Vol. 265: 227–234, 2003 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published December 31

Microhabitat use of juvenile Atlantic cod in a coastal area of Newfoundland determined by 2D telemetry

D. Cote[1,*], L. M. N. Ollerhead[2], D. A. Scruton[2], R. S. McKinley[3]

[1]Terra Nova National Park of Canada, General Delivery, Glovertown, Newfoundland and Labrador A0G 2L0, Canada
[2]Fisheries and Oceans Canada, PO Box 5667, St. John's, Newfoundland and Labrador A1C 5X1, Canada
[3]Centre for Aquaculture and the Environment (CAE), 123-2357 Main Mall, The University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

ABSTRACT: A location-finding acoustic telemetry system (resolution ±1 m) was used to map ocean substrates and to continuously monitor the habitat associations (substrate, water temperature, and depth) of 58 Age 2 to 3 juvenile Atlantic cod *Gadus morhua* from 11 August to 20 December 1999. Substrate use was studied in 2 stages to determine if it differed from the pattern expected given an absence of selectivity (substrate use proportional to substrate availability). The first level compared the proportions of substrate in the study-area home ranges of Atlantic cod to those of the entire study site. The second assessed if the time spent over specific substrates was proportional to the substrate availability within the study-area home ranges. Boulder substrate was incorporated into the home ranges of juvenile Atlantic cod more than would be expected given its availability within the study area. Kelp substrates were included in these home ranges less than expected while sand and gravel were used in proportion to availability. Time spent over substrates within study-area home ranges varied over the diel and seasonal periods. Within study-area home ranges, juvenile cod occurred in boulder substrates at levels greater than or equal to availability. Conversely, the proportion of time spent over open substrates (e.g. sand and gravel) was either less than or not different from those of substrate availability. Kelp substrates were used less than expected in August and December and more than expected in September and October. Over the diel period, it was found that nocturnally, associations with structure diminished except during September and December when boulder habitats were still used to a greater degree. Unlike younger conspecifics, Age 2 to 3 cod in Buckley Cove were not strictly associated with structurally complex substrates, which suggests that these fish experience less vunerability to predation. Also, unlike younger conspecifics, the distribution of Age 2 to 3 cod did not shift inshore nocturnally and therefore they did not benefit metabolically by moving through the thermocline that existed from August to mid-November. This study indicates that substrate use by juvenile cod is dynamic and the strength of associations with structural complexity varies over diel and seasonal temporal scales.

KEY WORDS: Atlantic cod · Juvenile · Habitat use · Telemetry · Substrate · Newfoundland

INTRODUCTION

The Atlantic cod is of considerable economic and cultural importance to the maritime regions of the North Atlantic, where it was, for hundreds of years, the mainstay of a lucrative commercial fishery. In the early 1990s, however, Atlantic cod stocks in the Northwest Atlantic collapsed, causing managers to implement a moratorium on commercial fishing for this species (Myers et al. 1996). Since the moratorium has been in place, Atlantic cod in the Northwest Atlantic have shown little recovery (Lilly et al. 2001) and in 2003,

*Email: david.cote@pc.gc.ca

populations off the east coast of Newfoundland and Labrador were declared 'endangered' (COSEWIC 2003).

Facilitating the recovery of the Atlantic cod depends upon an understanding of the essential habitats for all life stages (Langton et al. 1996). Studies of habitat use provide useful insights into aspects of the ecology of a species including feeding, predator avoidance, morphology, population dynamics, and resource partitioning (Kramer et al. 1997). Such information is valuable to managers, who can use it for population delineation and enumeration and for habitat enhancement or protection. Models have demonstrated that Marine Protected Areas (MPAs) can be effective tools for preventing over-harvesting (Guénette et al. 2000) and for increasing juvenile survival of Atlantic cod through habitat protection (Lindholm et al. 2001). However, to be effective, conservation initiatives such as the selection of sites for the establishment of MPAs require reliable knowledge of habitat use by those species requiring protection. Surprisingly, given the commercial importance of the species, little was known of the habitat use of juvenile Atlantic cod prior to the collapse of the Northwest Atlantic stocks. Since then several laboratory studies have shown the importance of substrate structural complexity for reducing predation-risk in juvenile life stages (Gotceitas & Brown 1993, Gotceitas et al. 1997, Lindholm et al. 1999).

In the wild, juvenile Atlantic cod utilize shallow coastal waters as nurseries (Templeman & Fleming 1965, Riley & Parnell 1984, Bergstad et al. 1987, Sinclair 1992, Pihl & Ulmestrand 1993, Dalley & Anderson 1995, Anderson & Rose 2001). As juveniles age, they move to progressively deeper water until, at 3 to 4 yr, they join adult conspecifics (Templeman 1974). Evidence also indicates that juvenile cod undergo ontogenetic shifts in substrate use and predator avoidance strategies (Gregory & Anderson 1997). While considerable gains have been made in understanding the ecology of these animals, conclusions regarding habitat use by juveniles are inconsistent. To date, substrate use by juvenile Atlantic cod has been studied primarily through underwater observation (e.g. Keats et al. 1987, Tupper & Boutilier 1995, Fraser et al. 1996, Gotceitas et al. 1997, Gregory & Anderson 1997, Cote et al. 2001). Unfortunately, older juveniles (Age 2 to 3) are difficult to study in this manner (e.g. Cote et al. 2001) because they generally occur at lower densities than younger age-classes. Telemetry lends itself well to studying more elusive and/or less abundant age-classes, while eliminating the potential for observer avoidance behaviour. Fixed-array hydrophone systems have been previously used to describe movement patterns (Hawkins et al. 1980, Clark & Green 1990, Sarno et al. 1994, Lokkeborg 1998, Lokkeborg & Fernö 1999) and general qualitative habitat use by gadids (Hawkins et al. 1980, Clark & Green 1990, Sarno et al. 1994). However quantitative examinations on substrate use are lacking. This is likely due to low concurrent sample sizes and/or the difficulty in obtaining adequate habitat information. Further, these studies were unable to describe population shifts in habitat use over a period of months because they were based upon few individuals tracked for short periods of time. In this study, a 2D location-finding telemetry system was used to describe distributions of Age 2 to 3 juvenile cod as they relate to substrate, macro-algae, depth and water temperature. Temporal variation of habitat use is examined across diel periods and months (August to December).

MATERIALS AND METHODS

Study area. The study area in Buckley Cove was approximately 5 ha and situated adjacent to the shore of inner Newman Sound; a glacial fjord on the northeast coast of Newfoundland (53.928° W, 48.576° N). The coast of inner Newman Sound is characterized by rocky shores interspersed with pocket beaches. Wave exposure ranges from sheltered to moderate. A shallow littoral shelf lies at depths of ~3 to 10 m and is characterized by sandy substrates, low bathymetric relief, and vegetative cover such as eelgrass *Zostera marina* and brown macroalgae *Laminaria* sp. This zone encircles the entire inner Sound, except in areas where submarine cliffs lie adjacent to the shore. Beyond the shallow littoral zone lies the basin slope (10 to 30 m depth), with greater bathymetric relief and a mixture of coarse and fine substrates. Macroalgae, such as colander kelp *Agarum cribrosum* and emergent epifauna (e.g. *Metridium* spp.), are also common within this zone. Finally, fine sediments (silt, mud and sand), low bathymetric relief, an absence of macroalgae, and low light penetration characterize the deepest parts of the inner Sound (30 to 60 m). The habitats incorporated into the study were characteristic of other shallow littoral and basin slope areas of Newman Sound.

Acoustic tracking. Age 2 to 3 juvenile Atlantic cod (n = 58; total length: 258 to 359 mm, 0 = 293 mm) were captured by angling, within the study area, and held in open water sea cages prior to surgery. Study animals were anaesthetized in a clove oil bath (Anderson et al. 1997) and acoustic transmitters (CAFT_11, Lotek Wireless; pulse rate: 10 s; 35 mm [length] × 11 mm [diameter], 6.5 g [in air], 3.35 g [in water]) were surgically implanted into the body cavity through the abdominal wall as described by Cote et al. (1999). Fish were allowed to recuperate in an open water cage for 24 h following surgery, and then released at the surface within the hydrophone array. Tracking commenced on the day of release. Transmitter longevity (approximately 60 d) was not sufficient to last for the duration of the study period; therefore, tagged fish were released in 4 deployments (August 5, n = 11; August 26, n = 13; September 7, n = 16; and October 9, n = 18).

The study area was continuously monitored for tagged individuals using an acoustic telemetry receiver (MAP_500; Lotek Wireless) from August 5 to December 20, 1999. The telemetry system was tethered to 4 subsurface omnidirectional hydrophones (model LHP-1; Lotek Wireless) that were capable of discriminating locations of tagged cod to within ± 1 m when the acoustic signal was detected by at least 3 hydrophones. The 300 to 400 m detection range of the hydrophones was sufficient to cover the designated study area.

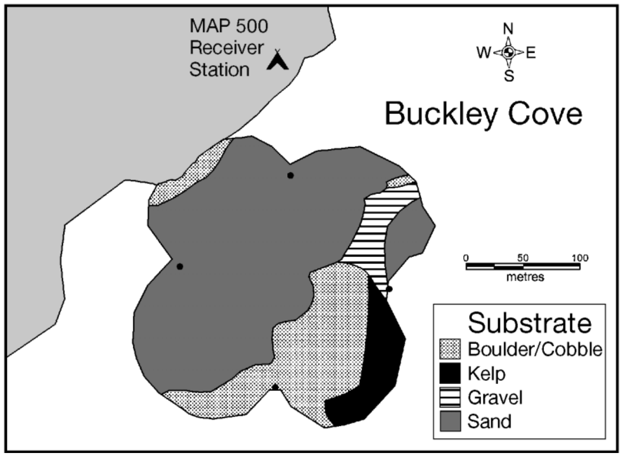

Fig. 1. Substrate of the study area in Buckley Cove, Newfoundland, and the locations of the fixed hydrophones (dots)

Habitat associations. Substrates in the study area were classified and mapped by divers carrying acoustic transmitters. Divers swam along the borders of substrate patches while being tracked by the telemetry system. The habitat features observed on the dives were linked via time stamps to the spatial data generated by the telemetry system with GIS (Mapinfo v. 6.0). The substrates were visually assessed and mapped according to the following classification: sand (particle size: <0.5 cm), gravel (particle size: 0.5 to 5 cm), boulder/cobble (particle size: >5 cm), and kelp (cover: >20%); (Fig. 1). Sand (64% of study area) was the dominant substrate, followed by boulder (24%), kelp (7%) and gravel (5%). Water temperature was measured each hour at 2 m intervals through the water column throughout the study period using 10 subsurface recording thermographs (Vemco Mini-Log TR). Ambient water temperature for each fish position was inferred from bottom water depth, assuming fish were within 1 m from the bottom. Qualitative observations of Age 2 to 3 cod, made during SCUBA dives, indicated that these fish remained in close association (<1 m) with the bottom throughout the diel period. Diel period was delineated based on subsurface light intensity at 3 m measured using a StowAway LI light intensity logger. Day (>0.36 lux), twilight (0.001 to 0.36 lux), and night (<0.001 lux) classifications were added to each fish location.

Statistical analysis. Movement of individuals was graphically examined for prolonged periods of inactivity. These cessations in activity were considered to have been the result of the expulsion of the transmitter or the mortality of the study animal. All such individuals were removed from the data set. Substrate use was studied in 2 stages (as per Aebishcher et al. 1993) to determine if it differed from the pattern expected given an absence of selectivity (substrate use proportional to substrate availability). The first stage compared the proportions of substrate in the study-area home ranges of Atlantic cod to those of the entire study site. The second assessed if the time spent over specific substrates was proportional to the substrate availability within the individual study-area home ranges. With this approach the sample size equalled the number of individuals detected for the time period in question (as opposed to the total number of locations measured for each fish). Significant deviations ($\alpha = 0.05$) from random habitat use within month and diel periods were determined using bootstrap techniques (Manly 1991). The difference between the proportion of habitat use and available habitat for individuals was randomly sampled with replacement to create a distribution of means (based on 1000 iterations) to which the null hypothesis value of 0 was compared (a zero value is expected if habitat is used according to availability). To reduce the effect of habitat specific differences in detectability (e.g. rocky environments may shield a fish from being detected by 1 or more hydrophones), the total time spent within a particular habitat was used in the analysis as opposed to the number of detected positions. Using the time spent in a particular habitat as a measure reduced the potential biases associated with intermittent detections that could be habitat specific. When a fish was not detected for >30 min it was no longer considered as being associated with a specific habitat. Study-area home ranges were calculated with the minimum convex polygon method (outlined in White & Garrott 1990). Although the true home ranges of most juvenile Atlantic cod in Newman Sound are small enough to fit within the study area (Cote 2002), tagged cod could move freely beyond the range of the telemetry equipment. Therefore, home-range area estimates are not reported.

RESULTS

Habitat use information was analyzed for 52 of 58 tagged individuals (Fig. 2). Of the remaining 6, 5 were removed from the data set because of suspected mortality/transmitter expulsion while the 6th was not relocated; likely the result of its immediate movement from the study area or a transmitter failure.

Of the Atlantic cod study-area home ranges, 94% included each of the available substrates; 6% of the home ranges did not include kelp, while 4% did not include gravel.

Boulder substrate was incorporated into study-area home ranges significantly more than would be expected, given its availability, while significantly less kelp was included. Areas of sand and gravel were incorporated according to their availability. Although time spent over habitats within study-area home ranges varied over months and diel periods, the following general trends were observed. Within study-area home ranges, boulder substrates were never utilized less than expected, given availability (Fig. 3), and were utilized significantly more than expected in 3 of 5 mo during diurnal and crepuscular periods (Table 1). Conversely, open substrates (gravel and sand) were never utilized more than expected in any month with sand being significantly under-utilized in 3 of 5 mo. Diurnal and crepuscular associations of Age 2 to 3 cod with kelp varied and were significantly less than expected during summer (August) and late autumn (December), and significantly more than expected during early autumn (September and October). Nocturnal associations with kelp were in proportion to availability, except in August when individuals spent significantly less time in kelp than would be expected.

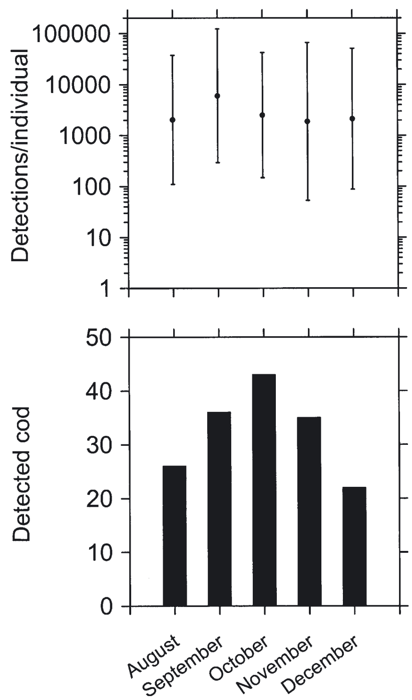

Fig. 2. Detections of juvenile Atlantic cod acquired with the fixed array telemetry system. Top panel: acoustic detections per individual (error bars represent the standard deviation). Bottom panel: the number of cod for which habitat use information was acquired

Table 1. Diel use of study-area substrates occupied by juvenile Atlantic cod in Buckley Cove, Newfoundland, from August to December 1999. Sig. – indicates statistically significant differences from expected use based on bootstrap analysis (1000 iterations; $\alpha = 0.05$); A = August, S = September, O = October, N = November, D = December

	Substrate	Sig. >	Sig. <
Day	Gravel	–	S, O, D
	Sand	–	S, O, D
	Boulder	S, O, D	–
	Kelp	S, O	A, D
Twilight	Gravel	–	D
	Sand	–	S, O, D
	Boulder	S, O, D	–
	Kelp	S, O	A, D
Night	Gravel	–	N, D
	Sand	–	S, D
	Boulder	S, D	–
	Kelp	–	A

No significant shifts in depth distribution of Age 2 to 3 cod were detected over the diel period from August to October (Fig. 4). Also, there was no difference in the water temperature occupied over the diel cycle. The water temperature range occupied by juvenile cod ranged from 1 to 18°C with average temperatures inhabited by cod being highest in September and lowest in December (Fig. 4).

DISCUSSION

The present study demonstrates that the strength of associations of Age 2 to 3 juvenile Atlantic cod with structural complexity is dynamic over diel and seasonal temporal periods, possibly reflecting the seasonal presence of predators and/or foraging opportunities that vary over space and time (Mattson 1990).

Study-area home ranges were established in areas with boulder substrates while kelp substrates were incorporated less than would be expected, given the availability of these substrates. Within study-area home ranges, cod showed a diurnal and crepuscular affinity for structurally complex substrates (boulder and kelp), particularly during September and October. Although time spent in boulder habitats remained high

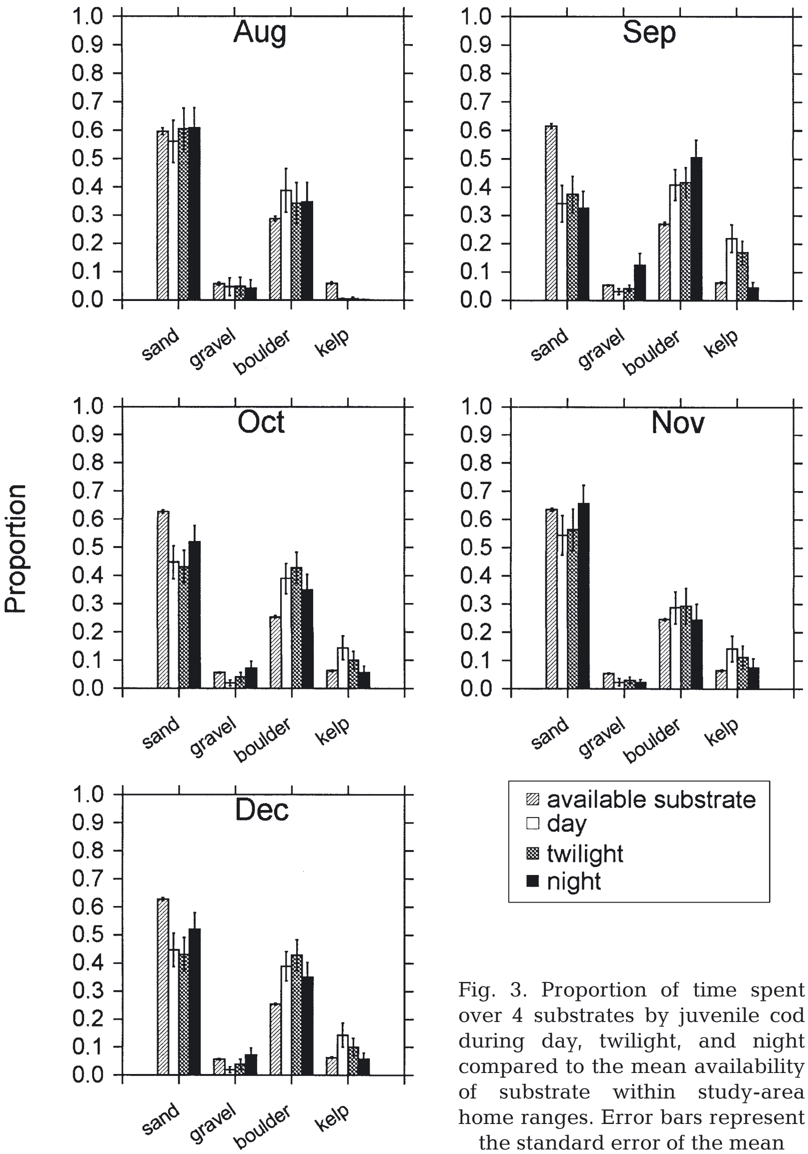

Fig. 3. Proportion of time spent over 4 substrates by juvenile cod during day, twilight, and night compared to the mean availability of substrate within study-area home ranges. Error bars represent the standard error of the mean

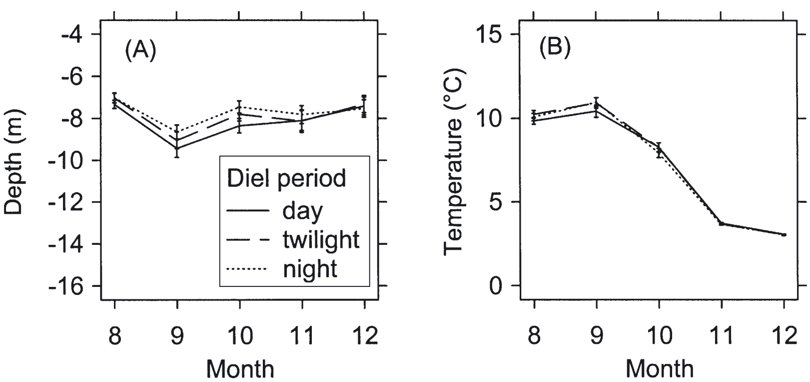

Fig. 4. Diel and seasonal variation of (A) depth and (B) temperature occupied by juvenile Atlantic cod in Buckley Cove, Newfoundland, 1999. Error bars represent the standard error of the mean

nocturnally, cod used kelp habitats within their study-area home ranges in proportion to availability. Age 2 cod have been observed in boulder substrates in the spring (Gregory & Anderson 1997) and from late summer to late autumn (Cote et al. 2001). Higher densities of cod in kelp have also been reported (Keats et al. 1987, Cote et al. 2001) although Gregory & Anderson (1997) found that older juveniles (Age 2–4) avoided kelp in spring. The latter study, however, indicated that this might have been an artifact of a seasonal depth preference. Although not examined explicitly in this study, older juvenile cod (Age 2 and older) have been reported to occur in areas of high bathymetric relief (Gregory & Anderson 1997, Cote 2002). Unfortunately, it is not clear which is more important—substrate complexity or bathymetric relief—since these attributes are highly correlated in Newman Sound (Cote 2002).

Open areas (sand and gravel) were underutilized by cod or used according to availability. These results are not in agreement with those of Clark & Green (1990), who described Atlantic cod of similar size (28 to 33 cm) to be diurnally active over sandy areas. However, because the dominant substrate in the study area was sand (64 %), the total time spent by cod over sand was still greater than over any other substrate except during September. In contrast, younger cod (Age 0 and 1) are known to exhibit a rigid diurnal association with structurally complex substrates (Keats et al. 1987, Gotceitas et al. 1997, Cote et al. 2001, Linehan et al. 2001), a habitat feature that has been shown to reduce predation risk (Gotceitas & Brown 1993, Fraser et al. 1996, Lindholm et al. 1999). The absence of a strict habitat association with structured substrates in Age 2 to 3 cod suggests they experience a reduction in predation risk, likely a result of their increased size (Lundvall et al. 1999, Kristiansen et al. 2000). Gregory & Anderson (1997) observed a strong association with structurally complex substrates in Age

2 to 4 cod; however, since they believed that cod were feeding little during their study period, predator avoidance was thought to be a greater priority. Cod feed actively in Newman Sound during late summer (Dietrich 1998) and autumn (D. Cote pers. obs.) and therefore may utilize sandy habitats opportunistically during foraging. Many studies indicate that fish manage foraging and predation risk in a way that maximizes food intake and minimizes predation risk (Lima & Dill 1990). Foraging in potentially 'dangerous' open habitats may become worthwhile if there is a reduction in predation risk (i.e. absence of predators) and/or prey is occurring at higher densities than in 'safe' habitats. The variation in strength of associations with structurally complex substrates exhibited by juvenile cod over monthly time periods may reflect the seasonal presence of predators. In Buckley Cove, angling efforts indicated that large cod (up to 95 cm in length) were actively feeding from late August until the end of October (D. Cote unpubl. data); a period that corresponds to the significant associations with structurally complex substrates exhibited by Age 2 to 3 cod.

Nocturnal migrations by juvenile cod to shallow water have been reported for Newman Sound (Keats 1990, Cote et al. 2001) and elsewhere (Pihl 1982, Clark & Green 1990). Clark & Green (1991) have shown that diel migrations through a thermocline can provide cod with metabolic benefits associated with digestion. It has also been suggested that these movements are related to predator avoidance (Clark & Green 1990). In this study, significant changes in depth distribution were not detected in any month despite the persistence of a thermocline until November. These results were not consistent with those of Clark & Green (1990) who observed that Age 3 juvenile cod exhibited nocturnal inshore migrations through a thermocline in late summer but ceased this behaviour when the water column became isothermal. Younger age-classes (Age 0 and 1) in Buckley Cove made inshore migrations through a thermocline, but continued to do so after the water column became isothermal, which suggests that other reasons for these movements exist (Cote et al. 2001), such as predator avoidance. Although large piscivores were present in Buckley Cove (namely large cod; Cote 2002) a lower vulnerability to predation by larger juvenile age-classes (i.e. Lundvall et al. 1999) could account for the age/size specific differences in migratory behaviour.

Concerns regarding altered behaviour of study fish resulting from transmitter effects were addressed by Cote et al. (1999) who found that transmitters had undetectable effects on study animals. The similar use of structurally complex substrates by juveniles in this study to those observed during SCUBA studies (Cote et al. 2001), support this view. The similarity in results also suggest that a fixed array telemetry system is ideally suited for collecting data for a habitat use study as it can provide long term continuous coverage which is not possible using divers.

Coastal habitats, where young cod are primarily distributed (Bergstad et al. 1987, Sinclair 1992, Anderson & Rose 2001), serve as important nurseries (Godø 1984). Within these zones it appears that juveniles show a general preference for structurally complex substrates, although greater flexibility is demonstrated as they age. Terrestrial wildlife has long been managed with a habitat-based approach (Koelin et al. 1996) but few examples exist in temperate/sub-arctic marine ecosystems. Recent developments in hydroacoustics (e.g. Anderson et al. 2002) make sea-floor habitat assessment and mapping possible. Such initiatives, coupled with a greater understanding of habitat use of young cod can be applied to many useful management exercises (e.g. prioritizing MPAs, Auster & Malatesta 1995; assessing productive capacity of habitats, Myers et al. 2001; stratifying research surveys, Perry & Smith 1994; modelling juvenile survival, Lindholm et al. 2001; and determining the potential for negative impacts from fishing, Auster 1998) that would allow for more responsible management of this species.

Acknowledgements. Financial and in-kind support of this research was provided by the Canadian Department of Fisheries and Oceans, Terra Nova National Park, and an NSERC grant to R.S.M. Thanks are given to J. Dietrich, R. Mercer, S. Moulton, C. Kelly, C. Pennell, L. Cole, and K. Clarke for field support. D. Rowsell, T. Lindstrom, E. Kennedy, and G. Niezgoda provided technical support for the MAP_500 and R. S. Gregory, and J. T. Anderson provided useful perspectives on this work. The authors are also grateful for comments on the manuscript by G. Power, J. Gosse and A. Cote and the anonymous reviewers.

LITERATURE CITED

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):1313–1325

Anderson WG, McKinley RS, Colavecchia MV (1997) The use of clove oil as an anesthetic for rainbow trout and its effects on swimming performance. N Am J Fish Manag 17: 302–307

Anderson JT, Rose GA (2001) Offshore spawning and year-class strength of northern cod (2J3KL) during the fishing moratorium, 1994–1996. Can J Fish Aquat Sci 58: 1386–1394

Anderson JT, Gregory RS, Collins WT (2002) Digital acoustic seabed classification of marine habitats in coastal waters in Newfoundland. ICES Mar Tech Ser 59:156–167

Auster PJ (1998) A conceptual model of the impacts of fishing gear on the integrity of fish habitats. Conserv Biol 12: 1198–1203

Auster PJ, Malatesta RJ (1995) Assessing the role of nonextractive reserves for enhancing harvested populations in temperate and boreal marine systems. In: Shackell NL, Willison JHM (eds) Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association, Wolfville, Nova Scotia, p 82–89

Bergstad OA, Jørgensen T, Dragesund O (1987) Life history and ecology of the gadoid resources of the Barents Sea. Fish Res 5:119–161

Clark DS, Green JM (1990) Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. Can J Zool 68:1434–1442

Clark DS, Green JM (1991) Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*) with evidence supporting an energetic basis for their diel vertical migration. Can J Zool 69:1302–1307

COSEWIC (2003) Canadian species at risk, May 2003. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Cote D (2002) Habitat use and movement patterns of juvenile Atlantic cod (*Gadus morhua*) in a coastal area of eastern Newfoundland. PhD thesis, University of Waterloo, Waterloo

Cote D, Scruton DA, Cole L, McKinley RS (1999) Swimming performance and growth rates of juvenile Atlantic cod intraperitoneally implanted with dummy transmitters. N Am J Fish Manag 19:1137–1141

Cote D, Moulton SS, Scruton DA, McKinley RS (2001) Microhabitat use of juvenile Atlantic cod (*Gadus* spp.) in a coastal area of Bonavista Bay, Newfoundland. Trans Am Fish Soc 130:1217–1223

Dalley EL, Anderson JT (1995) Distribution and abundance of demersal juvenile cod (*Gadus morhua*) in inshore and offshore areas of northeast Newfoundland (NAFO divisions 3KL) in the early 1990's. Atlantic Fisheries Research Documents 95/94 Department of Fisheries and Oceans, Canada, St. John's

Dietrich JP (1998) A comparison of the diets of juvenile Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) over late summer at an inshore site of Newfoundland. BSc dissertation, Wilfrid Laurier University, Waterloo

Fraser S, Gotceitas V, Brown JA (1996) Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Can J Fish Aquat Sci 53:305–314

Godø OR (1984) Cod (*Gadus morhua* L.) off Møre — composition and migration. Fl⊘d Rapp 1:591–608

Gotceitas V, Brown JA (1993) Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93:31–37

Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 54:1306–1319

Gregory RS, Anderson JT (1997) Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar Ecol Prog Ser 146:9–20

Guénette S, Pitcher TJ, Walters CJ (2000) The potential of marine reserves for the management of northern cod in Newfoundland. Bull Mar Sci 66:831–852

Hawkins AD, Urquhart GG, Smith GW (1980) Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array. In: Amlaner CJ Jr, MacDonald DW (eds) A handbook on biotelemetry and radio tracking. Pergamon Press, Toronto, p 461–470

Keats DW (1990) A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. J Exp Mar Biol Ecol 139:167–173

Keats DW, Steele DH, South GR (1987) The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can J Zool 65:49–53

Koelin GT, Cowardin LM, LL Strong (1996) Geographic information systems. In: Bookhout TA (ed) Research and management techniques for wildlife and habitats. Wildlife Society, Bethesda, MD, p 540–566

Kramer DL, Rangeley RW, Chapman LJ (1997) Habitat selection: patterns of spatial distributions from behavioural decisions. In: Godin JJ (ed) Behavioural ecology of teleost fishes. Oxford University Press, New York, p 37–70

Kristiansen TS, Otterå H, Svåsand T (2000) Size-dependent mortality of juvenile reared Atlantic cod released in a small fjord. J Fish Biol 56:792–801

Langton RW, Steneck RS, Gotceitas V, Juanes F, Lawton P (1996) The interface between fisheries research and habitat management. N Am J Fish Manag 16:1–7

Lilly GR, Shelton PA, Brattey J, Cadigan NG, Healey BP, Murphy EF, Stansbury DE (2001) An assessment of the cod stock in NAFO Divisions 2J+3KL. Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, Canada, Ottawa 2001/044

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lindholm JB, Auster PJ, Kaufman LS (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 180:247–255

Lindholm JB, Auster PJ, Ruth M, Kaufman LS (2001) Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Cons Biol 15:424–437

Linehan JE, Gregory RS, Schneider DC (2001) Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. J Exp Mar Biol Ecol 263:25–44

Lokkeborg S (1998) Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. Anim Behav 56:371–378

Lokkeborg S, Fernö A (1999) Diel pattern and food search behaviour in cod, *Gadus morhua*. Environ Biol Fish 54: 345–353

Lundvall D, Svanbäck R, Persson L, Byström P (1999) Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can J Fish Aquat Sci 56:1285–1292

Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman & Hall, London

Mattson S (1990) Food and feeding habits of fish species over a soft sublittoral bottom in the Northeast Atlantic. 1. Cod (*Gadus morhua* L.) (Gadidae). Sarsia 75:247–260

Myers RA, Hutchings JA, Barrowman NJ (1996) Hypotheses for the decline of cod in the North Atlantic. Mar Ecol Prog Ser 138:293–308

Myers RA, MacKenzie BR, Bowen KG, Barrowman NJ (2001) What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. Can J Fish Aquat Sci 58:1464–1476

Perry RI, Smith SJ (1994) Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Can J Fish Aquat Sci 51:589–602

Pihl L (1982) Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Neth J Sea Res 15(3/4):419–432

Pihl L, Ulmestrand M (1993) Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. ICES J Mar Sci 50:63–70

Riley JD, Parnell WG (1984) The distribution of young cod. In: Dahl E, Danielssen DS, Moksness E, Solemdal P (eds) The propagation of cod (*Gadus morhua* L.). Flød Rapp 1: 563–580

Sarno B, Glass CW, Smith GW (1994) Differences in diet and behaviour of sympatric saithe and pollack in a Scottish sea loch. J Fish Biol 45(Suppl A):1–11

Sinclair A (1992) Fish distribution and partial recruitment: the case of Eastern Scotian Shelf cod. J Northw Atl Fish Sci 13: 15–24

Templeman W (1974) Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of Newfoundland and adjacent areas from tagging in 1962–1966. ICNAF Res Bull 4:5–50

Templeman W, Fleming AM (1965) Cod and low temperature in St. Mary's Bay, Newfoundland. ICNAF Spec Pub No 6: 131–135

Tupper M, Boutilier RG (1995) Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 52:1834–1841

White GC, Garrott RA (1990) Analysis of wildlife radiotracking data. Academic Press, Toronto

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: February 3, 2003; Accepted: November 13, 2003
Proofs received from author(s): December 23, 2003