TEMPERATURE PREFERENCE AND ACTIVITY OF JUVENILE COD IN BROAD COVE, CONCEPTION BAY, NEWFOUNDLAND

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Temperature Preference and Activity of Juvenile Cod in Broad Cove, Conception Bay, Newfoundland

by

© Donald Stuart Clark, B.Sc. Hon.

A Thesis Submitted to the School of Graduate Studies in
Partial Fulfillment of the Requirements For the Degree
of Master of Science

Department of Biology
Memorial University of Newfoundland
May 1989

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ISBN 0-315-59253-2

ABSTRACT

Field tracking studies conducted in Conception Bay, Newfoundland employing ultrasonic telemetry, determined the activity patterns of juvenile (3 year old) cod (*Gadus morhua* L.) on a daily and seasonal basis. In conjunction with the tracking study, the temperature preference of juvenile cod throughout the year was determined in the laboratory, and the influence of holding temperature on temperature preference was assessed. The results of the temperature preference studies were compared with water temperatures inhabited by juvenile cod in the field to assess the role that water temperature might play in mediating movement and activity.

Juvenile cod exhibited seasonal variation in both temperature preference, and activity patterns. Temperature preference was highly correlated with seasonal changes in the temperature of the inshore waters inhabited by juvenile cod, both for fish acclimated to ambient temperature water, and those maintained at 10°C overwinter. This indicated that seasonal variation in temperature preference was initiated by factors other than changes in ambient water temperature. However, the temperature preference of these two groups differed significantly, indicating that thermal history also influenced temperature preference.

The tracking studies showed that during summer (May - September) juvenile cod were wide ranging, conducting a diel migration from deep cold water where they remained inactive diurnally, to shallow warm water where they actively fed nocturnally. In autumn (September - December) these fish were diurnally active within a restricted home range in shallow water over a sandy substrate. At night they were inactive and remained in a consistent night-resting site over a rocky substrate in close proximity to their diurnal home range.

The summer diel migration may result in increased growth since the movement of juvenile cod into deep cool water during non-foraging hours would effect a lower metabolic rate, and hence lower maintenance costs. In September when the water column becomes isothermal their switch to a non-migratory diel activity pattern is consistent with what would be predicted on the basis of energetic efficiency. It is unclear what selective factors may be involved in the switch in September from nocturnal to diurnal activity. However the most parsimonious hypothesis is that juvenile cod time their activity to reduce predation risk.

ACKNOWLEDGEMENTS

Throughout these studies I have been assisted by numerous people to whom I would like to extend my sincere gratitude. My thanks to my supervisor, Dr. John Green, for his help in the inception and execution of this study and his useful comments on this manuscript. Thanks also to the other members of my supervisory committee, Mr. H. Lear and Dr. D. Larson for their guidance and critique of this thesis. Statistical advice provided by Dr. D. Schnieder and Dr. G. Skanes was much appreciated.

Further thanks go to Dr. M. Bruce-Lockhart who provided the computer software to analyse the telemetry data, Bruce Cocker of Technical Services who built the hydrophones, the Ocean Science Centre divers who helped with placing the hydrophones in the ocean, and Adrian Walsh who skippered the Elsie G during my all night tracking vigils.

I would also like to thank the many graduate students, past and present, who provided freely of their time to assist me. Assistance with scuba diving was provided by Kevin Pauley, Lew Page, Mark Hawryluk, John Christian, Frank Boothroyd, and Chris Rogers. Above water assistance in my field studies was provided by Rob Dillinger, Tony Harold, and by Sarah Thatcher, who frequently chauffered me between the university and my study site. Thanks also to Dave Methven who recorded two days of temperature preference studies on video tape for me when I was getting married.

Special thanks go to my grandfather William Stuart, who first instilled in me an interest in fish and their activities. Thanks also to my wife Kirsten, who assisted me with all aspects of this study, from the collection of temperature preference data in the lab and around the clock tracking of juvenile cod in Broad Cove, to the typing and editing of this manuscript.

Financial support for this study came from NSERC grants awarded to Dr. John Green, and from a Memorial University Graduate Student Fellowship.

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INTRODUCTION

The Atlantic cod, *Gadus morhua* Linnaeus, is an important commercial species which has drawn fishermen to Newfoundland for four hundred and fifty years. As a result of its commercial importance, the activity and temperature affinities of Atlantic cod have been the subject of a great deal of study. However, this effort has been devoted almost exclusively to fish of commercial size, with little attention paid to juvenile fish. An understanding of the factors which influence the movements of adult cod can provide us with predictive powers with respect to the fishery; this is of immediate relevance in an economic sense. However, a complete understanding of this fish at all stages in its life history is a necessary prerequisite for proper management of the fishery and thus, daily and seasonal activity patterns of juvenile cod and their temperature preference are important topics for study.

Adult cod conduct a seasonal migration which brings them into inshore waters in summer. These fish generally spawn in March or April in the deep water along the continental shelf where the temperature is about 3°C, following which they disperse and move onto the banks (Templeman 1981). As the shallow inshore water becomes warmer in June, adult cod move through a cold (-1.5°C to 0°C) intermediate layer into the warmer shallow water (Lear and Green 1985). Thus in June, cod are found in water generally less than fifty metres deep at 1°C to 4°C (Lear et al. 1986; Jean 1964). As the surface waters warm to between 12°C and 14°C these adult cod move progressively deeper, usually remaining in 1°C to

4°C water (Templeman and Fleming 1956; Martin and Jean 1964). They continue to move deeper in the autumn and as the temperatures decrease inshore in early winter, cod move below the range of the cold water back into deep warmer water (Templeman 1974).

Seasonal migration is characteristic of adult cod from all areas and its timing and extent appear to be regulated, to some degree, by water temperature. Bear Island cod conduct a spawning migration which takes them to the Norwegian coast to spawn. These fish collect near Bear Island in winter along the boundary between the warm Atlantic water (2°C) and the cold Arctic water (0°C) remaining on the Atlantic side (Lee 1952; Beverton and Lee 1965). The location of other concentrations of cod in the Barents Sea depends on the extent of the cold arctic water. In warm winters they are found near Novoya Zemlya on the Goose Bank but in cold winters they move south and east avoiding water below 2°C (Maslov 1968). Similarly, the easterly extent of summer movement by southeast Barents Sea cod depends on the degree of intrusion by the annual warm tongue of Atlantic water (Midttun 1965). The relationship is so direct that the fishery can be predicted four to six months in advance (Konstantinov 1965; Legget 1977).

The appearance of cod in fjords of western Greenland also seems to be temperature dependent. Cod generally appear in May and June, along with schools of capelin, but following severe winters, cod do not migrate through the unusually cold coastal waters (<0°C) into the fjords (Horsted and Smidt 1965).

The majority of cod from the Labrador-Newfoundland stock complex spawn from March to May off the coasts of Labrador and Northeast Newfoundland along the slopes of the continental shelf (Templeman 1981). The fertilized eggs develop as they are carried south by the Labrador Current and hatch over the northern Grand Bank and along the Avalon peninsula (Templeman 1981). The larvae are then swept shoreward as a result of the influence of Coriolis forces on the Labrador Current, and are found in the bays along Newfoundland's east coast (Lear and Wells 1984; Lear and Green 1985). The seasonal movements of these fish are then little known until they approach maturity and join the adults in their spawning run. Some authors have suggested that these bays serve as nurseries for the young fish (Thompson 1943; Templeman 1981). However, it is evident that some degree of seasonal migration occurs, and it has been suggested that this increases with age.

Some studies suggest that cod are relatively stationary during their first few years of life (Hjort 1914; Strubberg 1916; Strubberg 1933; Russell 1937; Taning 1937). Strubberg (1916; 1933) tagged two year old fish and found that they remained within five miles of their release site during the following twelve to eighteen months. Hawkins et al. (1985) in their study of cod in a Scottish sea loch, concluded that underyearlings settle in the loch and may remain there until they are over three years old. Tracking studies conducted using ultrasonic telemetry indicated that during summer juvenile cod remained in a restricted home range (1 to 1.5 ha) in shallow, warm water and were generally active diurnally, although some fish were active nocturnally (Hawkins et al. 1980).

Tracking was not continued over winter, however in conventional tagging studies individual fish were caught in the same area of the loch both before and after winter (Hawkins et al. 1985). Thus, Hawkins et al. (1985) were not able to determine if fish remained in the loch over winter, but their results indicated that if an offshore winter migration did occur, at least some fish returned in subsequent years.

Other studies indicate that a degree of seasonal movement does occur. Trout (1957) reported that the distance moved by Bear Island Cod over winter was directly related to the age of the fish. Juvenile cod moved increasing distances from the summer grounds each winter, culminating in a "Dummy Run" prior to sexual maturation (Trout 1957).

Seasonal movement in juvenile cod has also been reported from other areas. Jean (1964) noted that small cod (<38 cm) from the Gulf of St. Lawrence move into deeper water over winter, and that distance moved from the summer grounds varies with size. Heesson (1983) and Riley and Parnell (1984) also found seasonal movement in young cod (<3 years) in the North Sea. Fish tagged close to shore in winter were captured in the summer in offshore locations a median of 80 km away (Riley and Parnell 1984) and then closer to shore again the next autumn.

In Newfoundland, Thompson (1943) suggested that the movements of juvenile cod are quite restricted during the first three years of life. By the end of three years they reach an average length of 29 cm (Wells 1968), and the scope of their activity begins to increase, although it remains somewhat circumscribed until they reach maturity at 6 - 9 years of age (60 - 80 cm in length) when they commence annual spawning migrations (Thompson 1943). Templeman and Fleming (1965) found cod between 11 and 30 cm in St. Mary's Bay over winter, which suggested that these fish reside year round in coastal waters. Also, Agget et al. (1987) proposed that cod less than 45 cm may overwinter in Conception Bay, with offshore migration occurring when the fish are larger.

One factor which seems to be critical in adult cod migration is water temperature. Adult cod generally remain in water between 1°C and 4°C, and avoid other temperatures (Jean 1964; Martin and Jean 1964; Midttun 1965; Woodhead and Woodhead 1965; Lear et al. 1986). However if juvenile cod remain inshore year-round, they must be able to tolerate a wider range of temperatures than the adults. Winter temperatures in inshore waters may drop as low as -1.8°C (Templeman 1965) which is below the plasma freezing point temperatures of adult cod (Choy et al. 1981; Fletcher et al. 1982). Fish can survive below this temperature in a supercooled state, but contact with ice, resulting in ice seeding in the fish, could be lethal (Choy et al. 1981). Juvenile cod have been found frequently at temperatures below -1°C, (Jean 1964; Templeman and Fleming 1965), and experiments on two and three year old cod suggest that cold temperatures are not lethal to them (Harden Jones and Scholes 1974). Kao and Fletcher (1988) have found that juvenile cod have higher levels of plasma antifreeze glycoproteins than adults, giving them greater resistence to freezing.

Temperature preference experiments with ages 0+ and 1+ cod (maximum size 15.8 cm) from the Sea of Murmansk suggest a winter temperature preference of about 3.5°C (Tat'yankin 1974a). However, these fish are not exposed to temperatures as cold as in Newfoundland so the temperature preference of young cod may differ here. Also, the experiments of Tat'yankin (1974a) provided a measure of acute temperature preference, which is highly influenced by acclimation temperature (Beitinger and Magnuson 1979), as indicated by subsequent investigations (Tat'yankin 1974b). A more useful measure of temperature preference is the final preferendum, defined by Fry (1947) as, "a temperature around which all individuals (of a given species) will ultimately congregate, regardless of their thermal experience before being placed in the gradient."

Final preferendum may be determined from a study of acute temperature preference as the point at which selected temperature and acclimation temperature coincide (Fry and Hochachka 1970). In this manner, Jobling (1988) has calculated a final preferendum of 13.5°C for cod. This value was arrived at by extrapolating from acute temperature preference of one and two year old cod, and as a result may overestimate final preferendum. Reynolds and Casterlin (1979) pointed out that a straight line extrapolation from acute temperature preference will overestimate final temperature preference, since the relationship between acclimation temperature and acute temperature preference deviates from linearity, particularly as the final preferendum is approached. Furthermore, temperature preference may vary both seasonally (Fry and Hochachka 1970;

Barans and Tubb 1973; Reutter and Herdendorf 1974) and with age (McCauley 1977; Reynolds and Casterlin 1978; Coutant 1985), so a single value may not give a realistic idea of temperature preference of all ages of cod throughout the year.

Summer surveys of cod abundance along the Canadian Atlantic coast have shown that small cod (<38 cm), unlike the adult fish, remain in shallow water as temperatures increase, and are abundant at 4°C to 8°C (Jean 1964). Temperature preference studies suggest that young cod (<2 yrs., maximum length 24.7 cm) exhibit a temperature preference of 9.5°C in summer (Tat'yankin 1974b). The preference for warm water is corroborated by tracking studies conducted by Hawkins et al. (1974) who followed juvenile cod in 11°C water during October. Small cod (<45 cm) were reported in similar temperatures (10°C to 12°C) in late summer in Conception Bay (Aggett et al. 1987). Thus, young cod are exposed to a wide range of temperatures over the year and may, as Tat'yankin (1974a) suggests, exhibit seasonal variation in temperature preference.

Thus, unlike adult cod which generally maintain a fairly constant thermal environment, juvenile cod inhabit warm water in summer and cold in winter. This places physiological demands on the fish, since a change in temperature alters the fish's respiratory requirements, and the efficiency of chemical reactions within the fish (Crawshaw 1977), necessitating an acclimatory response from the fish. The process of acclimation to an altered thermal regime may be quite lengthy, requiring feedback to the genetic material resulting in restructuring at both the cellular and tissue levels (Fry and Hochachka 1970; Hazel and Prosser 1974). The optimum temperature for physiological activity is thus altered to match the environmental temperature.

A fish may obviate the necessity of acclimatory responses by regulating body temperature through behavioural means. Temperature preference generally corresponds to a fish's thermal optimum (Crawshaw 1977; Magnuson et al. 1979); thus through behavioural thermoregulation a fish can maintain a physiologically appropriate temperature. Furthermore, the preferred temperature appears in many cases to be that which maximizes the growth rate (Beitinger and Magnuson 1979; McCauley and Casselman 1981; Coutant 1987). The temperature at which maximum growth is realized depends on the species in question and may be influenced by a variety of factors, particularly food abundance. Metabolic rate increases with temperature, thus increasing the amount of energy required for maintenance, but also increasing the ability to process food. This results in a high temperature optimum for maximum growth in fish fed to satiation, and a lower optimal temperature for growth when the food supply is restricted (Brett 1971; Hawkins et al. 1985).

For cod, maximum growth rate occurs between 13°C and 15°C (Jobling 1983). However, gross conversion efficiency (increase in body weight divided by weight of food consumed) is maximal at 7°C due to low maintenance requirements (Hawkins et al. 1985). Thus if diet is restricted, maximum growth is achieved at the lower temperature. Similarly, Brett (1971) found that maximum growth in sockeye salmon (*Onchorynchus nerka*) occurred at progressively lower temperatures when the food supply was decreased. Thus if maximal growth is to be achieved, temperature preference must be sensitive to food abundance.

In some cases diurnal variation in temperature preference is displayed. For goldfish the preferred temperature peaks in the four hours before dawn (Reynolds et al 1978). Similarly, Spieler et al. (1977) demonstrated that goldfish growth was maximized when the temperature fluctuated daily, peaking in the last four hours of dark. Thus temperature preference is responding to a physiological cycle to maximize growth. Sockeye salmon also exhibit diurnal variation in temperature preference. Young sockeye salmon conduct a daily vertical migration which takes them from deep, cold water by day, to warm, shallow water at night (Brett 1971). They feed crepuscularly near the surface, and spend daylight hours in cold water, which is energetically efficient since it results in a low metabolic rate during the non-feeding hours (Brett 1971). Thus it is apparent that for many fish, temperature is an environmental variable which is controlled by behavioural means in order to maximize growth.

While temperature seems to play an important role in regulating the movement of adult cod, it is uncertain what role, if any, it plays in the movement of juveniles. Tat'yankin (1974b) suggested that their temperature preference is quite plastic, simply reflecting acclimation temperature.

In this study I looked at diel activity patterns of juvenile cod in Broad Cove, Conception Bay, to see if these patterns are similar to those found by Hawkins et al. (1985) in Scotland, and to see if there is any seasonal variation in these patterns. Laboratory studies were conducted over a one year period to determine the temperature preference of juvenile cod, see if it varies temporally, and elucidate the influence of acclimation temperature on temperature preference. The results of laboratory and field studies were then integrated to assess the role temperature preference might have in mediating juvenile cod activity.

MATERIALS AND METHODS

2.1 Temperature Preference

Experiments were conducted at the Marine Sciences Research Laboratory (MSRL) using a four chambered temperature gradient tank (Appendix 1). A gradient was established by adding warm and cold water to adjoining chambers and blocking the intervening channel with an insulating styrofoam barrier. The 3 remaining passages were then partially blocked with plexiglass barriers to restrict water mixing between chambers, leaving a space 12 cm deep at the bottom of the channel. A regulated flow of warm water was supplied from a header tank maintained by a constant supply of seawater. Water in the header tank was heated to 10°C using a Neslab recirculating heater between November 1986, and July 1987, and in November 1987. In September and October of 1986 and 1987, ambient water in excess of 10°C was available, and the heater was not used. Airstones in each chamber kept the water mixed and assisted in preventing oxygen supersaturation.

Cold water was supplied from a header tank in trials from September 1986 to May 1987. The header tank was cooled with a neslab recirculating cooler from September to December 1986. The neslab was not used from December 1986 to May 1987, since ambient water temperature was less than 4°C, the lowest temperature the neslab could provide. From July 1987 to December 1987 the recirculating neslab was connected directly to the experimental tank, as this

To reduce disturbance of the experimental fish, the tank was surrounded to a height of 2 m with black plastic drapes, and observations were made from an adjoining room using a video camera suspended above the tank, and connected to a television monitor. A 30mm video recorder was also used to record activity sequences for later analysis. A Yellow Springs Instruments 12 channel telethermometer with a thermistor located in each chamber was used to monitor temperature. Temperature was recorded to the nearest 0.1°C.

The ambient light cycle was followed throughout the year. Full light was provided by a 15 watt frosted bulb suspended at the top of each chamber, and a flourescent light 235 cm above the centre of the tank. Dawn and dusk were simulated by using the flourescent light alone for 30 minutes at the beginning and end of the light cycle.

Illumination at night was provided by a 25 watt red light suspended above each chamber. As the visual range of cod does not include the red band (Anthony and Hawkins 1983) this lighting allowed for observations but did not interfere with normal scotopic conditions.

Subjects for the temperature preference studies were drawn from two populations; field or ambient water acclimated fish, and heated water fish. The former were brought directly from the field (Broad Cove) when possible. All fish used in these experiments were between 24 and 35 cm in length, and were likely three years in e Wells 1968 . The water temperature where these fish were caught was measured by a diver with a thermometer. Between January and May fish were not available from the field, so fish which had been held in the lab since the previous November were used as subjects. These fish were among fourty brought from Broad Cove and held at the MSRL in a 300 gallon tank which had a constant supply of fresh sea water pumped from a depth of 20 m in Logy Bay. Thus, holding temperature was representative of the temperatures these fish would experience over winter in nearshore waters. The water temperature in the holding tank was recorded each time fish from this tank were used in an experiment.

Heated water fish were held at the MSRL in a 300 gallon tank with a constant supplement of ambient sea water. Between October 1986, and May 1987, and during October, November, and December 1987, tank water was maintained at 10°C using a recirculating neslab unit. Between June 1987 and October 1987, these fish were held at lab ambient temperature, which was in excess of 10°C and peaked at 13°C.

Groups of 6 to 10 fish were placed in the chamber of the experimental tank which best approximated their acclimation temperature. The fish were then left for two to three days, a period sufficient for them to reach their final preferendum (Reutter and Herdendorf 1974; Richards et al 1977) before observations began. This also allowed time for adjustments to be made in the water temperatures present within the tank if the fish seemed to be congregating near one extreme of the gradient. Such adjustments were necessary since a gradient could not be maintained which included the full range of water temperatures available from the warm and cold water sources. The temperature range within the tank during an observation period varied between 2.0 and 7.9°C.

At least two sets of observations, each of two hours duration were conducted, during which the number of fish in each chamber, and water temperature in each chamber were recorded at five minute intervals. Observations were made in morning and afternoon, and in most cases, also at midnight. The mean occupation temperature was then calculated for each group of fish as a measure of temperature preference. Experimental trials were paired temporally for ambient acclimated and heated water fish, to allow comparisons of temperature preference of each group to be made throughout the year, and two sets of fish were tested from each group to assess within group variation in temperature preference.

Trials with ambient acclimated fish in April were conducted in an unheated fish holding building at the Marine Sciences Research Laboratory as this provided access to a colder (-1°C) supply of sea water. The experiments were conducted in a trough tank (40 cm deep, 60 cm wide and 150 cm long). The trough was divided using baffles into four 30 cm by 30 cm chambers, and an airstone was placed in each chamber to keep the water mixed. A 30 cm by 30 cm area at one end of the trough was sectioned off with a perforated plate, and an immersion heater was placed in this section to establish a temperature gradient. Two airstones were placed in this section to assist in distributing heated water to other portions of the tank. A constant volume of ambient sea water was added at the opposite end of the tank, and a standpipe, also at this end of the tank, drained off excess water. The number of fish in each chamber and the temperature in each chamber were recordeded as in other trials.

A series of gradient reversal experiments were conducted throughout the year to ensure that the selection of a region within the experimental tank was made with regard to temperature, and not position. After completion of a temperature preference trial, the temperature gradient was altered by changing the chambers which recieved warm and cold running water. A period of 4 to 20 hours was them allowed for the new gradient to be established and the juvenile cod to reorient themselves. A further one or two periods of observation were then undertaken and the mean occupation temperature calculated. The distribution of the fish within the experimental tank, along with their preferred temperature, could then be compared from before and after the gradient reversal, to ensure that the fish were responding to temperature and not position.

Statistical analyses of data were either conducted by hand using a pocket calculator, or on a computer using Minitab statistical software. A contingancy table test was used to determine the influence of gradient reversal on the selection of chambers within the experimental tank by juvenile cod. A binomial expansion was then used to see if gradient reversal influenced the preference of the juvenile cod for warm versus cold ends of the experimental tank.

A split plot analysis of variance was used to determine if temperature preference of juvenile cod varied with the time of year and if it varied between the two experimental groups (fish taken from ambient temperature water, and fish held in heated water). Finally, the relation between ambient water temperature and the temperature preference of fish from ambient and heated water was investigated through correlation.

2.2 Field Activity Studies

Field studies on the activity of juvenile cod were conducted in Conception Bay, Newfoundland. Tracking within Broad Cove was conducted using a spaced hydrophone array to precisely locate fish. This system is similar to that described by Hawkins et al. (1980) in conjunction with their cod tracking studies in Scotland. Four omnidirectional hydrophones, constructed by the electronics division of technical services at Memorial University of Newfoundland, were placed on the sea floor at depths of 8 to 17 m. Fish were tagged with a cylindrical hydroacoustic transmitter 50 mm long, and 12 mm in diameter. Reception of the signal by at least three hydrophones was necessary to determine the fish's position.

Hydrophones were connected by cable to a four channel telemetric receiver located in a field station at Broad Cove. The receiver deleted extraneous background noise and passed the cleaned signals to a four channel oscilloscope. The osciloscope displayed time intervals (or delay times) between reception of the signal by the first hydrophone, and its reception at subsequent hydrophones. Each delay time could be translated into a hyperbola between the two hydrophones (using the speed of sound in water) and two delay times resulted in two hyperbolae, whose intersection point indicated the fish's position.

Delay times were recorded by hand to the nearest millisecond, and analyzed using "Fishtrak," a computer program written by Michael Bruce-Lockhart (Department of Engineering, Memorial University of Newfoundland), which determined the fish's location. Fishtrak calculates the fish's position to within 0.1 m. However, delay times were only measured to the nearest millisecond, limiting the accuracy of positioning. Within the hydrophone array, positions were accurate to approximately one metre, however, due to the nature of hyperbolae, there are some areas outside the array, but still within tracking range, where accuracy may be further reduced due to imprecision in delay times.

The hydrophones could detect a signal at a range of 1000 m; however the range over which they could provide an accurate position was somewhat less than this. The arrangement of the four hydrophones used allowed the location of a tagged fish within an area about 300 m in diameter. This range was decreased when background noise was high due to heavy seas, or when the tagged individual was in a sheltered location. If large rocks or other objects severely obstructed the direct passage of the signal from the transmitter to the hydrophone, the range at which the fish could be accurately located was reduced. This distance could decrease practically to nil if the tagged individual was in a crevasse, or under a rock.

Eleven fish were tracked in Broad Cove using this system. For four fish, positions were recorded at two minute intervals throughout the active phase of their diel cycle, and the distance between successive readings was calculated, allowing a comparison of activity between fish, and among fish at different times of day. Also, positions were used to determine daytime home range area. Positions from throughout the day were plotted on a map, and the extreme points in the range were connected by lines, forming a complex polygon which represented the daytime home range. This polygon was traced on a Zeiss digitizer which then calculated the area within the boundaries. This was done on a daily basis for four fish, where positions were available from throughout successive days, and on an overall basis for 6 fish; plots from different days were overlayed on one another, and a polygon constructed which included positions from all days of tracking.

Fish which left Broad Cove were tracked from a 5 m aluminum boat using a VEMCO mobile receiver and directional hydrophone. When this boat was used, fish could only be tracked during the day. Using the directional hydrophone as a guide, the boat could be manouvered over the fish to within a few meters, and the approximate position of the boat was then recorded on a map of Conception Bay. Relocation on subsequent days was effected by checking from the boat at approximately 400 m intervals (the pinger could be detected from about 1 km) along the shoreline to a distance of 8 km east and west from Broad Cove. Initially, checks were also made along the same stretch of coastline over deeper water (50 to 200 m) 1 km and 2 km offshore. However, since the tagged juvenile cod were never found in deep water, these checks were discontinued. If the fish was not located it was assumed to have moved out of the tracking area.

The depth of water at which fish were captured or relocated was measured with a handline to the nearest foot and later converted to meters. All temperature measurements were made to the nearest 0.1°C with a Vemco depth and temperature sensitive hydroacoustic transponder, except in Broad Cove, where temperatures were also measured by divers with a thermometer.

In addition to the fish tracked from the small boat, two fish were tracked from the 12 m boat Elsie G. Use of this larger boat allowed tracking to continue at night. When using the Elsie G tracking was conducted in the usual manner, but the boat's location was determined to 0.01 minutes latitude and longitude using Loran C, and depth was measured with a sonic sounder.

Fish for tagging were caught on baited hooks at depths between 11 and 14 m, within an area about 30 m across in Broad Cove. This area was over the region of sandy substrate in which fish were subsequently tracked in the autumn (Figure 3, page 30). All fish tagged in this study were between 29 and 33 cm in length, and were likely all three years in age, as this size range stradles the average for three year old fish from this region reported by Wells (1968) as 29 cm in spring and 32 cm in autumn and by May et al. (1965) as 31 cm based on samples taken from April to September. The range of 29 to 33 cm falls well above the average length of two year old fish (22 cm), and well below that of four year olds (44 cm) (Wells 1968). When a fish of appropriate size was caught, it was anaesthetized with MS222, the transmitter was inserted orally and pushed down past the pharynx into the stomach. The fish was then placed in a bucket of seawater to recover from the anaesthetic. Following its recovery, the fish was placed in a cage and lowered to the sea floor near its capture site at a depth of 10 to 12 m, and held there for at least one hour. The fish was then released at the bottom by opening the cage door and allowing it to swim out. The fish generally left the cage within 5 minutes, at which point tracking commenced.

A two-way Kruskall-Wallis test was used to test the significance of differences in mean activity levels at different times of day of juvenile cod tracked in Broad Cove and also to test for differences in activity between fish. Preliminary results had suggested that activity peaked at the beginning and end of the daytime active phase, so a Scheffe Multiple Contrast test was employed to test for this.

RESULTS

3.1 Temperature Preference

Upon introduction to the experimental tank, fish generally went through a short period of inactivity during which they did not move from the initial chamber. This was followed by an exploratory period during which fish moved freely between chambers, after which they began to select an area within the temperature gradient. The gradient reversal experiments indicated that the region of the tank in which the fish congregated changed when the orientation of the temperature gradient was reversed (Table 1). However, although the position of greatest residency shifted, in all 10 reversal experiments the end of the temperature gradient which had the highest cumulative residency remained the same ($p=0.009$; Table 2).

The temperature preferred by fish held in ambient temperature water peaked in September and October, then declined over winter to a minimum in March and April (Figure 1). Fish held in 10°C water showed a similar pattern, but did not display as low a preferred temperature over winter. A split plot Anova (Table 3) indicates that temperature preference of juvenile cod differed significantly depending on time of year ($F=159.6$, $p<0.001$), and also differed significantly between the two holding conditions ($F=1420$, $p<0.001$). Furthermore, the interaction effect ($F=10.7$, $p<0.001$) indicates that there was significant variation in the difference between temperature preferenda of the two

Table 1 The influence of change in the orientation of the temperature gradient on the cumulative total number of juvenile cod observed in each chamber within the experimental tank. X^2 tests for the difference in distribution of fish before and after gradient reversal.

	Cumulative # of Fish in Each Chamber Before Gradient Reversal				Cumulative # of Fish in Each Chamber After Gradient Reversal				
	Chamber Number								
Date	1	2	3	4	1	2	3	4	X^2
Feb 20 - Feb 21	0	149	107	32	27	108	162	2	71.1
Mar 26 - Mar 27	248	38	12	2	0	2	36	262	548.5
Apr 1 - Apr 3	270	29	1	0	0	0	33	267	596.1
Apr 18 - Apr 21	260	125	15	0	5	36	141	182	577.9
May 13 - May 16	16	112	106	66	209	46	6	40	288.8
May 20 - May 22	123	160	1	16	36	5	195	63	413.2
May 26 - May 28	75	5	135	73	141	107	0	17	282.4
Sep 16 - Sep 17	162	66	5	17	11	72	138	29	258.9
Oct 29 - Nov 1	178	40	4	82	21	89	39	1	223.5
Nov 24 - Nov 25	147	99	9	45	4	127	118	51	232.8

$$X^2_{0.005(3)} = 12.838$$

Table 2 The influence of change in the orientation of the temperature gradient on the proportion of the total cumulative observations of juvenile cod made in warm and cold halves of the experimental tank.

	Before Reversal		After Reversal	
Experiment	Warm	Cold	Warm	Cold
Feb 20 - Feb 21	0.52	0.48	0.55	0.45
Mar 26 - Mar 27	0.05	0.95	0.01	0.99
Apr 1 - Apr 3	0.00	1.00	0.00	1.00
Apr 18 - Apr 21	0.04	0.96	0.11	0.89
May 13 - May 16	0.44	0.56	0.15	0.85
May 20 - May 22	0.06	0.94	0.14	0.86
May 26 - May 28	0.28	0.72	0.06	0.94
Sep 16 - Sep 17	0.28	0.72	0.33	0.67
Oct 29 - Nov 1	0.86	0.14	0.85	0.15
Nov 24 - Nov 25	0.36	0.64	0.44	0.56

Number of times preferred side remained the same = 10

Number of times preferred side changed = 0

Probability of occurrence by chance = $0.5^{10} = 0.00098$

Figure 1 Temperature preference of juvenile cod from ambient water and heated water over a one year period.

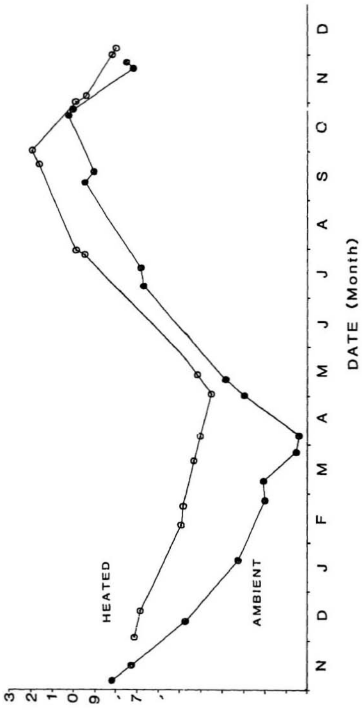

HEATED
AMBIENT
DATE (Month)
N
D
J
F
M
A
M
J
J
A
S
O
N
D
3
2
1
0
9
7

Table 3 Summary table for a Split Plot Analysis of Variance on the effects of temperature treatment and time of year on the temperature preference of juvenile cod from Broad Cove.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between Groups	35.7	3	11.9	1420.0*
Factor A (Temp. Treatment)	35.5	1	35.5	
Error (Between Groups Within Treatment)	0.2	2	0.025	
Within Groups	337.7	28		
Factor B (Time of Year)	312.9	7	44.7	159.6*
A x B Interaction	20.9	7	3.0	10.7*
Within Groups Error	3.9	14	0.28	

$^{*}p<0.001$

Figure 1, which shows that temperature preference of the two groups of fish was quite similar in October and November, when their acclimation temperatures differed by less than 1°C, but differed by over 4°C in March and April, when their holding temperatures differed by 11°C.

3.2 Tracking Experiments

Eighteen fish tagged with acoustic transmitters were tracked in Conception Bay for periods of up to 21 days (Table 4). This tracking revealed temporal variation in both habitat and behaviour. Fish tracked from late September through December (Autumn) remained within restricted home ranges in shallow water, and were active diurnally. Fish tagged from May to early September (Summer) were wide ranging in Conception Bay, generally remaining in deep (approximately 30 m) water, and were active nocturnally. No fish was tracked during both summer and autumn.

3.2.1 Autumn

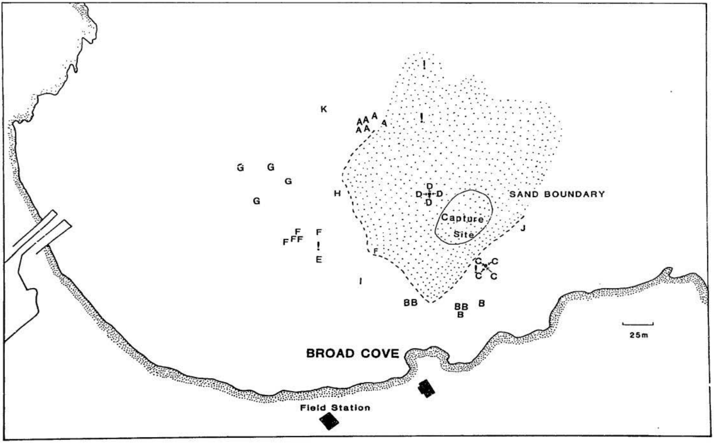
Eleven fish were tracked between September 23 and December 2 for periods of up to 12 days. In all cases the fish remained within Broad Cove for the duration of the tracking period (Table 4). Tracking ended either with the expiration of the tag's batteries, or the expulsion of the transmitter by the fish.

Fish were generally stationary nocturnally, with activity commencing at dawn and ending at dusk. Fish tended to return to the same locale each night, in some cases spending several nights in the same position, and for all but one fish

Table 4 Maximum distance moved from Broad Cove by 18 juvenile cod tagged in Broad Cove and the dates during which they were tracked.

Season	Fish	Length (cm)	Dates Tracked	Maximum Distance From Broad Cove
Summer	A	31.0	July 3 - July 24	>8 km
	B	30.0	July 8 - July 19	>8 km
	C	31.2	July 29 - Aug. 1	6 km
	D	30.5	Aug. 16 - Aug. 19	5 km
		33.0	July 1 - July 9	>8 km (found within tracking area only once after July 1)
		32.4	Sep. 5 - Sep. 18	500 m past Broad Cove mouth
		28.6	Sep. 10 - Sep. 12	Just past Broad Cove mouth
Autumn	A	30.0	Oct. 6 - Oct. 18	Stayed in Broad Cove
	B	30.8	Nov. 21 - Dec. 1	Stayed in Broad Cove
	C	30.8	Oct. 4 - Oct. 7	Stayed in Broad Cove
	D	30.7	Oct. 9 - Oct. 13	Stayed in Broad Cove
	E	31.5	Oct. 18 - Oct. 19	Stayed in Broad Cove
	F	32.6	Nov. 5 - Nov. 8	Stayed in Broad Cove
	G	31.7	Nov. 11 - Nov. 15	Stayed in Broad Cove
	H	31.4	Sep. 23 - Sep. 24	Stayed in Broad Cove
	I	30.5	Oct. 2 - Oct. 3	Stayed in Broad Cove
	K	32.5	Nov. 8 - Nov. 9	Stayed in Broad Cove
	J	31.3	Nov. 3 - Nov. 4	Stayed in Broad Cove

Figure 2 Nocturnal locations of tagged juvenile cod tracked in the autumn at Broad Cove. Letters indicate the positions selected by an individual fish each night. ! indicates the hydrophone positions.


SAND BOUNDARY
Capture Site
25m
BROAD COVE
Field Station
A
B
C
D
E
F
G
H
I
J
K

(D), the night resting spot was over a rock or rubble substrate (Figure 2). At first light fish became active and quickly moved to their daytime home range which was generally over sand and removed from the resting spot (Figure 3). Daytime home range remained consistent in size and location for a fish on successive days (Figures 4 and 5), although it differed between fish. Daytime home range area varied from 545.3 m^2 for fish C to 25816.0 m^2 for fish B (Table 5).

3.2.2 Nocturnal Behaviour

Although some fish spent several nights in precisely the same location (fish C and D in Figure 2 each spent four nights in a single location), others showed some variation in resting sites. Fishes A, B and F returned to the same general area each night, but not to exactly the same position. After two nights in one location, fish B moved approximately 51 m to another area where it stayed on the following four nights. Fishes F and B also moved during the night, B on one occasion and F on two. On these occasions, the fish settled in their accustomed locations at dusk, but eventually moved to a second position in deeper water over sand. On all three occasions a heavy gale with winds of 90 km/hr. was blowing, and the shallow water would have been quite turbulent. Thus, it is possible that these fish moved their resting site in response to adverse conditions. On one of these nights, the wind died down before dawn, and the fish (F) had returned to its usual resting site before observations commenced 1.5 hours before sunrise.

Fish G seemed to vary considerably in its selection of resting site (Figure 2, page 30). However, this appears to have been an artifact of the tracking system,

Figure 3 Positions of a juvenile cod in Broad Cove on October 6, 1987 plotted at 20 minute intervals. N indicates the nocturnal resting site; ! indicates the position of a hydrophone.

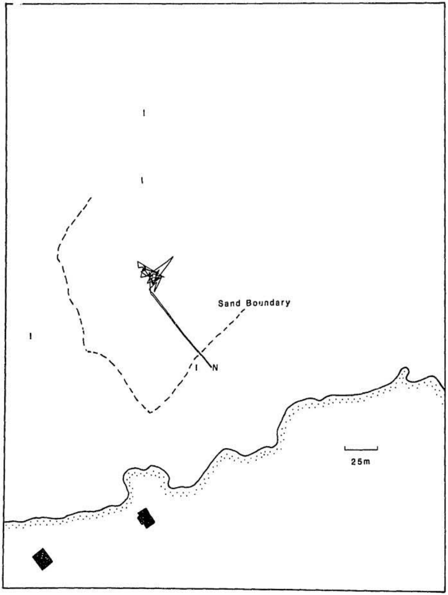

I
I
I
Sand Boundary
I
N
25m

Figure 4 Daytime home range of a juvenile cod in Broad Cove on four successive days, October 4 - 7. N indicates the nocturnal resting site; ! indicates the hydrophone positions.

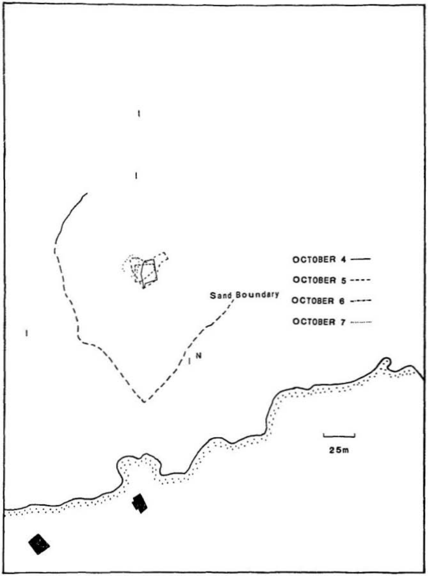

OCTOBER 4 ——
OCTOBER 5 ----
OCTOBER 6 -·-·-
OCTOBER 7 ········
Sand Boundary
N
25m

Figure 5 Daytime home range of a juvenile cod in Broad Cove on four successive days, October 9 - 12. N indicates the nocturnal resting site; ! indicates the hydrophone positions.

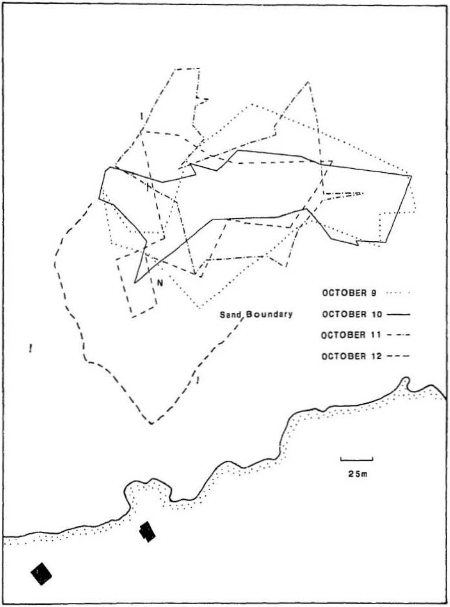

N
Sand Boundary
OCTOBER 9
OCTOBER 10
OCTOBER 11
OCTOBER 12
25m

Table 5 Daily, mean daily and total diurnal home range areas (m^2) of 6 juvenile cod in Broad Cove. The method for measuring the areas is described in the text.

Fish	Date	Daily Area m^2	Mean Daily Area m^2	Total Area m^2
C	Oct. 4	210.5	243.8	545.3
C	Oct. 5	176.4		
C	Oct. 6	448.0		
C	Oct. 7	140.1		
D	Oct. 9	15777.2	12548.7	25021.0
D	Oct. 10	11505.3		
D	Oct. 11	13401.6		
D	Oct. 12	9510.7		
F	Nov. 6	3932.3	4065.7	7846.1
F	Nov. 7	2905.1		
F	Nov. 8	5359.7		
G	Nov. 12	12095.3	11542.0	21858.7
G	Nov. 13	15250.1		
G	Nov. 14	7280.7		
G	Nov. 15	4076.1		
A	Oct. 6-18			13141.7
B	Nov. 21-29			25816.0

and not an accurate portrayal of the fish's behaviour. The transmitted signal from this fish would be clear as the fish approached its resting site, then would suddenly disappear, suggesting that the fish was moving into a sheltered rocky site. The sudden appearance and disappearance of the signal made it difficult to pinpoint the fish's location. Intermittent signal reception overnight, also suggested that the fish might have been in a sheltered site where rocks were blocking the signal's path. Fish F also appeared to be in a sheltered site at night. Although its resting area was very close to hydrophone 3 (Figure 2, page 30) signal strength varied considerably during the night, occasionally fading to the point that it no longer triggered the receiver. This strongly suggests that rock was blocking the transmission of the signal.

3.2.3 Diurnal Behaviour

Tagged juvenile cod commenced activity around first light, on average 45 min. ($s = 10.1$ min.) before sunrise (Table 6), and proceeded rapidly to their daytime home range. The fish were active within this area throughout daylight hours (Figure 4, page 35), then began to move back to their nocturnal resting site around sunset, and became inactive on average 53 min. ($s = 11.6$ min.) after sunset as darkness set in (Table 6).

In addition to variation in daytime home range size, juvenile cod displayed a great deal of variability in activity (measured as distance moved in two minute intervals). There was significant variation in activity levels both between fish ($p < 0.005$; Kruskal Wallis K), and among fish at different times of day ($p < 0.005$;

Table 6 Time before sunrise at which juvenile cod activity begins and time after sunset at which juvenile cod activity ceases.

Date	Before Sunrise (minutes)	After Sunset (minutes)
Sept. 24	25	45
Oct. 5	40	60
Oct. 6	37	49
Oct. 7	37	
Oct. 9		60
Oct. 10	43	58
Oct. 11	55	38
Oct. 12	52	73
Oct. 13	38	42
Oct. 18		69
Oct. 19	52	
Nov. 6	45	61
Nov. 7	62	59
Nov. 8	59	56
Nov. 11		65
Nov. 12		61
Nov. 13	41	41
Nov. 14	40	48
Nov. 15		31
Mean	45	54
s	10	12

Kruskal Wallis K). However, there was no significant interaction between the two variables tested (activity at different times of day, and for different fish), indicating that all tracked fish followed the same pattern of activity.

Fish were more active at the beginning and end of their diurnal activity cycle ($p < 0.05$, Scheffe's Multiple Contrast), than at other times during the day (Table 7). These periods were used by some fish to move between widely separated diurnal home ranges and night resting sites (Figure 3, page 33); however, in the instances where there was a short distance between home range and resting site, the fish still displayed their greatest activity at the beginning and end of their diurnal activity cycles (Fish D and F, Table 7).

3.2.4 Summer

Juvenile cod tagged between July and mid September exhibited a pattern of behaviour distinct from those tagged in the autumn. In summer juvenile cod were wider ranging, nocturnally active, and conducted a diel migration between deep cold water and shallow warm water.

Like the fish tagged in autumn, fish tagged in the summer were released near their capture site in 11 to 13 m of water in Broad Cove. However, unlike fish in autumn, they headed immediately into deeper water (approximately 20 to 26 m). Of the seven fish tagged in this period, one (tagged September 9) remained just outside the cove, in range of the stationary tracking gear, while six moved out of the area on the night of their release.

Table 7 Average distance (m) moved by four fish in ten consecutive two minute intervals at twelve times during the day beginning with the fishs' first two 20 minute periods of activity in the morning and ending with the last two periods of activity in the evening before the fish reached their nocturnal rest sites.

Fish C		Fish D		Fish F		Fish G	
Time	Distance (m)	Time	Distance (m)	Time	Distance (m)	Time	Distance (m)
0640-0700	11.6	0650-0710	20.7	0600-0620	22.9	0630-0650	21.3
0700-0720	4.1	0710-0730	17.7	0620-0640	20.1	0650-0710	19.5
0800-0820	2.8	0856-0916	17.6	0800-0820	12.7	0800-0820	12.9
1000-1020	3.0	1000-1020	16.7	0900-0920	15.0	0900-0920	11.1
1100-1120	4.1	1051-1111	12.4	1000-1020	14.3	1000-1020	11.9
1208-1228	11.0	1142-1202	10.9	1100-1120	13.0	1100-1120	12.4
1300-1320	7.3	1300-1320	19.5	1200-1220	12.8	1200-1220	14.1
1400-1420	3.5	1413-1433	10.6	1300-1320	14.5	1300-1320	11.7
1500-1520	2.8	1520-1540	11.8	1400-1420	13.2	1400-1420	9.2
1700-1720	3.4	1700-1720	14.4	1500-1520	9.5	1500-1520	15.6
1800-1820	5.6	1822-1842	16.9	1633-1653	20.5	1610-1630	16.4
1822-1842	12.8	1844-1904	20.5	1653-1713	13.2	1630-1650	26.2

Two of these fish, tagged on July 3 and July 8 1987, were monitored with mobile tracking gear on a daily basis for 21 and 11 days respectively. These fish moved extensively along the coast of Conception Bay, reaching distances of at least 8 km from Broad Cove, and moving in excess of 3 km in one day (Figure 6). They were monitored diurnally for periods of one to two and a half hours, during which they moved little or not at all. They did, however, move long distances between observation periods, probably moving nocturnally. Nocturnal activity was noted for these fish on the nights of their release, when both moved several kilometres from Broad Cove.

Diurnally, these fish were always found in water between 28 and 40 m deep, except on one occasion when fish A (Figure 6) was located in 16 m of water. This is much deeper than the water they are found in during the autumn, and exposed them to low temperatures (4.1°C to 4.6°C) even though the water temperature in the cove was similar to that found in autumn (12.9°C at 14 m, Figure 7).

These fish could not be tracked nocturnally, thus their locations on all nights except that of their capture are uncertain. They were caught at night in Broad Cove at depths between 11 and 13 m as were all juvenile cod caught during summer. Juvenile cod were feeding actively in Broad Cove nocturnally, and could easily be caught with a baited hook at this time while attempts to catch them before dark proved fruitless, the reverse of what was found in the autumn. Similarly, in the summer juvenile cod were not seen in Broad Cove during the day when scuba diving, whereas they were often seen in the autumn. On two dives in

Figure 6 Positions of two juvenile cod released in Broad Cove and tracked in Conception Bay during July 1987. The numerals indicate the number of days after release that the fish occupied a position. ? indicates that the fish could not be located on that day and was presumed to be outside the tracking area.

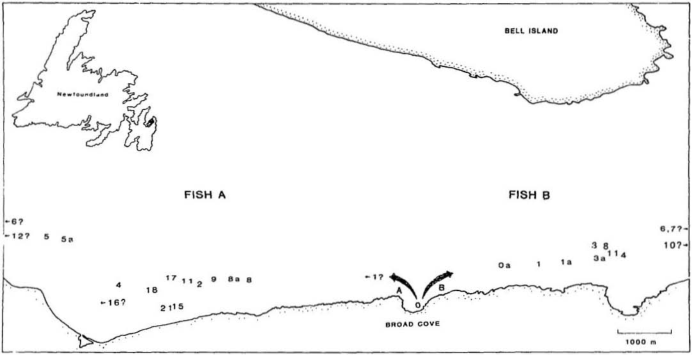
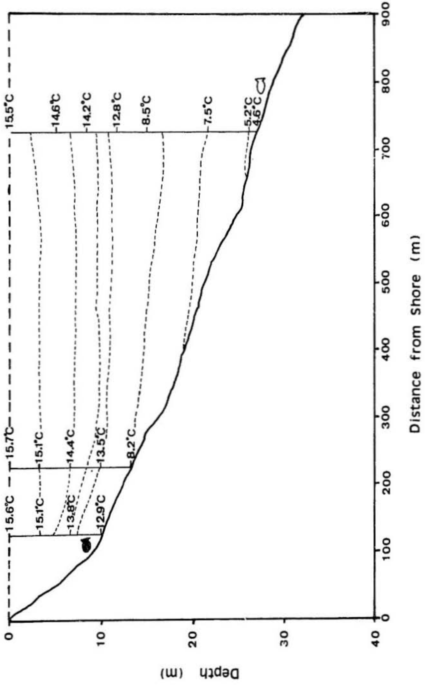

BELL ISLAND
Newfoundland
FISH A
FISH B
←6?
←12? 5 5a
4
←16?
18
17 11 2 9 8a 8
2115
←1?
A
O
B
BROAD COVE
0a 1 1a
3 8
3a 11 4
6,7?→
10?→
1000 m

Figure 7

Temperature profiles of Broad Cove in summer (Measured July 16). Black fish indicates the position of juvenile cod at night. White fish indicates the position of juvenile cod during the day.


15.5°C
14.6°C
14.2°C
12.8°C
8.5°C
7.5°C
5.2°C
4.6°C
15.7°C
15.1°C
14.4°C
13.5°C
8.2°C
15.6°C
15.1°C
13.8°C
12.9°C
Depth (m)
0
10
20
30
40
Distance from Shore (m)
0
100
200
300
400
500
600
700
800
900

May, 6 in June, 7 in July, and 4 in August, all to between 12 and 17 m depth in Broad Cove, no juvenile cod of the size range tagged were seen, although they were regularly sighted later in the year. Juvenile cod were first sighted during a daytime scuba dive on September 9. None were seen during dives to 12 m in Broad Cove on September 13, and 15, however, during twice weekly dives from September 21 to November 18 juvenile cod were always sighted, swimming in groups of from two to 12 fish.

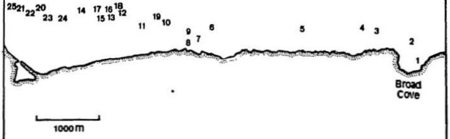
More detailed information on the activity of juvenile cod in summer was obtained for two fish tagged on July 28 and August 15, each of which was tracked for three days. These fish were tracked at night as well as during the day, giving a better indication of when they were active, and how far they moved. Fish C (Figure 8), tagged July 28, appeared to be inactive throughout most of the day. On the three nights that it was tracked, it became active between 2230 hr. and 2330 hr. It then moved extensively along the coast, five kilometres on the night of its release, and two and a half kilometres on the following night. It stopped moving by 1000 hr. on the first morning, and 0745 hr. on the second, and was inactive throughout the day. After release on July 28 it began to move west, staying in deep (22 to 30 m) water until 0300 hr. on July 29, when it moved close to shore in approximately 15 m of water. The fish remained close to shore until 0600 hr., when it moved further west and offshore. By 0900 hr. of July 29 it was again in shallow (9 m) water, and it stayed in shallow water for the duration of tracking.

Fish D moved 4 km east to the mouth of Portugal Cove on the night of its release

Figure 8 Locations of a juvenile cod tracked between July 29 and August 1. Numerals indicate position.

Position	Date	Time	Depth
1	July 29	1840	12 m.
2	July 29	1000	23 m.
3	July 29	1920-2330	30 m.
4	July 29	2400	31 m.
5	July 30	0150	30 m.
6	July 30	0230	30 m.
7	July 30	0315	16 m.
8	July 30	0330-0500	15 m.
9	July 30	0600	22 m.
10	July 30	0700	30 m.
11	July 30	0750	22 m.
12	July 30	0820	16 m.
13	July 30	0915	9 m.
14	July 30	0945	9 m.
15	July 30	1030-1600	9 m.
16	July 30	1600-2000	9 m.
17	July 30	2000-2200	9 m.
18	July 30	2230	9 m.
19	July 30	2330	?
20	July 31	0730	14 m.
21	July 31	0800-1000	14 m.
22	July 31	1000-2100	14 m.
23	July 31	2300	14 m.
24	Aug. 1	0130	14 m.
25	Aug. 1	0300-0700	15 m.

Tag evacuated Aug. 1 at 0700 hr.



(Figure 9); at 0730 hr. on August 16 it was in 16 m of water, but by 0800 hr. it had moved to 26 m and was no longer active. It had not moved by 1000 hr., when tracking was suspended, but was in shallow (14 m) water by 1900 hr when tracking recommenced. It remained in shallow water until 0500 hr. on August 17, when it moved out of the cove. At 0900 hr., when tracking was halted due to high winds, the fish was in deep water (30 m) slightly west of Portugal Cove. By 1900 hr. when tracking started again, the fish was back in the cove and in shallow water (13 m). It remained in shallow water, moving little until 0100 hr. on August 18 when it evacuated the tag.

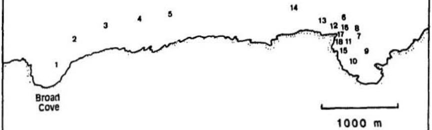
Fishes C and D moved extensively at night, and became inactive early in the morning, reinforcing the hypothesis that fish tagged in July but not tracked at night were active nocturnally. Also, the nocturnal behaviour of these fish supports the conclusion that juvenile cod regularly move into shallow water at night. Fish D moved into shallow water overnight, returning to deeper water diurnally. Fish C also moved into shallow water at night; however, after the night of its release it moved to a broad shallow basin, and did not leave shallow water during the day. This is counter to what was observed with all other tagged fish, which spent daylight hours in deep water, and to observations made at Broad Cove, where juvenile cod were not observed in shallow water diurnally at this time of year.

Fish C and D also varied in the time of day when they recommenced activity. Fish C remained stationary until late evening, well after sunset, while

Figure 9 Locations of a juvenile cod tracked between August 16 and 19. Numerals indicate position.

Position	Date	Time	Depth
1	Aug. 16	2300	13 m.
2	Aug. 17	0115	25 m.
3	Aug. 17	0200	30 m.
4	Aug. 17	0230	?
5	Aug. 17	0300	?
6	Aug. 17	0700	16 m.
7	Aug. 17	0830	25 m.
8	Aug 17	0915-1000	25 m.
9	Aug. 17	2100	16 m.
10	Aug. 18	0200	13 m.
11	Aug. 18	0330	15 m.
12	Aug. 18	0500	15 m.
13	Aug. 18	0510	?
14	Aug. 18	0800	27 m.
15	Aug. 18	1900	13 m.
16	Aug. 18	2100	14 m.
17	Aug. 18	2300	13 m.
18	Aug. 19	0030	13 m.

Tag evacuated Aug. 19 at 0030 hr.



fish D began moving some time prior to 1900 hrs, probably in the late afternoon as was seen with fish B. Fish B remained stationary throughout the afternoon of the day of its release, then became active between 1635 hr. and 1930 hr. Thus, although all fish tracked were inactive during the day, becoming stationary in early morning, the time at which they resume activity appeared to vary.

Results for fish tagged in early September indicated that a change between seasonal behaviour patterns was underway. The fish tagged on September 9 was active diurnally in deep water (26 m) over sand, and inactive nocturnally over a rubble bottom at 21 m Following its release, it moved to the mouth of the cove, unlike the fish tagged later, and did not move back in, staying in deeper water than fish tracked later, at the extreme range for the tracking gear. Similarly, the fish tagged on September 15 moved out to the mouth of Broad Cove after its release, out of range of the stationary array of hydrophones. It was then found in much the same area in 28 to 31 m of water on the next two days, not moving any great distance, unlike fish tagged earlier in the year.

3.3 Temperature Inhabited in the Field

Over the summer, juvenile cod were found generally in deep cool water during the day (4.1°C to 4.6°C) although warm temperatures were available in shallower water (Figure 7, page 47). In September, they were found in water of similar depth to that which they inhabit diurnally earlier in the year, but the temperature in this water was much warmer (10.5°C). Cooler temperatures were still present in slightly deeper water, but the juvenile cod did not inhabit it.

Over the autumn, water temperatures are quite constant throughout the water column to a depth of at least 30 m (Dobson et al 1985; Walker et al 1987). The juvenile cod inhabited the shallow water in the cove which was quite warm at the end of September (11.1°C); the temperature of this shallow water gradually declined to 5°C in December.

As no tracking was conducted over winter, the temperature of water that the juvenile cod inhabited in these months is uncertain. However, if, as seems likely, they remain in Conception Bay, the ambient temperature of seawater which is pumped into the MSRL from a depth of 20 m in Logy Bay, should accurately represent the temperatures juvenile cod experience over winter (Tables 8 and 9)

When seasonal preferred temperatures exhibited by juvenile cod in the lab are compared with ambient temperatures (temperatures at which they were tracked during summer and autumn, and MSRL ambient temperatures for winter and spring) it is apparent that these temperatures are generally quite similar. Environmental temperature is highly correlated with the temperature preference of fish from ambient water ($R = 0.95$, Table 8) and fish from heated water ($R = 0.89$, Table 9).

Table 8 Correlation of the preferred water temperature of fish caught at Broad Cove or held at ambient temperature at the M.S.R.L., with the ambient water temperature.

Date of Experimental Trials	Preferred Temp. (°C)	Ambient Temp. (°C)
Nov. 1 - Nov. 9	8.1	8.0
Nov 14 - Nov 17	7.2	6.0
Dec. 7 - Dec. 10	4.7	5.0
Jan. 17 - Jan. 22	2.2	1.0
Mar. 24 - Apr. 3	- 0.6	- 1.0
Apr. 26 - Apr. 30	1.9	1.0
May 9 - May 10	2.8	2.8
Jul. 11 - Jul. 18	6.7	5.2
Sep. 12 - Sep. 17	9.3	10.5
Oct. 22 - Oct. 26	10.1	10.0
Nov. 21 - Nov 25	7.3	7.8

t tests the significance of r; H_o $\rho=0$, H_a $\rho=0$

$r=0.98$, $t=14.6$, $p<0.001$

Table 9 Correlation of the preferred water temperature of fish held at 10°C over winter with ambient water temperature.

Date of Experimental Trials	Preferred Temp. (°C)	Ambient Temp. (°C)
Dec. 2 - Dec. 15	6.9	5.0
Feb. 11 - Feb. 21	4.9	- 0.5
Mar. 22 - Apr. 3	4.1	- 1.0
May 4 - May 16	3.9	2.2
May 26 - May 28	5.0	4.0
Jul. 25 - Jul. 28	9.7	5.2
Sep. 21 - Oct. 4	11.8	10.8
Oct 29 - Nov. 3	9.7	10.0
Nov 28 - Dec. 2	8.1	7.8

t tests the significance of r; H_o $\rho=0$, H_a $\rho=0$

$r=0.884$, $t=6.77$, $p<0.001$

DISCUSSION

The experiments conducted at the MSRL demonstrated that juvenile cod from Broad Cove exhibited seasonal variation in temperature preference. They also showed that this variation was not simply a response to changes in ambient temperature, since fish held at 10°C over winter showed a pattern of seasonal variation in temperature preference similar to fish from ambient temperature water. The decline in preferred temperature exhibited by heated water fish over winter suggests that there is some internal cycle operating independently of environmental temperature, which causes temperature preference to change seasonally. However, the fact that it does not drop as far as for ambient acclimated fish indicates that thermal history also exerts some influence on final temperature preference. The gradient reversal experiments demonstrated that the fish were selecting a position within the gradient on the basis of temperature rather than location in the experimental tank.

Tracking studies conducted in Conception Bay found both diurnal and seasonal variation in behaviour and habitat selection for juvenile cod. In summer juvenile cod conducted a diel migration which took them from deep cool water where they were largely inactive diurnally, to shallow warm water where they were active and feeding at night. Juvenile cod were not seen in Broad Cove during the day, and could only be caught there using a baited hook after dark. When tracked they were generally found in deep cool water during the day, but were found in shallow water at night. After the night of its release, one of the tracked fish (Fish C) moved into a broad shallow basin towards the head of Conception Bay, and stayed there in shallow water for the two remaining days of tracking. Its presence in shallow water diurnally is contrary to what was found with other tagged fish, and to observations in Broad Cove, where juvenile cod were not seen diurnally in summer. This may be indicative of some degree of variability in individual behaviour patterns, or may simply be a consequence of the fish's location over a broad shallow basin where the appropriate direction to swim in order to return to deep water was not readily apparent.

In autumn, when the water column had become isothermal throughout the depth range they had inhabited earlier in the year, juvenile cod switched to a diurnally active diel cycle, and restricted their movements to a small home range area, never leaving Broad Cove. This habitat selection exposed them to warm temperatures (10.8°C in September) which they avoided during their diurnal periods of inactivity earlier in the year. However, temperature preference of juvenile cod also varied seasonally in a pattern which was closely correlated with seasonal temperature changes in the shallow inshore water they inhabited. This seasonal variation in temperature preference is common in fish (Coutant 1977; Crawshaw 1977), and is thought to reflect a seasonal change in physiologically optimal temperature.

Temperature has a strong impact on physiological activity. To minimize the effects of alteration in the thermal environment, acclimatory responses are invoked which result in a change in enzyme variants to stabilize rates of catalyzed reactions, along with other cellular and tissue level restructuring (Fry and Hochachka 1970). These changes may be invoked by changes in temperature, or could be invoked by other cues in an anticipatory manner. In juvenile cod, it appears that these changes may be triggered by factors other than temperature change. Fish held in 10°C water over the winter showed a decline in temperature preference which corresponded to that of fish from ambient water, although the decline was smaller in magnitude. This suggested that they were anticipating seasonal temperature change, and physiologically preparing themselves for it. Whether this was accomplished through an endogenous annual cycle which was set prior to the beginning of the experiment, or was triggered by an alternate cue, such as day length, or a change in water chemistry, was not clear. However, it was clear that seasonal variation in temperature preference was not simply a response to ambient temperature.

By remaining inshore year-round, juvenile cod expose themselves to a broad thermal environment. Since temperature preference varies seasonally regardless of ambient temperature, these fish apparently anticipate temperature variation physiologically, and make seasonal adjustments to accommodate it. It is also apparent, however, that ambient temperature influences thermal preference, since fish exposed to cold water over winter express a much lower temperature preference. This suggests that the fish require some thermal stimulus before the physiological process of cold acclimation is completed. At the extreme in winter, fish held in ambient water preferred temperatures of less than 0°C. At this temperature, juvenile cod are producing plasma antifreeze glycoproteins at high levels (Kao and Fletcher 1988) and are thus cold tolerant. If they move into water above 0°C, antifreeze levels are not maintained, and production ceases above 1°C (Fletcher et al. 1987). Thus, it may be advantageous for the fish to remain in less than 0°C water during winter, thereby maintaining the level of plasma antifreeze glycoproteins.

Temperature preference for fish held in the lab peaked at 12°C in October, almost 2°C higher than for fish from ambient water. However, 12°C is coincident with temperatures which could be experienced in Broad Cove at that time of year (11.1°C on September 12). Temperature preference may have been influenced by the holding temperature of lab fish which reached 13°C in September, 2°C higher than in the field. Also, it is possible that the high food ration they were receiving may have influenced their temperature preference (fish held in the lab were fed to satiation every second day). Some studies have indicated that fish fed higher rations have a higher temperature preference (Javaid and Anderson 1967; Stuntz and Magnuson 1976) and satiated fish have a higher temperature preference than hungry fish (Reynolds and Casterlin 1979). This fits with a strategy of maximizing growth, since temperature for maximal assimilation declines with a decline in ration (Brett et al. 1969; Hawkins et al. 1985; Jobling 1988). Juvenile cod on unlimited ration experience maximum growth between 13°C and 15°C (Jobling 1983). Thus it is possible that the exhibited temperature preference of 12°C may show the influence of the high ration and holding temperature, resulting in a temperature preference that is somewhat higher than expected.

During the year, tracked fish showed two distinct patterns of activity. In summer they were nocturnal and wide ranging between deep cold resting sites, and shallow warm feeding areas. In the autumn, they maintained a home range in shallow water over sand, and were inactive nocturnally, resting in shallow rocky areas. The switch between these two very distinct behaviour patterns occurred in mid to late September. This period coincides with a marked shift in the thermal environment of near shore water. Over summer a strong thermocline builds up in shallow coastal water. In mid July the temperature at 11 m in Broad Cove was 13.8°C, versus 4.4°C at 33 m. This strong thermocline is a regular feature in shallow Newfoundland waters (Dobson et al. 1985; Walker et al. 1987). The thermocline can be influenced by wind induced upwelling which can reduce shallow water temperatures (Schneider and Methven 1988), but generally remains strong until mid September, after which the thermocline drops below 40 m (Powell et al. 1987; Walker et al. 1987). At this time the entire water column in depths less than 40 m is about 11°C and cooling during the autumn is uniform throughout the column. It seems likely that the shift in behaviour displayed by juvenile cod in September is related to this major environmental change.

Although the shift in behaviour coincides with this thermal event the adaptive significance of the change in seasonal behaviour patterns is not entirely clear. The fish seem to feed in much the same area regardless of season, since all juvenile cod caught for these experiments were captured at the same site. Also, observations from the Lora II underwater habitat in Broad Cove, showed that juvenile cod were actively feeding at night in shallow (<10 m) water (J. Green, pers. comm.), the same area in which they were found in this study to feed diurnally in the autumn.

The diel migration from deep to shallow water exhibited in the summer requires a horizontal move of several hundred metres at Broad Cove, an energetic cost which is eliminated in the autumn. This behaviour pattern is likely a response to the existing thermal stratification. The temperature preference experiments conducted in the lab showed that in July, juvenile cod exhibit a preference for water of 6.3°C, similar to that found in deep water, and considerably cooler than temperatures in shallow water, which may exceed 14°C (Powell et al. 1987). Temperature preference may thus serve as the proximate cause for a return to cold water during non-feeding periods. The ultimate cause underlying this behaviour may be energetic efficiency.

Metabolic rate increases with temperature, thus increasing maintenance costs (Brett et al. 1969; Stuntz and Magnusen 1976; Jobling 1988). Thus, although maximum growth may be achieved at relatively high temperatures given a sufficient supply of food, as food supply is decreased, the temperature at which maximum growth will be achieved is similarly reduced (Brett et al 1969; Hawkins et al. 1985) due to lower maintenance requirements.

Where a thermocline exists, it has been proposed that fish may acrue energetic benefits by moving into deep cold water to digest their food (Brett 1971). This is supported by experiments which demonstrate that when food is limited, maximum growth for sockeye smolt is experienced under a cycled temperature regime (Biette and Geen 1980). Similarly, goldfish (*Carassius auratus*) experience maximal growth when exposed to a cycled temperature regime in which the temperature peaks during the four hours before dawn (Spieler et al. 1977).

Clark and Levy (1988) have criticized the energetic explanation for vertical migration, noting that Alexander (1972) has calculated that more than half of the energy saved in metabolic costs by moving to cooler water would be required for hydrodynamic compensation in deeper water. In his calculations Alexander (1972) has assumed that the swim bladder cannot be inflated quickly enough to maintain bouyancy, thus the fish must be constantly swimming, and using its fins for lift to prevent further sinking. The swimming speed he calculated would be necessary was 1.08 km/hr. Since this study indicates that in the summer juvenile cod appear to remain stationary or move very little during the day, this cost would not apply, and the full energetic benefit of thermal selection should acrue.

Cod which are fed to satiation experience maximum growth between 13°C and 15°C (Jobling 1983); however, when the ration of cod between one and three years of age is held at a moderate level, growth is maximal at about 7°C (Hawkins et al 1985). This is very similar to the temperature preference of juvenile cod in summer found in this study (6.3°C). At 15°C, close to the temperature in Broad Cove over summer, maintenance costs are more than tripled (Hawkins et al 1985). Since the only apparent cost of vertical migration for juvenile cod is that associated with swimming, an activity which seems to be of negligable cost to these fish (Soofiani and Priede 1985), it should be energetically beneficial for them to move to deep cold water in non foraging hours.

A pattern of vertical migration should continue as long as there is a thermocline above the daytime depth of juvenile cod; however, when isothermal conditions exist throughout their range, vertical migration should cease, since it no longer provides any metabolic saving. This is what is seen in the seasonal behaviour of juvenile cod. In September, when the thermocline drops to 40 m. and deeper, vertical migration ceases. However, there is also a reversal in daily activity schedule, which cannot be accounted for as easily.

In the autumn juvenile cod are active diurnally rather than nocturnally. This pattern of seasonal reversal in diel activity cycles has also been found in studies on a number of other fish species, including *Myoxocephalus quadricornus* (Westin 1971), *Cottus poecilopus* and *Cottus gobio* (Andreasson 1973), *Salmo trutta* (Muller 1969), and *Lota lota* (Muller 1978a). However, these studies provide little insight into what adaptive significance this behavioural change may have for the fish in question, focusing instead on illucidating the zeitgeber which triggers the change.

For all these species, the factor which appears to trigger the reversal is light intensity (Erickson 1978; Muller 1978b). *Cottus gobio* in the lab switched from nocturnal to diurnal activity if daylength was less than 12 hours, and maximum light intensity did not exceed 20 lx (Muller 1978b). Similarly, *C poecilopus* and *Lota lota* switch from nocturnal to diurnal activity in the autumn, only in the low light conditions experienced close to the Arctic Circle, while in more southerly locations (55°35'N) they remain nocturnal throughout the year (Andreasson and Muller 1969; Muller 1978b). North of the Arctic Circle activity of these fish also becomes arhythmic during the 24 hour daylight of the summer (Andreasson 1973; Muller 1978b).

However, the reversal is not a simple response to low light intensity. *Lota lota* held at low light intensity throughout the year continued to display the seasonally appropriate behaviour pattern, becoming diurnal only during the winter months (Muller 1978b). Similarly, it is not possible to induce a reversal in *Cottus gobio* outside of the appropriate season. In both of these cases, the reversal seems to be linked to an endogenous seasonal activity pattern (Muller 1978b).

Muller (1978a; 1978b) has hypothesized that changes in diel periodicity in these northern fish may be linked to variation in diel food availability. In the autumn, nocturnal activity by these species corresponds with the timing of insect larval drift, while a lack of diel periodicity in summer may reflect a similar lack of periodicity in food avaiability. However, this does not account for the shift to diurnal activity over winter, and at present his hypothesis is still quite speculative.

Reversal of diel activity cycle is not restricted to fish north of the Arctic Circle. *Myozocephalus quadricornus* has been found to switch from being nocturnally active in summer to being diurnally active in winter at 58°50'N (Westin 1971). Coincident with this is a move from deep (20-25 m) water over summer to shallow (11 m) water in winter, which is similar to what was found for juvenile cod in Broad Cove in autumn, and a concomitant shift in diet (Westin 1970). Westin (1970) suggests that the vertical migration may be a response to water temperature; *M quadricornus* remains in cold deep water over summer, and moves into shallow water in the autumn only after surface temperatures have declined to 5°C, making the water column isothermal. However, light intensity seems to be the proximate cause of reversal in diel activity pattern (Westin 1971), as with *Cottus poecilopus*. What the ultimate cause of this change is, and what relationship it may hold with the shift in habitat and diet remains unclear.

Although change in light intensity could be the cue which triggers the reversal of diel activity pattern in juvenile cod at Broad Cove, it seems unlikely due to the southerly location of the research site (49°55'), and the early date of the switch. It seems more parsimonious that the switch from nocturnal to diurnal activity is linked to the other seasonal changes in behaviour, as is suggested for *Lota lota* and *Cottus gobio* (Muller 1978b).

After the switch from nocturnal to diurnal activity, juvenile cod continue to feed in much the same area as before, but spend nights in shallow water over a rocky substrate. All but one of the 11 juvenile cod tracked in the autumn spent their nights in an area with a rocky substrate. Moving to a rocky area at night from the [illegible] w [illegible] cover, particularly as some fish seem to select very sheltered sites between or alongside rocks, where signal transmission from the sonic tags was partially blocked. This may indicate that they were hiding from potential predators.

The main predators of young cod are older cod, pollock (*Pollachius virens*) and squid (*Illex illecebrosus*) (Scott and Scott 1988). Of these, the only species which would be present in significant numbers in Broad Cove during the autumn is squid. Squid feed nocturnally (Vinogradov and Noskov 1979); they are generally present in Conception Bay from late July and may be abundant from August to November (Squires 1957; Dawe et al 1981). Young cod constitute a large proportion of the squid diet, and it has been suggested that squid may have a significant impact on recruitment of young cod (Dawe et al. 1981; 1983). Squid do not generally prey on cod over two years of age (Dawe et al. 1983); they will, however, eat almost any fish shorter than their mantle length (O'Dor et al. 1980) which reaches an average of 25.1 cm for females in October and a maximum of 33.0 cm (Squires 1967). Thus, they may be capable of consuming three year old cod. This risk would however be slight as these fish fall well outside the size range reported from squid stomach contents (Dawe et al. 1983) and any tendency to avoid squid would likely be a holdover from previous years when they posed a greater threat. It is thus apparent that the benefits accrued by switching activity cycles to reduce the risk of predation by squid would be minimal.

One and two year old fish follow a diurnal activity pattern throughout the summer moving into cover at night (Keats et al. 1987). This may reduce predation by squid and would allow them to use visual cues to locate food. The use of visual cues may also be an advantage to older cod. Cod can locate food using olfactory stimuli received by the barbel and pelvic fin rays, which are extended and moved across the substrate (Brawn 1969). However, Brawn also found that cod used vision to locate and follow prey, and some authors suggest that cod are primarily visual feeders (Woodhead 1966; Brunel 1972); thus it seems likely that vision could be of assistance in locating food items.

Nocturnal activity is well documented for young cod (Arntz 1973; Pihl 1982; Hawkins et al. 1985). Hawkins et al (1974; 1985) found that most cod (>30 cm to a maximum of 63 cm) tagged with sonic transmitters were active diurnally, but some were active nocturnally. Since they do not indicate the time of year at which each pattern of behaviour was seen, it is not clear whether nocturnal and diurnal activity patterns were separated temporally. Researchers in Kiel Bay, Sweden, found small cod (26 to 30 cm; one year old) fed nocturnally (Arntz 1973; Pihl 1982). Zarkeschwari (1978) and Pihl (1982) also found that nocturnal feeding followed a migration into shallow water which is similar to what was found in this study.

The nocturnal activity displayed over summer by juvenile cod in Conception Bay may be a strategy which reduces predation risk from adult cod. Adult cod will prey on younger cod up to 30 cm in length (Daan 1973). Thus, three year old cod, which average 29 cm in length in spring in the Conception Bay region (Wells 1968) may be subject to predation by adult cod.

Adult cod are present in Conception Bay from May until the thermocline drops in September (Aggett et al 1987). If the adults are feeding nocturnally, juvenile cod would avoid predation, since they are moving into shallow warm water which adults avoid. However, it is not completely clear when adult cod feed. Some authors suggest that they feed mainly diurnally (Trout 1957; Brunel 1972), but most reports suggest that they feed throughout the day (Woodhead 1966; Daan 1973; Turuk 1973; Turuk 1975). If adult cod do feed throughout the day, then predation by adults should not place a selective pressure on juvenile cod favouring any diel variation in activity.

However, there is some indication that adult cod feed on fish primarily at night (Turuk 1973; Turuk 1975) making it advantageous for juvenile cod to move out of the deep water at night. Turuk (1973) found two distinct patterns of vertical migration in cod off Labrador, which was similar to what Brunel (1972) observed in the Gulf of St. Lawrence. However, Turuk conducted an extensive study of cod stomach contents throughout the day which revealed that the different patterns of vertical migration reflected variation in diel feeding patterns. He found that cod feeding primarily on benthic organisms ascended into the pelagic zone by day, and returned to the benthos at night, while cod feeding primarily on actively swimming pelagic organisms ascended into the pelagic zone by night and descended to the benthos during the day. Thus, predation by cod on actively swimming organisms was much higher at night.

Therefore, by moving out of deep water at night, juvenile cod may reduce the risk of being preyed upon by adults. This advantage, however, is dependent on adults consistently following the feeding pattern reported by Turuk (1973; 1975). Although Turuk's results are compelling, there is no consensus in the literature; thus, it is not clear that predation by adult cod would provide a consistent selection pressure favouring nocturnal activity by juvenile cod during the summer.

Another factor that could influence diel activity patterns is prey selection. Muller (1978a) suggested that annual changes in activity patterns of some fish species in northern Sweden may be related to seasonal variation in the diel periodicity of maximum prey abundance. Changing their foraging hours to correspond with the times of peak prey abundance would increase the foraging efficiency of these fish. The switch in diel periodicity exhibited by juvenile cod in Broad Cove may reflect a similar selective pressure.

Pihl (1982) found seasonal variation in stomach contents of young cod in Kiel Bay, although the timing of feeding remained constant throughout the year. Similarly, Hawkins et al (1985) reported some seasonal variation in stomach contents of juvenile cod in Loch Torridon. It is possible that the diet of juvenile cod in Conception Bay also changes seasonally, making nocturnal foraging favourable in summer, but rendering it unsuitable in the autumn. Nocturnal feeding would also serve to reduce competition, since sculpins, cunners (*Tautogolabrus adspersus*) and winter flounder (*Pseudopleuronectes americanus*), all of which may compete with juvenile cod for food, feed diurnally. All these species are present in the autumn however, and if prey selection remains the same, they would presumably be competing with cod at this time as well. However, seasonal data on the diet of juvenile cod in Conception Bay is not available, thus it remains unclear whether or not it bears any relation to seasonal changes in their activity.

Thus it is possible that juvenile cod are timing their activity in summer to reduce the risk of predation by adults, then switching to diurnal activity in the autumn to improve visual foraging after the adults leave the inshore area. This hypothesis relies on adult cod feeding on free-swimming prey mainly nocturnally, which is not certain. More detailed information on the activity of adult cod is required to assess this possiblity. If prey selection of juvenile cod changes seasonally, it is conceivable that nocturnal feeding to reduce competition may be optimal in summer whilst a diurnal pattern may be preferential in the autumn if the prey selected then are more easily located visually. An examination of prey selection over both seasons is required to determine the applicability of this hypothesis.

CONCLUSIONS

Juvenile cod from Broad Cove, Conception Bay exhibit seasonal variation in temperature preference and activity patterns. Laboratory studies on temperature preference show juvenile cod from ambient temperature water prefer temperatures which correlate closely with seasonal changes in the temperature of the inshore waters which they inhabit. A similar pattern is shown by fish held in 10°C water over winter, indicating that variation in temperature preference is not simply a response to changing ambient temperatures.

Field activity also changes seasonally. During summer juvenile cod are active nocturnally and wide ranging. Days are spent inactive in deep cold water, and at night they move into shallow water to feed. This diel vertical migration may result in increased growth. Fish feed in warm shallow water, then move back to cold deep water while food is digested. This diel vertical migration reduces metabolic costs by removing the fish from warm water, where maintenance costs are high, during non-feeding hours, thus increasing energy available for growth. After the depth of the thermocline drops in September, resulting in isothermal conditions throughout the range of juvenile cod, vertical migration ceases. The metabolic savings afforded by vertical migration in summer are now gone, thus it is more energetically efficient to remain in shallow water.

In the autumn juvenile cod maintain a restricted home range in shallow water, they are active diurnally over a sandy substrate, and at dusk return to a consistant resting site over a rocky bottom, where they remain stationary until dawn.

The shift from nocturnal to diurnal activity could be a response to seasonal changes in diet. However, it is unknown if diet of juvenile cod in Conception Bay varies seasonally in a manner which might lead to this change in feeding strategy. A more likely hypothesis is that the timing of activity varies seasonally to reduce the risk of predation. In summer diurnal activity would take juvenile cod out of deep water when adult cod are foraging, thus reducing the risk of predation from this source. In autumn the adult cod move out of Conception Bay, and juveniles could revert to the diurnal activity pattern followed by one and two year old cod, which would allow them to forage visually. Also, diurnal activity in autumn may reduce the risk of predation from squid, a nocturnal predator which is abundant in Conception Bay from August to November.

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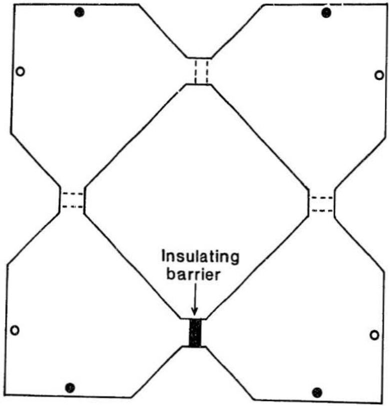
APPENDIX

Appendix A Diagrammatical representation of the four chambered temperature gradient tank. The overall dimensions of the tank were 150 cm X 150 cm X50 cm and the area of each chamber was 3734 cm^2. The water depth was 30 cm.



●: Red light

○: White light