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Variant colourations of Atlantic cod (*Gadus morhua*) in Newfoundland and Labrador nearshore waters

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Adult cod (*Gadus morhua*) inhabiting continental shelf waters of the Northwest Atlantic typically display a countershaded colouration: a dark back gradating to a light underbelly. Some cod in Newfoundland and Labrador inshore waters have predominantly brown or red pigmentation. Cod inhabiting Gilbert Bay in Labrador often have golden-brown colouration, likely the result of an invertebrate diet rich in carotenoids, and are known in the vernacular as the "golden cod of Labrador". To determine the stability of these variant colourations, we captured cod from Gilbert Bay, held them in a net pen and fed them a diet of fish. Over the 12-week experimental period, the variant coloured cod lost much of their brown or red pigmentation, and became countershaded. Because of its impermanence when cod switch from invertebrate to fish prey, variant colouration of cod can provide only provisional information about stock origin.

Keywords: Atlantic cod, body colouration, carotenoids, diet.

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Introduction

Adult Atlantic cod (*Gadus morhua*) in continental shelf waters of the Northwest Atlantic are typically countershaded, with a dark back gradating to a light underbelly. Fish dorsal and lateral surfaces are overlaid by numerous, rounded brown spots (Scott and Scott, 1988). Post-settlement juvenile cod inhabiting nursery grounds nearshore are typically brown dorsally and laterally (Methven and McGowan, 1998). Adult cod that are not countershaded are here regarded as having a variant colouration.

Variant colouration has been reported in the coastal waters of southern Norway. Cod in shallow water of the Norwegian skjærgård are rich in red pigmentation over their jaws, fins, and dorsal and lateral integument, whereas Norwegian deep-sea cod completely lack such red pigmentation and are countershaded (Dannevig, 1953; Love, 1970, 1974). Cod in Norwegian fjords are described as often having greenish (Dannevig, 1953) or brown pigmentation (Eythorsson, 1993).

Similar red and brown colour variants among cod in Newfoundland and Labrador coastal waters have been reported by natural historians (Cormack, 1826), and noted in accounts of local ecological knowledge (Hutchings *et al.*, 2002). Cormack (1826) mentioned "red cod" found nearshore, and "shore cod" from bays around Newfoundland that were "dusky brown dorsally and yellow or silvery ventrally". Munn (1922) stated that cod with a distinct "golden tinge" migrated through the Strait of Belle Isle.

Body colour of cod is not routinely recorded in Newfoundland fishery science surveys. Here, we document colouration variants in nearshore Labrador waters, similar to the variants in shallow Norwegian waters described by Dannevig (1953) and Love (1970, 1974). By investigating the stability of these variant colourations, we demonstrate that colouration provides only provisional information about stock origin (resident bay stock vs. migrating offshore stock).

Material and methods

Gilbert Bay, on the coast of southern Labrador (Figure 1), is approximately 30 km long and 0.5–2 km wide, with a total area of 60 km^2. Its mouth is an archipelago, with two

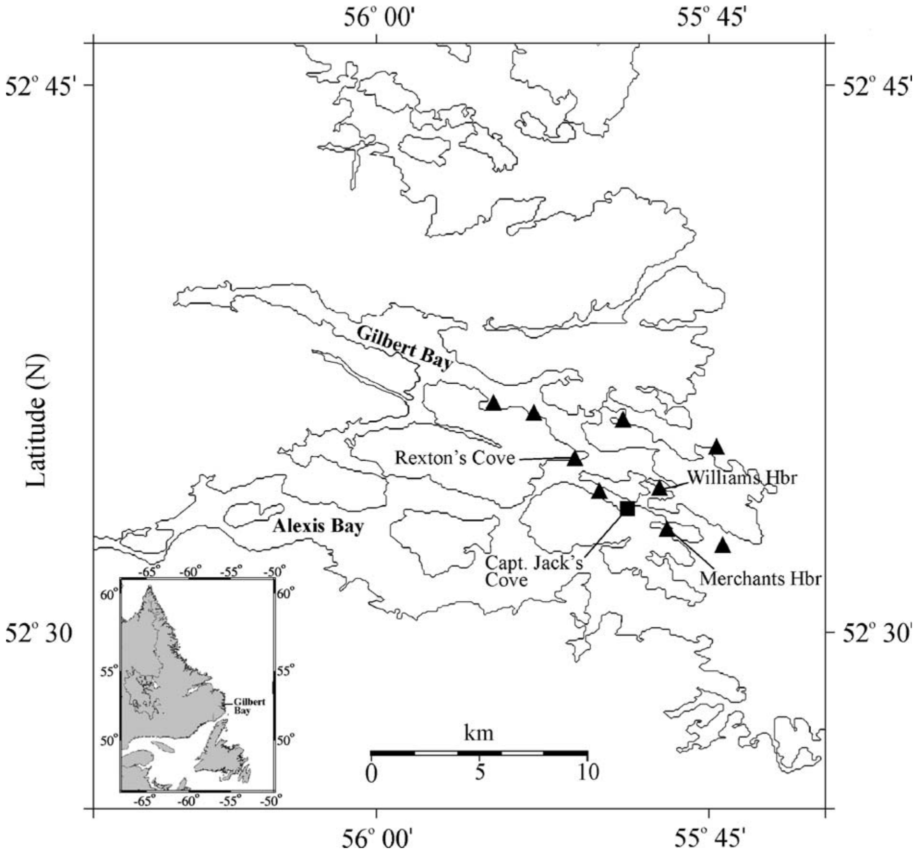

Figure 1. The Gilbert Bay study area in Labrador, eastern Canada (inset). Triangles denote locations where Atlantic cod were captured in early August 2001 and their body colouration recorded. The square marks the location of net pens in Captain Jack's Cove, where captured cod were held and fed a diet of fish to observe change in body colour over a 12-week experimental period.

narrow passages opening to the North Atlantic. Depths range from approximately 80 m near the mouth of the bay to approximately 20 m at the inner reaches. By December, most of the bay is frozen over with landfast ice. Entire water column temperatures remain subzero from December to May. Landfast ice usually melts by mid-May. During summer, surface seawater temperatures rise and reach 15 °C at their maximum in July (Morris and Green, 2002).

Experimental fish

Gilbert Bay supports a genetically distinguishable (Ruzzante *et al.*, 2000; Beacham *et al.*, 2002), resident population (Green and Wroblewski, 2000) of Atlantic cod that are red, brown, or golden-brown in colour and are known locally as the "golden cod of Labrador". Gilbert Bay cod can access the North Atlantic, but apparently do not leave the bay (Green and Wroblewski, 2000; Morris and Green, 2002). However, during summer, Newfoundland–Labrador shelf cod ("offshore cod") migrate to the coast, and may enter the outer portion of Gilbert Bay (Wroblewski, 2000).

Specimen cod were collected during the first week of August 2001, when both resident bay cod and migrant offshore cod were expected in the outer portion of Gilbert Bay. Fish were angled from depths <30 m at various sites within the bay and off adjacent headlands (Figure 1), using a fishing rod with an unbaited lure. Immediately on landing, the colour of the fish was scoredz on a scale of 1–5 (Table 1), such a scale being considered appropriate for assessing variant colouration by eye in the field. To create a permanent record of the colour, each cod was photographed on a white background using 35-mm slide film and flash. There was no evidence of stress-induced colour change in the fish within the first few minutes of handling, when colour was recorded.

Total length (TL) of the specimen was measured to the nearest 0.1 cm, and weight to the nearest 100 g, to minimize handling. Fish were then marked externally with uniquely numbered T-bar anchor tags (Floy Tag Manufacturing Inc., Seattle, Washington), and transported to a holding pen (Figure 1) within 1 h of capture. Specimens ≥ 35 cm TL were placed in a pen with 5 cm mesh netting (herein referred to as pen 1) and fish <35 cm TL were placed in a pen with 3 cm mesh netting (pen 2).

Table 1. Colouration scores assigned to Atlantic cod angled in Gilbert Bay.

Score	Colouration	Vernacular name
1	Countershaded pattern present. Dark back with grey sides, gradating to a light underbelly. Spots on dorsal and lateral skin are black or dark brown.	Offshore cod
2	Countershaded pattern present. Dark back gradating to a light underbelly. Spots on dorsal and lateral skin are brown.	Offshore cod
3	Countershaded pattern is absent, or contrast is reduced. Predominantly brown pigmentation of the dorsal, lateral, and ventral integuments, and fins. Spots are brown.	Brown cod, Bay cod
4	Countershaded pattern is absent or contrast is reduced. Golden-brown pigmentation of the body integument. Spots are brown.	Golden cod
5	Countershaded pattern is absent or contrast is reduced. Red pigmentation of the integument and fins. Spots brown to red-brown.	Red cod, Foxy cod, Iron-ore cod

The dimensions of each pen were 4.5×4.5×4.5 m, and the netting was of black twine.

Experimental conditions and control

Seawater temperature in Captain Jack's Cove (Figure 1) was recorded using a VEMCO Ltd (Shad Bay, Nova Scotia) Minilog-T data logger attached to the bottom of net pen 1. The temperature at the pen remained at 8–10°C until mid-September, when seasonal cooling started, and had dropped to 6°C by the end of the experiment in late October. Secchi depth readings (D_s) of water column turbidity near the net pens ranged from 5 to 8 m, which convert to a light extinction coefficient ($k = 1.7/D_s$) of 0.2–0.3 m^{-1}, typical values for coastal waters (Parsons *et al.*, 1984). The turbidity of the water reduced the visibility of the seabed 20 m below the bottom of the net pens.

Cod held in the net pens were not offered food during the first two weeks of captivity. Thereafter, they were offered a diet of capelin (*Mallotus villosus*) or herring (*Clupea harengus harengus*) 2–3 times per week for 8 weeks (Table 2). The food was weighed before dispensing. Food was withheld from the experimental fish during the last two weeks of the study. After 12 weeks in captivity, the colour of each cod was re-scored (Table 1), and the fish photographed, and measured for length and weight gain. The cod in pen 1 were sacrificed and otoliths removed for age determination. The experimental fish lengths used in the length-at-age analysis were lengths at the time of collection from the field. Age determination of the experimental cod took into consideration fish growth during the experimental period. Otoliths were read by Canadian Department of Fisheries and Oceans (DFO) personnel with extensive experience in age determination of farmed Atlantic cod.

As a control group for comparison with the experimental cod, free-living cod were angled from the inner portions of Gilbert Bay in early November, following the conclusion of the experiment (late October 2001). The colour of those cod ($n = 30$), which had remained in the wild for the duration

Table 2. Diet offered and quantity consumed per week by experimental cod in pen 1 ($n = 67$, cod initially ≥ 35 cm TL) and pen 2 ($n = 54$, cod initially < 35 cm TL).

	Pen 1		Pen 2	
Experimental week	Food offered	Amount consumed (% of body weight per week)	Food offered	Amount consumed (% of body weight per week)
1	Not fed	–	Not fed	–
2	Not fed	–	Not fed	–
3	Capelin	17	Capelin	Fish not feeding
4	Capelin	19	Capelin	Fish not feeding
5	Capelin	36	Capelin	12
6	Herring	24	Capelin	24
7	Herring	26	Herring	24
8	Herring	16	Herring	41
9	Herring	13	Herring	38
10	Herring	34	Herring	55
11	Not fed	–	Not fed	–
12	Not fed	–	Not fed	–

– Denotes food was withheld.

of the experiment, was also scored using the 5-point scale described in Table 1. Stomach contents were examined in the field.

Results

Cod collected from the field in early August ranged in colour score from 1 to 5 for cod ≥35 cm TL (Table 3), and from 2 to 5 for cod <35 cm TL (Table 4). The collection contained typical countershaded Atlantic cod and variant coloured cod with predominantly brown, golden-brown, and red pigmentation. The fish were viewed and described by two local fishers as a mixture of offshore cod and Gilbert Bay cod (J. and W. Russell, pers. comm., Williams Harbour).

While in captivity the fish consumed a fraction (range 0.12–0.55) of their total body weight per week (Table 2) and increased in size. The average weight of a cod in pen 1 was initially 0.90 kg (±0.37 kg s.d.), and increased on average by 0.38 kg (±0.23 kg s.d) over the 12-week experimental period. Lengths increased by 5.0 cm (±1.3 cm s.d.) from an initial average size of 44.5 cm (±5.4 cm s.d.). The average weight of a cod in pen 2 was initially 0.21 kg (±0.10 kg s.d.), increasing by 0.15 kg (±0.11 kg s.d.) over the 12-week experimental period. Lengths increased by 5.9 cm (±1.7 cm s.d.) from an initial average size of 27.5 cm (±4.0 cm s.d.).

Variant colouration changes

Overall, 121 specimens were monitored (Tables 3, 4). Pen 1 held several fish of each colouration score initially. Pen 2 held smaller cod, mostly brown (score 3). The lowest colour score (countershaded with dark spots) was initially absent among the small cod. Only one small cod had red colouration (score 5).

Table 3. Change in colour of Atlantic cod in pen 1 (n = 67; cod ≥35 cm TL) offered a diet of fish for 8 weeks. Cod were assigned a colour score immediately upon capture using the scale presented in Table 1. Individuals were re-scored after withholding food during experimental weeks 11 and 12.

		Colour after 12 weeks				
Initial colour	n	1	2	3	4	5
1	7	6	1			
2	26	13	13			
3	11	1	8	2		
4	14		3	11		
5	9		4	5		

Entries along the shaded diagonal indicate no change in colouration.

Table 4. Change in colour of Atlantic cod in pen 2 (n = 54, cod initially <35 cm TL) offered a diet of fish for 8 weeks. Cod were assigned a colour score immediately upon capture using the scale presented in Table 1. Individual cod were re-scored after withholding food during experimental weeks 11 and 12.

		Colour after 12 weeks				
Initial colour	n	1	2	3	4	5
1						
2	11	4	7			
3	35	9	25	1		
4	7	1	6			
5	1		1			

Entries along the shaded diagonal indicate no change in colouration.

Most cod generated a change in colouration score when held for 12 weeks and fed a diet of fish. Scores decreased for all cod that were initially red (n = 9 in pen 1; n = 1 in pen 2) and golden-brown (n = 14 in pen 1; n = 7 in pen 2). Cod that were initially brown (n = 11 in pen 1; n = 35 in pen 2) decreased in colouration score (43 fish) or remained unchanged (3 fish). Cod that were initially countershaded with small brown spots (n = 26 in pen 1; n = 11 in pen 2) maintained their countershaded appearance throughout the 12-week experiment, though the spots of about half these fish darkened. Only one countershaded cod (in pen 1) had lighter brown spots at the end of the experiment than it did at the start.

Cod in Gilbert Bay mature at a TL of 31–42 cm and an age of 4–8 years (Morris and Green, 2002), so based on size and age, most cod in pen 1 were adults (Figure 2). Length-at-age data for 66 cod fall within the 95% confidence intervals of known relationships for Gilbert Bay cod (Smedbol, 1999), and for cod from NAFO Division 2J (Shelton *et al.*, 1996). Stock origin (continental shelf or Gilbert Bay) of a cod cannot be discerned from length-at-age analysis.

The change in colour of a typically countershaded Atlantic cod held in pen 1 is shown in Figure 3. This fish was countershaded when captured from the wild and maintained its colour pattern over the 12-week period. However, the spots on its dorsal surface blackened, and the ventral integument darkened slightly, but still contrasted with the dorsal surface (Figure 3, below).

Figure 4 shows the change in colour of an initially brown cod; it changed to a countershaded colouration. When captured, the rounded brownish spots on its dorsal surface were inconspicuous against similarly coloured integument (Figure 4, above), but by the end of the experiment, the spots and fins had noticeably blackened and the colour of

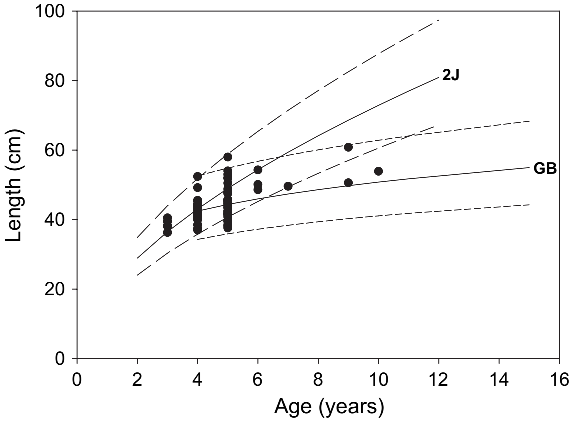

Figure 2. Length-at-age of Atlantic cod in pen 1 (n = 66; data from one fish was lost) compared with known relationships for Gilbert Bay (GB) cod (after Smedbol, 1999) and offshore cod in NAFO Division 2J (after Shelton *et al.*, 1996). The solid curve is the regression relationship, and the dashed curves the upper and lower 95% confidence intervals. The regression equation for Division 2J cod is $L = 22.1A^{0.482}$, and for Gilbert Bay cod is $L = 22.4A^{0.195}$.

the integument between the spots had lightened (Figure 4, below). Brown pigment was also lost from the belly of that fish.

The change in colour of an initially red specimen (score 5 on capture) is shown in Figure 5; clearly, it lost its red pigmentation. The colour of the spots darkened, from red to almost black. Red pigment was lost from the fins and

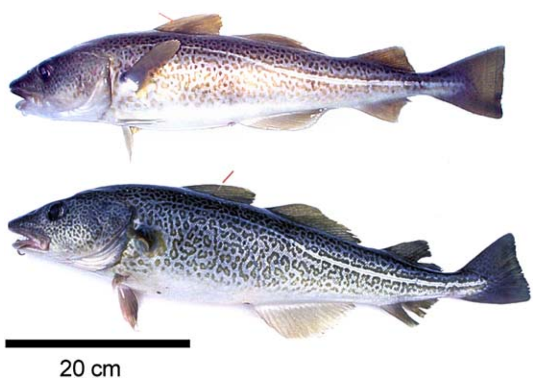

Figure 3. Above: Countershaded pattern of Atlantic cod typical of fish migrating inshore from the Grand Banks of Newfoundland and Labrador, known in the vernacular as "offshore cod". This fish (54 cm TL, 1.3 kg wet weight), captured near Merchants Harbour on the headlands of Gilbert Bay (Figure 1), was assigned a colour score of 2 (see Table 1). Below: Appearance of the same cod after 12 weeks in net pen 1 and fed a diet of fish. Body length increased (3 cm) to 57 cm TL and body weight increased (0.3 kg) to 1.6 kg. Colour score decreased to 1. Note the darkening of the initially brown spots, the enlargement of the spots and the greying of the entire body integument.

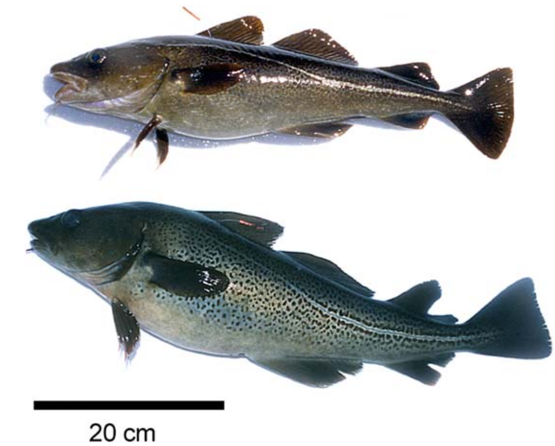

Figure 4. Above: Brown colouration of Atlantic cod commonly observed in Gilbert Bay and less often in nearshore waters of Newfoundland, known in the vernacular as "brown cod" or "bay cod". This fish (45 cm TL, 0.9 kg wet weight), captured near Williams Harbour (Figure 1), was assigned a colour score of 3 (see Table 1). Note the skin is dark brown over most of the body, including the underbelly. Below: Appearance of the same cod after 12 weeks in net pen 1 and fed a diet of fish. Length increased (7 cm) to 52 cm TL and body weight increased (0.3 kg) to 1.2 kg. Colour score decreased to 1. Note the darkening of the initially brown spots, greying of the side, and lightening of the underbelly.

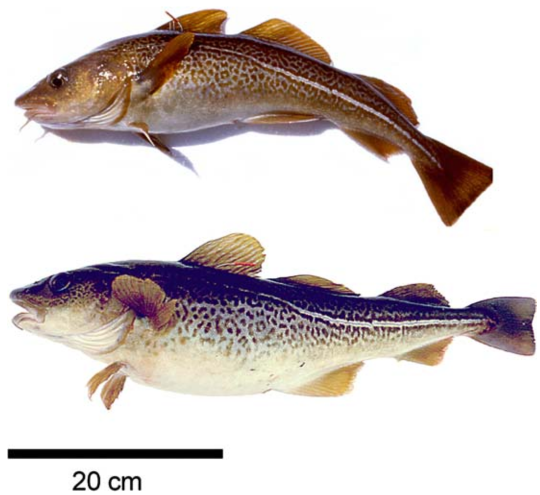

Figure 5. Above: Red colouration of Atlantic cod commonly observed in Gilbert Bay and more rarely in nearshore waters of Newfoundland, known in the vernacular as "red cod", "foxy cod" or "iron-ore cod". This fish (46 cm TL, 0.8 kg wet weight), captured near Rexton's Cove in Gilbert Bay (Figure 1), was assigned a colour score of 5 (see Table 1). Below: Appearance of the same cod after 12 weeks in net pen 1 and fed a diet of fish. Length increased (4 cm) to 50 cm and body weight increased (0.7 kg) to 1.5 kg. Colour score decreased to 2. Note the loss of red pigmentation from the integument. The initially red-brown spots and fins have become brown. The underbelly has lightened.

integument, most notably on the ventral surface (Figure 5, below).

Based on size, the majority of cod in pen 2 (initial average length 27.5 cm $\pm$ 4.0 cm s.d.) were juveniles. An overall loss of brown, golden-brown, and red pigmentation and a change to a countershaded pattern was observed in these cod (Table 4). Only one cod remained brown at the end of the 12-week experiment.

After termination of the experiment, the colour of free-living Atlantic cod in Gilbert Bay was observed. All fish angled (n = 30; > 35 cm TL) in the inner portion of the bay near Rexton's Cove (Figure 1) during the first week of November 2001 were either brown (n = 3), golden-brown (n = 24), or red (n = 3), suggesting that experimental fish of Gilbert Bay origin could have maintained their variant pigmentation if they had remained in the wild. No countershaded cod were caught. Examination of stomach contents revealed that those cod were feeding on invertebrates: mysids, limpets, shrimp, scallops, and clams.

Discussion

Colour in fish is primarily attributable to pigments in the skin. Brown and black pigments (melanins), found in many fish species, are contained within melanophores (Fox and Vevers, 1960; Waring, 1963; Bagnara and Hadley, 1973). Carotenoids, found in erythrophores and xanthophores, are responsible for red, orange, and yellow colours. When conjugated with proteins, carotenoids may also produce a brown colour (Fox, 1976). The carotenoids leutin and taraxanthin are found in the skin of Atlantic cod (Goodwin, 1950).

Carotenoids are synthesized by plants and enter animal tissues through diet (Fox and Vevers, 1960; Weedon, 1971; Bagnara and Hadley, 1973). A diet rich in carotenoids results in enhanced red, orange, and yellow pigments in fish (Steven, 1948; Mori *et al.*, 1987; Meyers and Sanderson, 1992; Ahilan and Prince Jeyaseelan, 2001). The red colour of Norwegian coastal cod was attributed by Fox and Vevers (1960) to a supply of carotenoids from its diet of predominantly shore crab (*Carcinus maenas*). Consequently, a diet of carotenoid-rich invertebrates could explain the brown, golden-brown, and red colour of Gilbert Bay cod. Indeed, Gilbert Bay cod feed predominantly on a diet of benthic invertebrates such as shrimp, mysids, amphipods, and various crab species (Morris and Green, 2002).

Steven (1948) studied the relationship between diet and colour in brown trout (*Salmo trutta*). He demonstrated that trout kept in aquaria and fed horseflesh lost their characteristic red and yellow pigmentation. Total carotenoids in the tissue of experimental trout were reduced to 10% of the value found in wild trout. When carotenoids were introduced back into the diets of de-pigmented fish, their red and yellow pigmentation increased visibly within 35 days (Steven, 1948).

Similar relationships between diet and colour have been demonstrated for other fish species. Pacific killifish (*Fundulus* sp.) fed a diet of fish experienced a decrease in concentrations of carotenoid pigment in the integument (Sumner and Fox, 1935). Garibaldi (*Hypsypops rubicunda*) gradually lost their characteristic yellow-brown to orange colour when kept on a carotenoid-free diet of fish for periods of 3.5–11 months (Fox, 1976). The results of our 3-month experiment using Atlantic cod are therefore seemingly consistent with these observations for other fish species.

The overall colour pattern of an individual fish depends partially on the combination of melanophores, xanthophores, and erythrophores. The distribution, density, size, and relative motility of each cell type will affect the display (contrast) of the patterning (Burton, 2002). Generally, melanophores appear in far greater numbers on the dorsal integument of fish than on the belly, and hence the white undersides of many species (Bagnara and Hadley, 1973). Localized variations in the number of chromatophores can often account for the patterns of spotting or mottling observed in many species (Bagnara and Hadley, 1973).

When held in net pens for 3 months and fed a diet of fish, Atlantic cod in this experiment underwent a change in colour of the dorsal, lateral, and ventral integuments, fins, and the spots (highly pigmented areas) on the dorsal and lateral surfaces (Figures 3–5). Experimental fish lost brown, golden-brown, and red pigmentation. They also darkened in the net pen environment. Melanin pigments are synthesized directly within the melanophores and are responsible for rapid change in colour (Bagnara and Hadley, 1973). Numerous studies have demonstrated that when a fish is kept on a dark background, melanin pigments disperse intracellularly, making it appear darker (Fox and Vevers, 1960; Grove, 1994). Prolonged exposure to a dark background may result in an increase in the total amount of melanin pigment present (Fox and Vevers, 1960; Bagnara and Hadley, 1973). Given the turbidity of the water in Gilbert Bay, the sea bottom would likely not have been very visible to cod in the net pens. However, the slight possibility remains that change of substratum may be implicated in the colour changes recorded during this work.

In this experiment countershaded cod darkened, but remained countershaded (Figure 3). Dorsal spots blackened and the ventral integument became slightly greyer. The observed darkening could be explained as a response to the black netting of the holding pen. The biofouling algal species *Ectocarpus siliculosus* and *Pilayella littoralis* colonized the netting within a week of deployment, creating a black-brown background. In response to this, melanin pigments in the skin of the experimental cod perhaps dispersed, or increased in quantity, resulting in a darker skin.

Brown variants in our experiment had the least countershading (Figure 4). Pigmentation was dominant over the entire body integument, including areas such as the underbelly, where there is usually little pigmentation. The brown colour of these cod is likely attributable to a combination of carotenoids from the diet and melanins produced in response to a dark, benthic habitat. Juvenile and young adult cod, both inshore and offshore, feed predominantly on euphausiids, mysids, shrimps, small lobsters, crabs (Scott and Scott, 1988), annelids, and molluscs (Keats and Steele, 1992, as cited in Steele and Lilly, 1999), and are brown. During the 12-week experiment, the brown colour was generally lost from the body integument, presumably as a consequence of the restriction of carotenoids in their diet. The dorsal spots of these fish darkened, likely in response to the dark background of the net pen.

Similar to countershaded cod, the dorsal spots and fins of red cod darkened (Figure 5), also perhaps in response to the net pen environment. The most notable change, however, was the loss of red colour from the lateral and ventral integument. That all initially red cod lost red pigmentation during the experiment is considered to exemplify the role of a carotenoid-rich diet in the colour of Gilbert Bay cod.

Cod inhabiting deep (>100 m) continental shelf waters off Newfoundland and Labrador consume mainly capelin (Lilly, 1991), and are countershaded. In recent years capelin have appeared off the headlands of Gilbert Bay, but they have not migrated into the bay (Morris and Green, 2002, pers. obs.). The free-living cod collected in Gilbert Bay as a control group in autumn were feeding exclusively on invertebrates, so it is assumed that fish prey were not available or selected.

Figure 3 (above) shows the countershaded pattern typical of cod migrating inshore from deeper continental shelf regions. Figures 4 and 5 (above) show brown and red variants of Atlantic cod common in Gilbert Bay (though less so in Newfoundland inshore waters). The brown and red colourations likely result from an invertebrate diet rich in carotenoids. Within weeks of a switch to a fish diet, brown and red variants lost their pigmentation, becoming more countershaded. Therefore, brown or red colour can be used to discriminate invertebrate-eating, nearshore cod from fish-eating, offshore cod that recently arrived at the coast. Atlantic cod preferentially feed on capelin when available in abundance (Lilly, 1991), so a nearshore cod feeding on newly available capelin will quickly become indistinguishable from a migratory offshore cod. Moreover, a brown or red cod found inshore late in autumn could be a bay resident or a migrant cod feeding on invertebrates.

The results of this study show that colour cannot be used as a reliable discriminator of stock structure, owing to its impermanence when cod switch from invertebrate to fish prey. Variant colouration of cod can provide only provisional information about stock origin. However, the field study presented here will hopefully provide a stimulus for controlled experiments in the laboratory. Such studies may involve cod of variant colourations fed different diets, with microscopic examination of the chromatophores to determine the cell nature of observed colour changes.

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