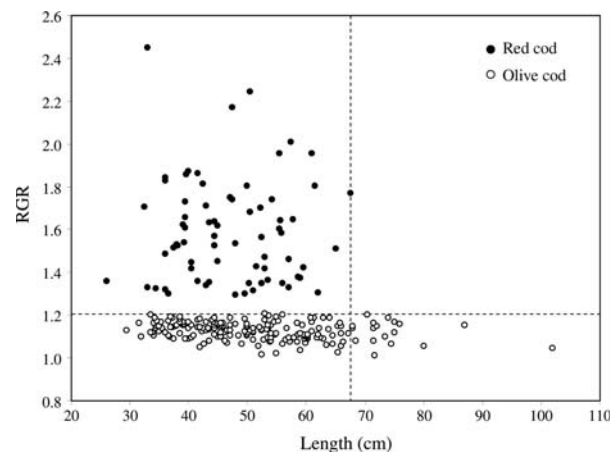


Figure 4. RGR plotted against length for cod from Cashes Ledge. The dashed vertical line represents the upper bound of high RGR values, and the horizontal dashed line the maximum RGR for what are considered to be olive cod. Cod with intermediate RGR values (1.2–1.3; $n = 34$) are not shown and were excluded from all analyses.

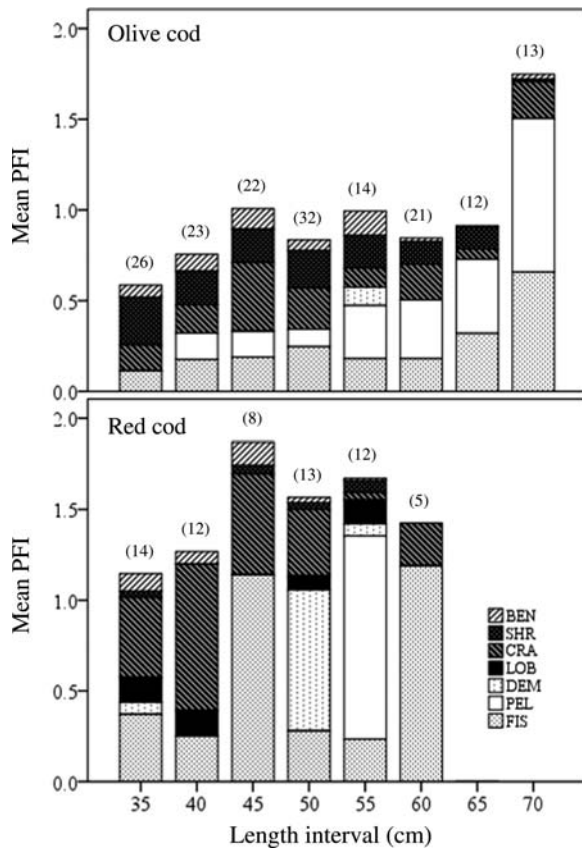


Figure 5. Mean PFI of various prey items in the diet of olive and red cod by 5-cm length interval. Prey categories are BEN, benthos; SHR, shrimp; CRA, crabs; LOB, lobster; DEM, demersal fish; PEL, pelagic fish; FIS, unidentified fish. Samples sizes are given in parenthesis.

Diet

Ontogenetic trends in diet of both colour types of cod (Figure 5) revealed some differences in feeding habits. First, a common pattern in diet ontogeny in cod, i.e. a 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 own development. In addition, only red cod apparently fed on lobsters, although these did not account for a very large proportion of the diet. Non-parametric tests (the 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 always were 64 for red cod and 163 for olive cod. Overall, smaller red cod than olive cod appeared to target larger benthic and demersal prey.

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 $\delta^{13}\text{C}'$ (ANOVA, $F_{1,134} = 46.5$, $p < 0.0001$) and $\delta^{15}\text{N}$ (ANOVA, $F_{1,134} = 14.9$, $p < 0.0001$). There was an effect of size on $\delta^{15}\text{N}$ ($F_{2,134} = 23.2$, $p < 0.0001$), but not on $\delta^{13}\text{C}'$. In addition, there was a significant interaction effect of size class \times colour type on both $\delta^{13}\text{C}'$ ($F_{3,134} = 3.9$, $p < 0.05$) and $\delta^{15}\text{N}$ ($F_{3,134} = 5.0$, $p < 0.01$). Notably, $\delta^{13}\text{C}'$ values were more pelagic in red cod than

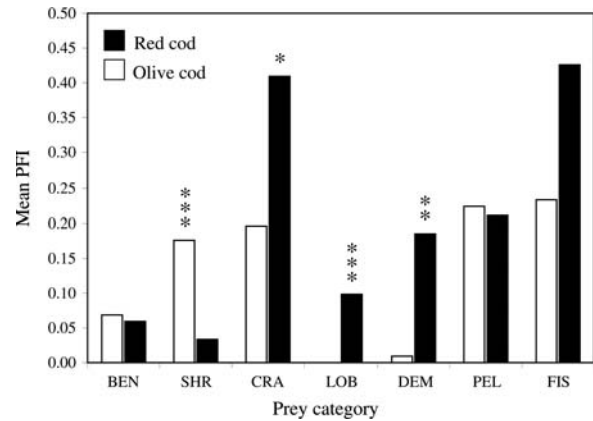


Figure 6. Mean PFI by prey category and colour type. The asterisks represent significant differences among types (the Mann–Whitney *U*-test): *** $p < 0.0001$; ** $p < 0.01$; * $p < 0.05$. Prey categories are BEN, benthos; SHR, shrimp; CRA, crabs; LOB, lobster; DEM, demersal fish; PEL, pelagic fish; FIS, unidentified fish.

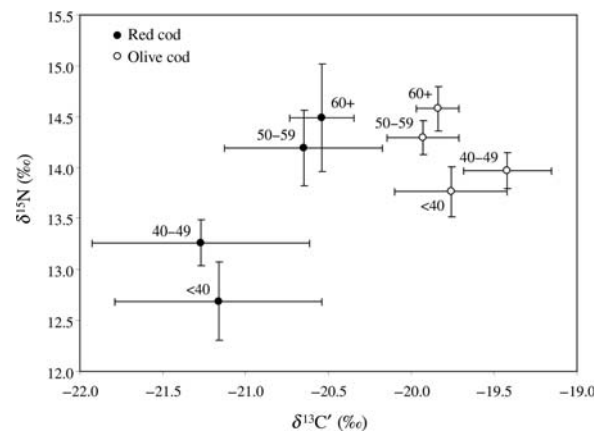


Figure 7. Mean (\pm 95% CI) $\delta^{13}\text{C}'$ plotted against mean $\delta^{15}\text{N}$ (\pm 95% CI) for red and olive cod by size class (cm).

in olive cod at all sizes. $\delta^{15}\text{N}$, on the other hand, was significantly higher in olive cod only for smaller sizes (<50 cm).

Growth, distribution, and morphometrics

VBGFs varied among colour types (Figure 8). Despite low confidence in the VBGF parameter estimates (Table 1), the curves were significantly different among colour types (ARSS, $F_{3,241} = 6.19$, $p < 0.001$); red cod seemingly do not grow as large as olive cod (L_{inf} for red and olive cod: 92 and 143 cm, respectively, although there was 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.

The distributions of red and olive cod on Cashes Ledge differed (Figure 9a). ANOVA revealed a significant effect of depth on RGR values ($F_{2,53} = 18.0$, $p < 0.0001$), which were significantly higher at the shallowest depth sampled (<20 m) than at either of the

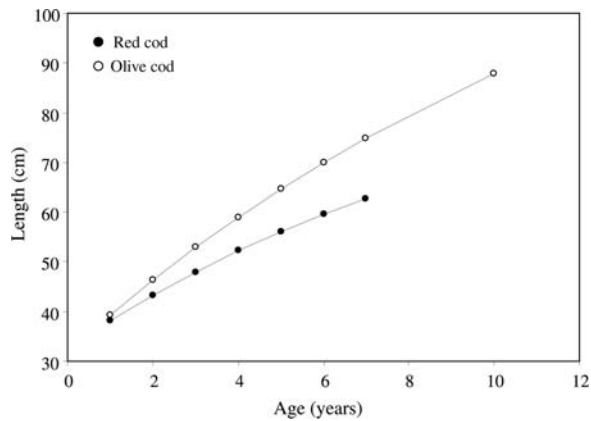


Figure 8. Modelled growth (VBGF) for red and olive cod from Cashes Ledge.

Table 1. Parameter estimates and standard error (s.e.) for the von Bertalanffy growth curve fits, where RSS is the residual sum of squares.

Parameter	Red cod		Olive cod		All cod	
	Estimate	s.e.	Estimate	s.e.	Estimate	s.e.
L_{inf}	92.6	101.9	143.0	117.6	163.2	180.0
k	0.10	0.22	0.07	0.09	0.05	0.08
t_0	-4.3	4.9	-3.6	1.7	-4.1	1.9
r^2	0.32		0.52		0.46	
RSS	3 851		11 747		16 800	
n	70		177		247	

two greater depths (20–30 and >30 m), showing that red cod were apparently located largely on the top of Cashes Ledge (Ammen Rock). Additionally, red cod were scarce over larger scales in the central Gulf of Maine (Figure 9b); high values of RGR were seen only in very proximity to Ammen Rock.

The DFA 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 DFA revealed the following three dimensions as the 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 centre 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 is more robust (i.e. D8: red > olive cod), that red cod have shorter snouts (i.e. D1: red < olive cod), and that the posterior portion of their body is more slender than that of olive cod (i.e. D22: red < olive cod).

Discussion

We believe that we have found evidence for what we interpret as significant life-history variation among colour types of Atlantic cod in the Gulf of Maine (at Cashes Ledge). Gosse and Wroblewski (2004) concluded that red colour in a coastal population of cod in Labrador was attributable 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 was no more than an expression of diet and habitat preferences, which could vary over a cod's lifetime. The results of this study indicate that although 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 and 6), habitat preferences (distribution around Ammen Rock; Figure 9a), growth (Figure 8), and body shape (Figure 10) are all consistent with the existence of alternative life-history strategies in cod (and possibly ecotype variation), as shown for other species of fish (Jonsson and Jonsson, 1993; Bernatchez *et al.*, 1996; Morinville and Rasmussen, 2003; Kerr *et al.*, 2009). 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 (Trudel *et al.*, 2001; Boughman *et al.*, 2005). Ecotypes usually imply or arise from some level of genetic isolation (Bernatchez *et al.*, 1996; Baker *et al.*, 2005). 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 rates (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 from any other location in the Gulf of Maine, so it is too early to conclude that these cod represent a distinct (genetic) ecotype. The fact that they coexist 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 the timing of spawning (Wirgin *et al.*, 2007). It is suspected, in this case, that early spawners (winter) are more migratory, as a corollary to greater dispersion of eggs and larvae in winter (J. Churchill, WHOI, unpublished data) than in spring, when the late spawners are active. Similarly, differences in egg characteristics (buoyancy) can be correlated with the sub-population structure in cod (Stenevik *et al.*, 2008). It is hypothesized here that potential differences in the timing and the location of spawning, and potentially egg buoyancy and other early life-history characteristics, may lead to genetic isolation in Cashes Ledge cod. Therefore, although red cod may coexist with olive cod at Cashes Ledge, there are mechanisms (oceanographic and biological) that could lead to genetic differentiation of colour types; this hypothesis requires further investigation.

The alternative hypothesis is that colour variation at Cashes Ledge, and possibly at 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 vs. 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 heritable (Zimmerman and Reeves, 2002), although usually heritability remains unclear

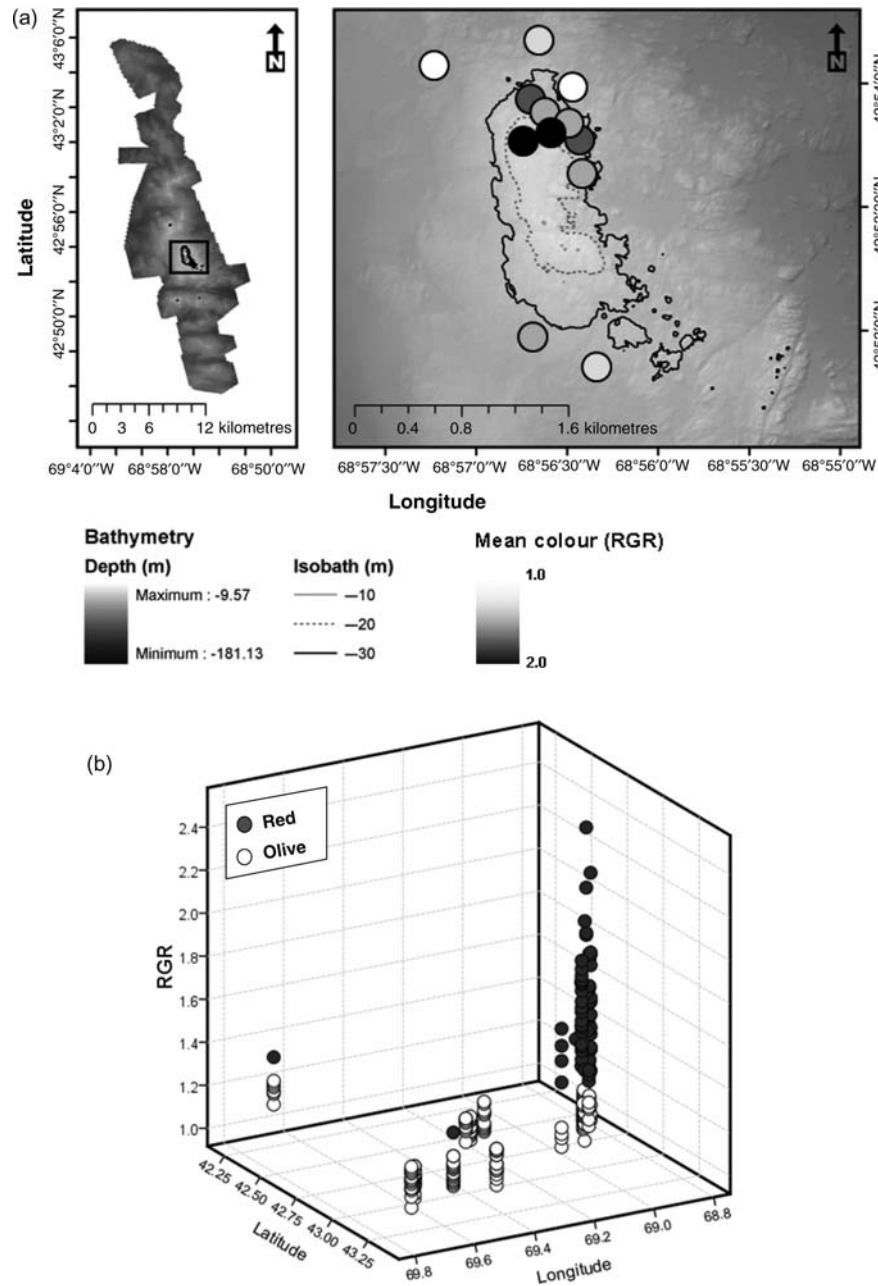


Figure 9. (a) The distribution of red and olive cod captured on Cashes Ledge during angler surveys from 2007 to 2009. The circles denote the locations where fishing was conducted during the surveys, and the shading of circles represents the mean RGR value of the catch (see legend). Note how high mean RGR values are largely confined to depths < 30 m, an area of some 2×1 km. (b) Three-dimensional plot indicating spatial variation in RGR values near Cashes Ledge. The maximum distance between sampling sites is 77 km.

(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 centre 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 all directions. 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 then 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 residence behaviour, spawning times, and population genetics.

Regarding residence, our results are consistent with red cod residing at Cashes Ledge. Resident fish among and within populations tend to have more robust bodies (Morinville and Rasmussen, 2008) and attain smaller sizes (Gross, 1987) than migrant fish, the situation for red vs. olive cod at Cashes Ledge (Figures 10 and 8, respectively). Furthermore, we hypothesized

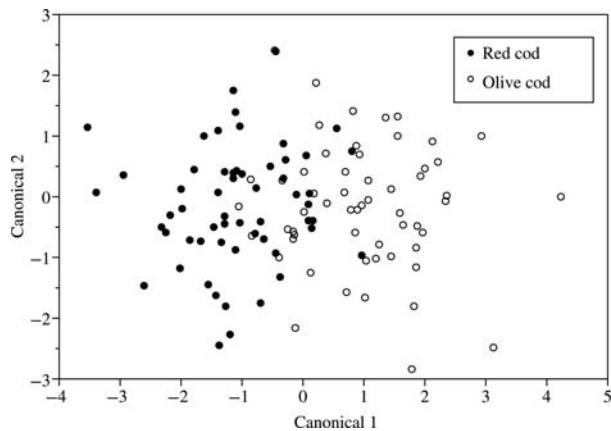


Figure 10. DFA of morphometric characters classified 84% of red and olive cod correctly.

Table 2. The number and percentage of red and olive cod classified correctly using DFA after correcting for differences in size among fish.

Actual	Predicted		% correct
	Olive	Red	
Olive	48	10	83
Red	9	49	84
Total			84

that red cod would also have a more-benthic diet, indicative of feeding on locally derived food sources (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 (such as shrimp) to fish (Figure 5). Red cod, on the other hand, consumed larger proportions of demersal fish at smaller size, as well as more crabs. Only red cod fed on lobsters. The lack of shrimp in red cod diets was likely due to their isolation on the top of Ammen Rock (Figure 9a). Shrimps such as *Pandalus borealis* are typically distributed over and in fine-grained bottom sediments at depth (Haynes and Wigley, 1969), i.e. not on the top of Ammen Rock. Shrimp are important in the diet of cod generally (Sherwood *et al.*, 2007) and their absence from 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 could be adaptations to feeding on large prey.

Stable isotope signatures differed among cod types (Figure 7), but the sign of the difference was the opposite of that expected. In particular, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were more depleted (lower) in red cod than olive cod. Given that the diet results showed no obvious focus of red cod on pelagic or lower trophic level prey, it is our opinion that the stable isotope differences we observed simply represent a 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values in red cod may be more of an indication of residence at Cashes Ledge than real differences in feeding. Natural gradients in $\delta^{13}\text{C}$ have been used elsewhere to infer residence and movement in fish (Rasmussen *et al.*, 2009). A logical next step for addressing the question of cod residence at Cashes Ledge would be to tag individuals acoustically and to track their movements via a fixed acoustic receiver array (e.g. Lindholm *et al.*, 2007).

The distributions of red cod at Cashes Ledge (Figure 9a) and their scarcity at sites distant from Ammen Rock (Figure 9b) are further suggestive of residence 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 colour 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 their 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 a red colour (e.g. crabs and lobsters at Cashes Ledge; Figure 5). However, Sherwood *et al.* (2007) presented the results of an analysis of diet of more than 16 000 cod from various regions around Newfoundland and Labrador. Despite major differences in the diet (from 80% by weight shrimp, *P. borealis*, in offshore Labrador to mostly fish in southern Newfoundland), there were no differences in colour. All the cod in this study displayed the typical counter-shaded pattern (GDS, pers. obs.) shown by Gosse and Wroblewski (2004). These contrasting situations illustrate that whereas fish need to consume a diet rich in carotenoids to express colouration (Ahilan and Prince Jeyaseelan, 2001), they only do so under certain circumstances. In every case, including in the present study, red cod inhabit shallow water (mostly inshore; this study may be the only example of red cod being found up to 100 km offshore, owing to the uniqueness of the Cashes Ledge habitat). Why cod express colour in shallow water is unknown. We speculate that the 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 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, the red colour may protect cod from ultraviolet light, which can influence 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

The 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). Our results suggest that red cod are highly localized on the top of Cashes Ledge, whereas olive cod extend deeper and grow larger, 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. As 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 the reduced total cod biomass by slowing the rate of rebuilding in the Gulf of Maine (assuming that resident fish are less productive). Moreover, 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 before collapse (Collins and Rathbun, 1887; Rich, 1929; Bigelow and Schroeder, 1953). Fecundity is typically correlated positively 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 the historical levels of productivity despite efforts being made to reduce fishing pressure in the Gulf of Maine. Therefore, managers need carefully to consider such perverse and unintended consequences for life-history variation within and among populations when implementing future management initiatives.

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