BEHAVIOUR, RESOURCE USE, AND CONDITION OF DEMERSAL AGE 0 ALTANTIC COD (Gadus morhua) IN COASTAL NEWFOUNDLAND: COMPONENTS OF SURVIVAL RISK IN THE NEARSHORE ENVIRONMENT

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Behaviour, resource use, and condition of demersal age 0 Atlantic cod (*Gadus morhua*) in coastal Newfoundland: components of survival risk in the nearshore environment.

by

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A thesis submitted to the School of Graduate Studies in
partial fulfilment of the requirements for the degree of
Doctor of Philosophy in the Faculty of Science

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17 January 2000
St. John's, Newfoundland, Canada

ABSTRACT

It is well established, that following a pelagic phase age 0 Atlantic cod (*Gadus morhua*) settle to the bottom to assume a demersal habit. However, risks to juvenile cod survival in the coastal zone of the northwest Atlantic are not well understood. A better knowledge of factors affecting survival of age 0 cod during the transition to a demersal habit in shallow (<10 m deep) nearshore regions of Newfoundland has broad ecological applications and will improve our understanding of the role of coastal habitats to the rebuilding of north Atlantic cod stocks. In this thesis, I investigated the importance of nearshore regions in coastal Newfoundland as rearing grounds for age 0 cod by examining their behaviour, resource use, and condition in relation to diet for the first several months post-settlement.

Day-night differences in catch and diet of age 0 and age 1 cod were examined to delineate the diel peak in foraging activity and resource use in eelgrass (*Zostera marina*) habitat. Cod exhibited a size-related shift (age 0 to 1) from feeding predominantly on zooplankton by day to benthos at night. Intercohort cannibalism occurred when age 1 cod were approximately three times larger than their prey. Diet composition and catch data revealed that concentrations of age 0 cod foraged in the water column during the day, ceased feeding at night, and appeared to move to the bottom. Seasonally decreasing day length and prey size contributed to a decline in daily ration, yet age 0 cod maintained a strictly diurnal foraging cycle. The nocturnal decrease in feeding coincided with an increase in the catch of older conspecifics (age 2 and 3) and increased foraging activity of age 1 cod suggesting that avoidance of older conspecifics is an important factor influencing the survival of age 0 cod in the nearshore.

Capture-mark-recapture experiments and seasonal sampling were conducted to examine the movement levels, spatial distribution, behaviour, and abundance of age 0 cod in eelgrass and no-eelgrass habitat over two years. Cod remained localized for several weeks (September-December) after settling from a pelagic habit and may remain localized during their first winter. Marked cod did not appear to move further than a few hundred metres within eelgrass habitat, but moved up to 1.2 km in no-eelgrass habitat. Slope values for variance-mean density relationships indicate that age 0 cod aggregated during the day, while high within and between site variation in catch at the scale of hours and weeks provide evidence of localized lateral movements. These patterns in the catch rates are interpreted to reflect social behaviour in the form of mobile shoaling aggregations during the day. Day-night comparisons of ratios of variance to mean density were also indicative of aggregative behaviour during the day. Day-night patterns in the catch rates are interpreted to be due to a decrease in activity and local dispersal of shoaling aggregations at night. A significant increase in abundance of age 0 cod in less suitable habitat (no-eelgrass) when settlement strength was high is consistent with the hypothesis of density dependent habitat selection.

Diet composition and simple indices of condition were compared during the autumnal settlement of age 0 cod. Laboratory experiments were also conducted to determine whether simple indices of condition reflect differences in energy intake (ration level) and to determine minimum index of condition values for age 0 cod that died due to exhaustion of their energy reserves. Results agreed with published literature on the value of simple indices to assess condition of cod. Liver and contractile muscle energy reserves of wild age 0 cod varied seasonally, however, their condition was well above that of cod that died in the laboratory. Laboratory studies revealed that condition of cod differed significantly over time and between daily ration levels. Indices of condition representing variation in muscle energy reserves exhibited a steady decline once the hepto-somatic index fell below a value of about 2.0, which I interpret as evidence of a pattern of depletion of lipids and then proteins, similar to that observed for larger juveniles and adults. I conclude that as long as age 0 cod are above a "safe" level of condition their body length may still increase despite a decline in condition.

Condition of a laboratory cultured and wild juvenile cod population from coastal Newfoundland were compared to determine whether small juveniles develop enlarged fatty livers in captivity. Cultured cod developed enlarged fatty livers, exhibiting significantly higher liver and contractile muscle energy reserves than wild cod. Cultured cod of similar age exhibited a high divergence in body size over time. Indices of liver energy reserves were positively correlated with body size suggesting that a size-related social hierarchy had developed in the laboratory. In the wild, indices of liver energy reserves were negatively correlated with body size, suggesting high utilization of dietary lipids by larger juveniles in association with increased metabolic expenditure when feeding on small prey items.

I conclude, from studies of condition in relation to diet, that shallow water coastal environments may serve as trophically adequate rearing grounds for age 0 cod for the first several months post-settlement. Behaviour patterns exhibited by age 0 cod, i.e., restricted movements in shallow nearshore waters, diurnal shoaling, and preference for structurally complex habitat, are mechanisms for predator avoidance, suggesting that predation risk is high in coastal Newfoundland. Predation risk, particularly from older conspecifics, in the nearshore environment and its potential to influence cod recruitment warrants further investigation.

ACKNOWLEDGEMENTS

I would like to take this space to thank my supervisor, Joe Brown, for his friendship and good natured support throughout the production of this thesis. He supplied insight and encouragement. I thank members of my committee, Pierre Pepin and Dave Schneider, for their review and criticism of earlier versions of the manuscript. Many thanks to Carole Bradbury, Jacques Gagné, Bob Gregory, and anonymous reviews for their critical review of published manuscripts which resulted from these studies.

I truly would have been hard pressed without the help of these illustrious field and laboratory assistants: Dan Boyce, Carole Bradbury, Sandy Fraser, Peter Hennebury, Francis Hennebury, Adrian Jordaan, Dave McKeown, Jack Temple, and Tom Therriault. I thank Mr. Sing Hoi Lee for his valuable assistance in identifying the various copepods. I thank Hong Chen and Trevor Avery for their assistance in statistical analysis. The catch values for juvenile cod captured in October 1993 appear courtesy of Dave Methven. John Christian prepared Figure 3.1.

Thanks to all at the MSRL. Jim Devereaux and the boys in the workshop, Terry Harris, Betty Hatfield, Trevor Keough, Connie Short, Donna Somerton, Steve Sooley, Ross Wilson, Winnie Sparkes, Delores Wheeler, and all of the custodians.

This study would not have seen the light of day without the monetary support obtained through the Early Life History Initiative of the Northern Cod Science Program, Department of Fisheries and Oceans Canada, Newfoundland region.

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CHAPTER 1. General Introduction

The acquisition of food is a fundamental requirement of all fish. The variety of morphological and behavioural adaptations that have evolved to meet this basic requirement and conversely, to avoid being preyed upon are astounding. Many foraging decisions, such as feeding location, search area, whether to feed in a group or alone, and when to cease feeding are directly and indirectly linked to the natural environment. Theoretically motivated consideration of animal behaviour in relation to their natural environment began approximately three decades ago when Tinbergen (1963) emphasized the importance of studying the behaviour of animals in their natural surroundings. One conclusion from such studies was that animals possess the ability to assess and behaviourally control their risk of predation (Lima and Dill 1990). Alterations in foraging and anti-predator behaviour in fish can occur at various life history stages and reflect environmental conditions during developmental and evolutionary time (Lima and Dill 1990).

The comparative approach is very useful for investigating the general relationship between behaviour and ecology, generating hypotheses that can be used as predictions for other species and species groups. Helfman (1986) has illustrated this approach in a review of the diel behaviour of fish, noting, "many fish appear to separate the day into an active, food gathering phase and a relatively inactive, resting phase that is ultimately linked to predator avoidance". For example, on coral reefs where predation risk is high (Hixon 1991), small zooplanktivorous fish generally feed over refuge sites within large, relatively stationary aggregations during the day and individually seek cover during periods of increased activity of nocturnal fish (Helfman 1986). Although diel behaviour patterns are well known for coral reef fish, Helfman (1986) suggested that convergent patterns in fundamental activities can be expected in almost any fish assemblage; behaviour patterns that successfully reduce predation risk while maintaining adequate food intake may have evolved numerous times, transcending geographic and taxonomic boundaries.

Nursery grounds for juvenile fish should present a useful location for testing Helfman's (1986) hypothesis regarding convergent behaviours. Additionally, ecological investigations on the interactions of juvenile fish in their natural environment can provide information on processes affecting survival and improve our understanding of the importance of nurseries as rearing grounds (Suthers et al. 1989; Smedstad et al. 1994). Two potentially important sources of mortality are high predation rates and low food availability, especially in nursery grounds. Nurseries are characterized by high numbers of young juvenile fish, which may provide a seasonal source of food for potential predators. High densities of young fish may also result in high intra- and interspecific competition for food resources. Investigations on behaviour under natural conditions can help to establish whether the risk of predation mortality is high, especially when behaviours are associated with the presence or absence of potential predators. Analysis of fish condition, which can be defined as the state of physical fitness, is a valuable method of indirectly examining success of the individual or population in finding food in relation to prey availability.

The recent collapse of Atlantic cod (*Gadus morhua*) stocks in the northwest Atlantic (Sinclair et al. 1994; Taggart et al. 1994) has served to highlight many ecological questions regarding factors affecting survival at various life history stages of this economically important species. A report on the state of the northern cod stock (Harris 1990), located off the northeast coast of Newfoundland (NAFO Divisions 2J3KL), identified a general lack of information on even the basic ecology of juvenile cod throughout the inshore area. The inshore area is defined by large bays along the northern coast of Newfoundland, including White Bay, Notre Dame Bay, Bonavista Bay, Trinity Bay, and Conception Bay. A general lack of historical investigations in the inshore area reflected the view that fish from these locations were not a critical component of the northern cod stock, contributing <10% of the population compared with offshore (Anderson et al. 1995), and that these fish represented small "bay" populations (Hutchings et al. 1993). However, the importance of nearshore nurseries for demersal juvenile cod has been well documented in European waters (Daan 1978; Riley and Parnell 1984; Godo et al. 1989), and evidence of high numbers of juvenile cod in shallow nearshore waters of the northwest Atlantic (Keats et al. 1987; Methven and Bajdik 1994; Tupper and Boutilier 1995a; 1995b; Dalley and Anderson 1997; Ings et al. 1997; Methven 1997) suggest that these areas may represent important nursery and rearing grounds. Lack of information on even the basic ecology of juvenile cod from nearshore regions represents a serious impediment to our ability to reliably forecast their recovery.

For example, following the collapse of Atlantic cod stocks, it became apparent that the development of a reliable index of year-class strength at an earlier age than that derived from age 3 abundance data available from off-shore bottom trawl surveys would be of value. The ability to locate and adequately sample juvenile cod is essential to the development of a reliable index of year-class strength. Delineation of nursery areas and a description of the behaviour of young cod, with emphasis on how behaviour patterns and external factors create spatial and temporal variation in abundance and catchability will aid in the identification and evaluation of potential monitoring methods.

Following a pelagic phase, age 0 juvenile Atlantic cod settle to the bottom to assume a demersal habit. Recent studies on juvenile cod occurring in coastal regions of the northwest Atlantic have focused on behaviour and substrate use by age 0 cod under the risk of predation in the laboratory (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996; Gotceitas et al. 1997) and in the wild (Tupper and Boutilier 1995a; 1995b; Gotceitas et al. 1997). *In situ* behavioural observations conducted in coastal Nova Scotia, revealed that demersal age 0 cod may be solitary, site attached, and defend territories (Tupper and Boutilier 1995a). These juveniles appeared to be uniformly distributed at settlement, but survival was highest in cobble and rock reef habitats. The behaviour of demersal age 0 cod inhabiting coastal regions of Newfoundland is not well understood. However, in contrast to the findings in coastal Nova Scotia, a recent study on habitat use in coastal Newfoundland showed that age 0 cod are found primarily in eelgrass habitat (Gotceitas et al. 1997). These contrasting habitat preferences have been attributed to the greater risk of predation from larger co-occurring conspecifics in coastal waters of Newfoundland (Gotceitas et al. 1997). Cannibalism is common among cod and increases with predator size, density of young cod, and degree of overlap in distributions among age-groups (Ponomarenko 1968; Bogstad et al. 1994). Presence of newly settled age 0 cod in shallow (<20 m deep) nearshore environments has been attributed to predator avoidance (Riley and Parnell 1984) and evidence of restricted distributions of age 0 cod within the 4-7 m depth zone in coastal waters of Newfoundland (Methven and Schneider 1998) may be related to a relatively high risk of predation in deeper coastal waters. Studies in coastal regions of Newfoundland suggest that larger 1 to 3 year old juvenile cod make shoreward migrations into shallow nearshore regions occupied by age 0 cod at night (Clark and Green 1990; Keats 1990; Methven and Bajdik 1994; Cote et al. 1998). Thus, if older juveniles represent a serious predation risk to newly settled and post-settled age 0 cod then a corresponding change in the behaviour and (or) distribution of age 0 cod is expected at night.

Little is known of the importance of nearshore environments as rearing grounds and hence their potential for contributing to the recovery of cod stocks. Through the series of studies presented in this thesis, I hoped to augment ecological information on how demersal age 0 cod use the nearshore environment in coastal Newfoundland and examine processes affecting their survival. Specifically, this thesis uses indirect methods to examine whether predation and variation in prey quality and quantity affect the survival of demersal age 0 cod in the nearshore environment of coastal Newfoundland over the first several weeks/months post-settlement. Indirect studies examine end results or products of activities such as foraging, to infer species interactions and effects of feeding on other animal populations in space and time (Keast and Welsh 1968; Keast 1977; Helfman 1986). In Chapters 2 and 3, I examine the diet, activity patterns, and movement of marked age 0 cod in the natural environment to determine their primary prey, spatial distribution, distribution in the water column, level of movement, and behaviour in relation to predation risk in the nearshore environment. In Chapters 4 and 5, I examined the condition of demersal age 0 cod in relation to diet over the first several weeks/months post-settlement to determine whether variation in prey quality and quantity are factors limiting survival in the nearshore environment. To better interpret field data on feeding, condition, and survival I conducted laboratory studies to determine whether simple indices of condition are suitable for assessing the physical fitness of small juvenile cod and to identify the critical condition at which small juvenile cod die due to exhaustion of their energy reserves.

Laboratory studies have documented a habitat shift by age 0 cod in the presence of actively foraging older conspecifics (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996; Gotceitas et al. 1997), suggesting that the presence of older cod may influence the distribution and possibly the food intake of young cod in the wild. Much of our current understanding of the ecological role of fish populations is derived from analysis of stomach contents of wild fish (Keast and Welsh 1968; Keast 1977; Thorpe 1977; Pihl 1982; Keats 1990). However, it is as important to know when fish are eating as it is to know what they are eating. As such, analysis of stomach contents collected at regular time intervals over 24-h periods are particularly valuable as they can be used to establish foraging cycles and changes in resource (food and habitat) use that are ultimately related to variations in prey availability and (or) predation risk (Ide 1942; Thorpe 1977; Hall et al. 1979; Helfman 1986; Naud and Magnan 1988). Moreover, a series of collections conducted over a 24-h period represent a fundamental first step in diet studies of fish, establishing the best time of day to collect fish in order to maximize the amount of information obtained per individual. In Chapter 2 of this thesis I investigate age-class differences in behaviour and resource use among age 0 and age 1 cod in the nearshore environment. Qualitative and quantitative analysis of stomach contents were conducted on both age-classes at regular time intervals over 24-h periods throughout the autumnal settlement of age 0 cod and compared with catch rates of age 0 and

1 to 3 year old cod to determine whether behaviour, distribution, and activity patterns were related to presence of potential predators. Because predator to prey size ratios of piscivorous fish are typically 2:1 to 4:1 (Nursall 1973; Bogstad et al. 1994), I expected mechanisms of predator avoidance such as foraging time and location to be more evident in small individuals (i.e., age 0 cod). Additionally, inferences on periods of low prey availability and low condition were derived from seasonal estimates of food intake rates of age 0 cod.

Our current understanding of the distribution, movement levels, and behaviour of demersal age 0 cod in coastal Newfoundland is limited to underwater observations and capture rate studies that can only describe occurrence or absence at specific sites. In Chapter 3, I conducted capture-mark-recapture experiments and seasonal capture rate studies on post-settled age 0 cod, to determine relationships between distribution, behaviour, activity patterns, and predation risk in the nearshore environment. Capture-mark-recapture experiments were designed to provide information on the degree of nearshore movements of post-settled age 0 cod in two nearshore habitats (eelgrass and no-eelgrass) over two consecutive years, while variation in catch data was used to infer distribution and behaviour patterns. Results from investigations presented in Chapter 2 provided evidence that day-night differences in foraging behaviour of age 0 cod were related to increased nocturnal abundance and activity of older conspecifics in shallow nearshore waters, suggesting that the availability of refuge sites, in the form of protective bottom habitat, may influence the distribution of age 0 cod in the nearshore. These conclusions are supported by recent findings on the influence of habitat on the distribution of small juvenile cod in coastal waters throughout the north Atlantic (Støttrup et al. 1994; Tupper and Boutilier 1995b; Gotceitas et al. 1997; Methven and Schneider 1998). MacCall (1990) hypothesized that fish select habitats due to differing levels of density-dependent resources (i.e., food and shelter). Evidence of density-dependent distributions in adult and large juvenile cod occurring in the Gulf of St. Lawrence and east of Newfoundland (Swain and Wade 1993; Taggart et al. 1994) lead me to examine habitat selection at high and low densities of demersal age 0 cod in the nearshore environment of Newfoundland.

Changes in the condition of fish will reflect variations in environmental conditions such as abundance and availability of food (Love 1970; Edwards et al. 1972; Holdway and Beamish 1984; Black and Love 1986; Jobling 1988; Pedersen and Jobling 1989). Thus, condition can be considered an index of success because food energy is required to fuel all metabolic processes (Winberg 1956). Variation in condition of fish results from storage of excess energy under conditions of optimal food intake and conversely, drawing on these energy reserves during periods of food limitation (Love 1970). It is generally assumed that fish in good condition will have better chances of survival than fish in poor condition. For example, they should survive longer during food shortages (Wilkins 1967), have a higher resistance to disease, and have a greater swimming capacity, which can enhance their ability to evade predators, catch prey, and move out of marginal habitats (Booman et al. 1991). A decline in condition is generally attributed to reduced food intake, which is usually a consequence of poor feeding conditions (Pedersen and Jobling 1989). However, seasonal variation in food quality alone may affect condition (Black and Love 1986; Jobling 1988), yet fish may still be at a "safe" level of condition. Studies document seasonal variations in fish condition (Bulow et al. 1981; MacFarlane et al. 1993; Smedstad et al. 1994), yet the critical condition at which fish die due to exhaustion of their energy reserves has not been well established. Field studies pertaining to feeding, condition, and survival can only be interpreted meaningfully when condition has been assessed for fish that have exhausted their energy reserves. Only recently have studies acknowledged the importance of knowing the critical condition at which fish exhaust their energy reserves (Lambert and Dutil 1997).

Chapter 4 reports a field investigation on the seasonal variation in condition in relation to diet of demersal age 0 cod in the nearshore environment. A laboratory component examined the influence of varying ration levels on simple indices of condition and a field study was conducted in conjunction with the analysis of foraging behaviour reported in Chapter 2. The laboratory experiment examined whether simple indices of condition reflect differences in energy intake and established minimum condition values at which age 0 cod died due to exhaustion of their energy reserves. Critical values provided a meaningful criterion for interpreting field data on feeding, condition, and survival of age 0 cod.

Chapter 5 reexamines the variation in condition of demersal age 0 cod in relation to diet during a second field season in order to verify conclusions and test hypotheses presented in Chapter 4. In Chapter 5, field collections were extended to include winter sampling to determine condition and whether juveniles consumed lipid-rich prey over the winter. These follow-up studies are important to the general theme of the importance of nearshore nurseries as rearing grounds. Research outlined in Chapter 5 focuses primarily on the phenomenon of enlarged fatty livers in captive, small juvenile cod. This aspect of the study is timely, as the collapse of cod stocks has increased interest in cod aquaculture and grow out programs in the Newfoundland region.

The development of corpulent livers in large juvenile and adult cod has been documented under captive conditions (Lie et al. 1986; Jobling 1988), and is caused by an excessive build-up of lipid reserves when cod are fed high lipid diets. The excessive build up of lipids is undesirable as it may divert growth energy away from optimal body length increases and has the potential to increase costs to juvenile cod aquaculture and grow out programs. However, if young juvenile cod build up excess lipid reserves in captivity, then nearshore grow out and stocking programs may benefit by feeding lipid-rich food for a short period prior to release, as high lipid reserves may provide a buffer, increasing survival of newly released fish until they become established in natural populations.

CHAPTER 2: Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland

ABSTRACT

In coastal Newfoundland, age 0 Atlantic cod (*Gadus morhua*) settle in shallow, nearshore regions occupied by older conspecifics. Although intercohort cannibalism is common, little is known of the behavioural processes that reduce interactions among juvenile cod cohorts in the wild. I examined the day-night differences in diet and catch of age 0 and age 1 cod to delineate peak foraging activity and resource use in eelgrass (*Zostera marina*) habitat. Cod exhibited a size-related shift (i.e., age 0 to 1) from feeding predominantly on zooplankton by day to benthos at night. Intercohort cannibalism occurred when age 1 cod were approximately three times larger than their prey (i.e., age 0 cod). Concentrations of age 0 cod foraged in the water column during the day, ceased feeding at night, and appeared to move to the bottom. Seasonally decreasing day length and prey size contributed to a decline in daily ration, yet age 0 cod still maintained a strictly diurnal foraging cycle. A lack of nocturnal feeding by age 0 cod coincided with an increase in the catch of older conspecifics (age 2 and 3) and increased foraging activity of age 1 cod suggesting that avoidance of older conspecifics is an important factor influencing the diel feeding behaviour and activity cycle of age 0 cod in shallow coastal waters of Newfoundland.

INTRODUCTION

Since the recent collapse of the north Atlantic cod (*Gadus morhua*) stock, young juveniles have largely been confined to inshore areas of coastal Newfoundland (Dalley and Anderson 1997). In the coastal environment, age 0 cod typically settle in areas occupied by larger conspecifics (Clark and Green 1990; Methven and Bajdik 1994). One to 3 year old juveniles are typically found further away from shore during the day and show a nocturnal movement into shallow coastal waters where age 0 juveniles are concentrated (Pihl 1982; Riley and Parnell 1984; Clark and Green 1990; Keats 1990; Methven and Schneider 1998; Cote et al. 1998). It has been suggested that this shoreward movement by older juvenile cod is associated with increased foraging activity (Pihl 1982). Intercohort cannibalism is common when small and large cod occur together (Bogstad et al. 1994), yet how small cod balance the trade-offs of predation risk against the choice of when and where to forage is not well understood. A better knowledge of the processes that reduce interactions between small fish and potential predators has broad ecological applications and will improve our understanding of the role of coastal habitats to the rebuilding of Atlantic cod stocks (Taggart et al. 1994).

The feeding requirement of small, rapidly growing fish often forces them to occupy the same habitat as larger potential predators. When distributions overlap, predator avoidance may be expected to have a greater effect on the foraging time and location of smaller individuals. Laboratory studies document a habitat shift by age 0 cod in the presence of actively foraging 1 to 3 year old conspecifics (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996; Gotceitas et al. 1997), suggesting that age 0 cod perceive larger juveniles as a threat. Thus, the presence of older cod may influence the distribution and possibly the food intake of young cod in the natural environment.

Analysis of diet is a valuable tool for exploring interactions among fish. The feeding behaviour of most fish is highly structured within the diel cycle (Johnson and Dropkin 1993) and processes underlying changes in behaviour, distribution, and foraging activity, such as prey availability and predator avoidance, may be reflected in diel or seasonal changes in diet (Keast and Welsh 1968; Keast 1977). The presence of a predator may modify the foraging behaviour of small fish by inducing shoaling behaviour and (or) restricting feeding time and location (Helfman 1986; Lima and Dill 1990). High predation pressure could potentially reduce food intake, condition, and ultimately survival of small fish.

Generally, logistic requirements influence the ecologist's choice of sampling design for diet studies. As such, many researchers resort to point-in-time sampling study designs. However, diel variation in diet composition and feeding frequency and intensity (i.e., stomach fullness) can influence the accuracy of the sampling frequency and dietary analysis such that randomized point-in-time sampling may miss daily and (or) seasonal feeding patterns (Hodgson et al. 1989). If point-in-time sampling programs are to maximize the amount of information gained per fish collected, than fish should be collected during, or shortly after, periods of intensive feeding (i.e., when stomachs are fullest; Bowen 1996). Subsequently, the first step in diet studies should be a 24-h series of collections conducted at regular intervals to establish whether stomach fullness, or diet composition changes according to time of day. Ultimately, the study objectives will dictate the sampling design, however, to better understand the ecological role of fish in their natural environment, diet should be considered over 24-h periods, particularly for opportunistic feeders and during ontogenetic shifts in resource (i.e., food and habitat) use.

The ecological significance of daily patterns of foraging in demersal age 0 and age 1 cod, determined from sampling at regular time intervals throughout a 24-h period, have not been considered in shallow coastal waters of Newfoundland. In this study, I investigated stomach fullness and diet composition of demersal age 0 and age 1 cod at regular time intervals throughout a 24-h period on a monthly basis during August-December to delineate possible age-class differences in feeding behaviour and resource use in a preferred coastal habitat of age 0 cod. Autumnal changes in food intake were also established using field estimates of rates of gastric evacuation and mean stomach fullness over 24-h periods. Inferences on predation risk were derived from diet studies and diel patterns in the catch of age 0 to 3 year old cod in standardized hauls with a beach seine.

MATERIALS AND METHODS

Study location

The bulk of this study was carried out at a shallow water site (~ 5.5 m depth) in Goose Cove (47°50.5'N, 53°53.9'W), which is located in Bull Arm of Trinity Bay, Newfoundland (see Site 2, Chapter 3, Fig. 3.1). The substrate type at the study site consisted of sand and gravel (0.1-2.0 cm), and the bottom was dominated by a dense bed (~ 75% cover) of eelgrass (*Zostera marina*) to a depth of about 5.0 m. A complete description of the study area is provided in Chapter 3.

A preliminary study was carried out in a small, shallow water (1-2 m deep) inlet at the southeast entrance to Goose Cove. Substrate type at this site consisted of sand and gravel with approximately 5% eelgrass cover.

Preliminary study

On August 26-27 1993, cod were collected in standardized hauls with a 30 m beach seine (BS-I; see below) at 3-h intervals throughout a 24-h cycle. This seine was deployed by a single individual. One warp-end was secured on shore, then the net was deployed by slowly walking the second warp-end out into the water to a maximum depth of 1.2 m. The shoreline was parallelled at this depth to the full length of the net, then the second warp-end was brought to the location of the first warp-end and the net was hauled to shore. Captured cod were sorted by length-class, killed in an overdose of anaesthetic (tricaine methane sulfonate; MS 222), placed on dry-ice, and stored (-20°C) for later analysis.

Cod were captured in too few numbers throughout the 24-h cycle to determine age-class differences in peak foraging activity (Table 2.1). However, a qualitative analysis of diet composition (presence/absence of prey) indicated that age 0 cod were consuming calanoid copepods, while age 1 cod were consuming large benthic invertebrates. These results on diet composition are consistent with those reported for a 1.2 m deep site located nearby in Trinity Bay (Lomond et al. 1998). Catch results, reported in Table 2.1, provide evidence of a shoreward movement into very shallow waters at night by both age 0 and age 1 cod. These juvenile cod catch results are consistent with findings (Methven and Bajdik 1994) at the same shallow (1.2 m) water site studied by Lomond et al. (1998).

Samples conducted during the day-light period at a deeper (5.5 m) water site in Goose Cove (Site 2; see Fig. 3.1) on August 27, revealed that both juvenile cod age-classes could be captured in high numbers at this location. For the remainder of the study the 24-h collections were conducted at this site (see below).

Diel variation in stomach contents

Cod were collected at 3-h intervals over 24-h periods on September 13-14, October 04-05, November 13-14, and at 4-h intervals on December 14-15. Sampling was carried out using one of two types of beach seine modified to fish 50 m from shore. Beach seine I (BS-I) had head rope and foot rope lengths of 30 m and a stretched mesh size of 9 mm throughout. Beach seine II (BS-II) was first described by Lear et al. (1980) and had a 9 mm mesh size in the codend. The wings of both seines were fitted with 75 cm poles that maintained the wings in an upright position while the net was hauled to shore. Limited access to sampling gear required the use of BS-I during the September and December diel sampling program and BS-II during October and November.

The seine was deployed from a small (6 m) motorized boat at a distance of 50 m from shore. During each set, the head ropes were located at the same location on shore (16 m apart), thereby keeping the area sampled fairly constant (i.e., 16 m × 50 m = 800 m^2). The seines sampled the lower 2 m of the water column. Water temperature was measured 50 m from shore, within 1.0 m of the bottom. Low beam flash-lights, which were directed away from the water (i.e., placed on and directed onto the ground or directed into the bottom of the boat), were used during night sampling. Thus, effects of the artificial light source on the feeding and distribution of fish at night was considered to be negligible.

Once the seine was brought to shore, fish were placed in a large tub filled with seawater and sorted by length-class. Up to fifteen age 1 cod (7.9-14.3 cm) were immediately removed from the catch, followed by a sample of ten age 0 cod (4.2-7.4 cm). Fish were killed in an overdose of anaesthetic (MS 222), placed on dry ice, and stored (-20^0 C) for later analysis.

In the laboratory, individual fish were thawed, blotted, measured for standard length (SL; ±1.0 mm), and weighed (±0.01 g). The stomach was removed and food items identified, counted, and weighed. Relative position of dominant prey within the stomach was recorded during dissection. There was no evidence of regurgitation (i.e., food in the buccal cavity or empty, yet distended stomach). Preliminary analysis revealed that calanoid copepods dominated the diet of age 0 cod, while larger invertebrates dominated the diet of age 1 cod. In order to assess diel changes in diet composition of age 0 cod with more precision, calanoid copepods were identified to genus or species. A haphazard sample of up to 20 copepods from each taxon identified in the diet of age 0 cod were measured for length on a monthly basis according to standard measurement techniques (Bottrell et al. 1976; Mason 1977; Rosen 1981). Harpacticoids in the diet of age 0 cod were combined to form a single taxon. All copepods were combined into a single taxon for age 1 cod. The remaining food types were identified to the same taxonomic level for both cod age-classes. For example, crustaceans were identified to order; annelids to class; gastropods and pelecypods pooled into Mollusca; and fish were considered a single group.

Food items in the stomach of individual age 0 cod were separated into one of the taxa outlined above, placed on a glass filter and dried to a constant weight (± 10 μg) at 60°C. Unidentified food material was treated in a similar manner.

Due to the predominance of larger food items in the diet, the method used to obtain the total weight contribution of small zooplankton differed for age 1 cod. Small zooplankter taxa, specifically copepods, cladocerans, and pelecypod veligers, were counted for each individual fish. An average weight was estimated for an individual within each zooplankter taxon by pooling a haphazard sample of 200-300 individuals from no fewer than three cod. The remaining zooplankters from each stomach were then pooled with the unidentifiable food material from that stomach. Larger food items in each stomach were separated and grouped into one of the taxa outlined above. Food groups, identified for each fish, were dried separately to a constant weight (± 100 μg) at 60°C. For each diel sampling program, the total weight contribution of copepods, cladocerans, and pelecypod veligers to the diet of each age 1 cod was estimated from the average weight and number of individuals counted. The weight of unidentifiable food material was obtained by difference. That is, weights obtained for all zooplankton taxa were subtracted from the combined dry weight measure of the unidentifiable food and zooplankton. This value was always positive.

An index of relative importance (IRI), developed by George and Hadley (1979), was used to estimate the importance of each prey taxon in the diet of age 0 and age 1 cod. The IRI is derived from an index of absolute importance which combines three standard diet measures (% frequency of occurrence, % total number, and % total weight) into a single index for each taxon. The IRI incorporates all three methods into a single index which is derived from an index of absolute importance (IAI) as follows:

2.1)
$$IAI_a = \text{\% frequency of occurrence} + \text{\% total number} + \text{\% total weight for food item } a;$$

2.2)
$$IRI = \frac{IAI_a}{\sum_{a=1}^{n} IAI_a} \times 100;$$

where, *a* is the specific prey group and *n* is the number of different prey groups.

To account for variation in body size, weight of the stomach contents at time t was adjusted for fish size by establishing an index of stomach fullness, expressed as:

2.3)
$$C_t = \frac{G_t}{W_t} \times 100,$$

where G_t, is the dry weight of the stomach contents (grams) and W_t is the total wet body weight (grams). The average stomach fullness at time t was estimated by including fish with empty stomachs.

Gastric evacuation and daily ration

Exponential rates of gastric (i.e., stomach) emptying have been described for young cod (Tyler 1970), and the exponential model has been identified as giving the best description of the rate of gastric evacuation of fish, particularly when feeding on small (i.e., planktonic Crustacea and benthic invertebrates) food items (Jobling 1986; 1987). The exponential model defines gastric evacuation as:

2.4) $$\bar{C}_x = \bar{C}_o e^{-RT}$$

where, $\bar{C}_o$ and $\bar{C}_x$ are, respectively, the average stomach fullness (g dry · g wet^{-1}) at the beginning and end of time interval T (i.e., 3 h in September, October, and November, and 4 h in December) and R is the instantaneous evacuation rate (g dry · gram wet^{-1} · hour^{-1}). In its logarithmic form equation 2.4 is written as:

2.5) $$\ln \bar{C}_x = \ln \bar{C}_o - RT.$$

The evacuation rate was estimated for age 0 and age 1 cod for each diel survey as the slope of the relationship between ln $\bar{C}_x$ and time. This was accomplished by identifying the greatest peak in stomach fullness for a diel survey and calculating R over the subsequent series of observations where $\bar{C}_x < \bar{C}_o$.

Daily ration was determined using the Eggers (1977) model, which assumes an exponential evacuation function to estimate the average daily ration of all fish collected during a given day ($\bar{D}$; grams dry · g wet^{-1} · day^{-1}). The Eggers (1977) model defines daily ration as:

2.6) $$\overline{D} = \overline{C} \times R \times 24$$

where $\overline{C}$ is the average stomach fullness of all fish collected over a 24-h period, R is the prevailing gastric evacuation rate, and 24 is the number of hours in a day.

Eggers (1979) suggested that daily ration values derived from his model may be biased when the stomach contents at the beginning and end of a 24-h period are not equal. Therefore, I performed a paired t-test (PROC TTEST, Cochran and Cox approximation, SAS 1988) on the difference between stomach fullness of C_0 and C_{24}, to verify whether Eggers' (1979) correction should be used.

RESULTS

Size and catch of juvenile cod

The size of age 0 cod retained for analysis in this study ranged from 4.2 to 7.4 cm SL while age 1 cod ranged from 7.9 to 14.3 cm SL (Fig. 2.1). Larger conspecifics ranged from 16.6 to 27.5 cm SL, which corresponds to 2 and 3 year old cod (May et al. 1965; i.e., age > 1, Table 2.2). Age 0 cod dominated the autumnal catch in Goose Cove and the catch of this age-class was always highest during the day (Table 2.2). Conversely, 2 and 3 year old cod were rarely captured during the day but were well represented at night, which is when the catch of this age-class was highest. The catch of age 1 cod did not show a consistent diel pattern. The Mann-Whitney *U* test was used to test for day-night differences in the capture rate (number of fish per haul) of each juvenile cod age-class (Siegel 1956). Under the null hypothesis the Mann-Whitney U test assumes that the day and night catch rates have the same distribution. If the evidence supports the alternate hypothesis, it implies that the bulk of the catch rates from one light period is higher than the bulk from the other light period. Catch rates differed significantly between all light periods tested for age 0 cod (September $U = 0$, $p = 0.008$; October $U = 0$, $p = 0.018$; November $U = 0$, $p = 0.008$; December $U = 0$, $p = 0.028$) and all but one (October) for cod > age 1 (September $U = 0$, $p = 0.008$; October $U = 4$, $p = 0.286$; November $U = 0$, $p = 0.008$; December $U = 0$, $p = 0.028$). Catch rates of age 1 cod were significantly higher at night in September ($U = 0$, $p = 0.008$), but did not differ between light periods in October ($U = 5$, $p = 0.286$), November ($U = 5$, $p = 0.143$), or December ($U = 3$, $p = 0.200$).

In addition to juvenile cod, four other fish species (Greenland cod, *Gadus ogac*; three-spine stickleback, *Gasterosteus aculeatus*; winter flounder, *Pleuronectes americanus*; and short-horned sculpin, *Myoxocephalus scorpius*) were also recorded in the catches. Of these four species, *Gadus ogac* was most prevalent. When very small, *G. morhua* and *G. ogac* are morphologically similar, however, these two species can be distinguished at a size of about 3.0-4.0 cm SL (i.e., in 1997, suspected differences in eye diameter and anal fin pigmentation were verified in the laboratory from artificial fertilization and raising of young from known brood stock; S. Grant, unpubl. data).

Two autumnal influxes (i.e., August-September and October-November) of small (3.5 to 6.0 cm) recently settled age 0 cod have been reported in coastal Newfoundland (Methven and Bajdik 1994). This study confirms these findings. However, high numbers of recently settled cod were also observed in the catches during December (Fig. 2.1), indicating that in some years nearshore settlement may extend beyond November. Age 0 *G. ogac* were also captured in Goose Cove, however, they appear to settle only in August-September.

Diel feeding cycle and diet composition

Mean stomach fullness of age 0 cod showed a marked diel cycle that did not vary during the autumn months (Fig. 2.2). Mean stomach fullness increased throughout the day, peaked at dusk, and declined until dawn. Mean stomach fullness at dusk ranged from 0.16 to 1.09 g dry · g wet^{-1}. Generally, the proportion of fish with empty stomachs increased throughout the night and peaked at the last sample taken just before dawn, suggesting that age 0 cod did not feed at night. Stages of food digestion and constriction of the stomach also provide evidence that age 0 cod did not feed at night. For example, after sunset, there was a gradual constriction of the anterior region of the stomach and as digestion progressed food formed a bolus in the posterior region of the stomach. Only the central region of the bolus contained identifiable prey items, suggesting a peripheral action of digestion.

Throughout autumn, the diet of age 0 cod was dominated by small (<4 mm) planktonic Crustacea (Fig. 2.3). In order to obtain an estimate of the seasonal variation in zooplankter importance an IRI was calculated for all cod captured during the daylight period (Table 2.3), which was when fish were actively feeding (Fig. 2.3). Cladocerans (*Podon* sp. and *Evadne* sp.) dominated the diet during September, followed largely by copepodite stages of *Acartia* sp. and pelecypod veligers. These zooplankters were very small (<1 mm). Cladocerans maintained a moderate importance to the diet to November. During October, pelecypod veligers and *Acartia* sp. were replaced by larger calanoid genera (1.0 - 4.0 mm). Larger adult stages of *Temora longicornis* dominated in October and *Calanus finmarchicus*, particularly copepodites with a high incidence of oil sacs, were also important. Importance of small copepodites of *Pseudocalanus* sp. and *Acartia* sp. increased during November and December, and coincided with an increase in the consumption of smaller copepodite stages of all calanoids.

Benthic and epibenthic prey were generally of minor importance to the diet of age 0 cod (Fig. 2.3). Benthic cumaceans were the largest prey items consumed (<9 mm). Small benthic (gammarid) and pelagic (hyperiid) amphipods (<7 mm) were also consumed as well as epibenthic Harpacticoids (<3 mm). All amphipods found in the diet during September were pelagic and small (2-3 mm). For the remaining months it was generally observed that pelagic amphipods were consumed during the day, while benthic amphipods and cumaceans were consumed at dusk and dawn, suggesting a movement out of the water column by age 0 cod at night. After sunset benthos was observed in the anterior region of the stomach and as digestion progressed throughout the night these larger prey were typically found in the centre of the gastric bolus, being surrounded by partially digested food.

Distinct changes in the position of dominant zooplankton taxa in the stomachs of age 0 cod during the daylight period appeared to correspond with changes in the tidal cycle, suggesting a tidal influence on diet composition and feeding behaviour. For example, on September 13, low and high tide occurred at approximately 10:00 and 16:30, respectively. Position in the stomach revealed that cladocerans and pelecypod veligers were largely consumed during ebb tide, while *Acartia* sp. were consumed during flood tide. At 08:00, cladocerans and pelecypod veligers dominated the diet (Fig. 2.3). By 11:00, *Acartia* sp. dominated the anterior region of the stomach and exhibited an increase in dietary importance throughout the flood tide. During flood tide, cladocerans and pelecypod veligers were found in the posterior region of the stomach of all fish sampled. At 17:00, cladocerans and pelecypod veligers dominated the anterior region of the stomach and showed an increase in importance throughout the ebb tide (Fig. 2.3). On November 13, low and high tide were at approximately 13:15 and 19:00, respectively. The position of dominant prey in the stomach revealed that *Pseudocalanus* sp., *Acartia* sp., and cladocerans were consumed during ebb tide while *T. longicornis* and *C. finmarchicus* were consumed during flood tide. These observations were supported by diel changes in the importance of these prey types (Fig. 2.3). In October, *T. longicornis* and cladocerans generally dominated the anterior region of the stomach during ebb tide. However, I could not establish distinct trends on the influence of tide on feeding during October and December, which I attribute, in part at least, to the distinct diurnal foraging cycle of age 0 cod and the initiation of these diel surveys during mid to late afternoon (Fig. 2.2).

Age 1 cod fed predominantly at night (Fig. 2.4). However, prey items in "fresh" (i.e., showing little or no digestion) condition were observed throughout the diel period suggesting that intake was not zero when stomach fullness declined between sampling intervals (i.e., when $\bar{C}_x < \bar{C}_o$). A decrease in the proportion of fish with empty stomachs between sampling intervals when $\bar{C}_x < \bar{C}_o$ also suggests that food intake was not zero (Fig. 2.4). Feeding frequency (i.e., periods of intensive feeding) of age 1 cod varied during the night (Fig. 2.4). Mean stomach fullness showed a single nocturnal peak at approximately two hours of midnight in September, October, and December. In November, two nocturnal peaks in stomach fullness were observed; one after sunset and a second before sunrise. Peaks in mean stomach fullness ranged from 0.72 to 1.18 g dry · g wet^{-1} (Fig. 2.4). Overall, the highest proportion of fish with empty stomachs was observed during the day.

Small planktonic crustacea were of minor importance to the diet of age 1 cod in September, peaked in importance during October and were of limited importance during November and December (Fig. 2.5). Greatly increased predation is commonly associated with increased prey abundance (Keast 1977) and fish select the largest zooplankters (Noble 1975; Brooks and Dodson 1965). The sharp increased in importance of calanoid copepods to the diet of age 1 cod in October coincided with a switch to large calanoids by age 0 cod providing evidence of an increase in the abundance of this prey resource.

Diet composition of age 1 cod varied between sampling intervals of each diel survey, however, mysids and gammarid amphipods generally dominated the diet during September, November, and December, and increased importance of mysids (Fig. 2.5) was associated with the peaks in mean stomach fullness (Fig. 2.4). Even the October peak in stomach fullness (Fig. 2.4), resulted from a few cod (40%) that had consumed a large quantity of mysids, indicating that increased foraging activity was associated with the nocturnal consumption of large benthic and epibenthic prey.

During November and December, seven age 1 cod stomachs contained fish. State of digestion indicated that these fish were not consumed in the net during the current sampling event. Five cod consumed fish that were identifiable as age 0 cod. The length (cm) of the age 0 cod and age 1 cannibals (in parentheses) were as follows: 4.0 (11.6), 4.2 (12.4), 4.4

(12.3), 4.7 (13.9) and 5.0 (13.6). Age 1 cannibals were on average 2.9 times larger (2.7 - 3.0) than their prey. This is in agreement with findings that suggest piscivorous fish must be at least 2-4 times larger then their prey (Nursall 1973; Bogstad et al. 1994).

Gastric evacuation and daily ration

Field estimates of rates of gastric evacuation ranged from 0.092 to 0.248 g dry · g wet^{-1} · h^{-1} for age 0 cod and 0.111 to 0.258 g dry · g wet^{-1} · h^{-1} for age 1 cod (Table 2.4). Most methods used to estimate gastric evacuation in fish follow the general approach introduced by Bajkov (1935). To determine the time taken for stomachs to empty, Bajkov (1935) suggested that fish be caught, placed in holding tanks without food, and sampled at regular time intervals. Bromley (1994) suggested that in principle, measuring gastric evacuation by this method in the field is the ideal situation because the fish have been subjected to natural environmental conditions and diet. However, Bromley (1994) also noted that stress caused from the capture process may suspend the normal digestion process for several hours during these kinds of field experiments (Lockwood 1980; Köster et al. 1990). Therefore, I used a field method introduced by Boisclair and Leggett (1985), whereby the greatest peak in stomach fullness for a diel survey is identified and values for the gastric evacuation are calculated over the subsequent series of observations where stomach fullness declined between sampling intervals (i.e., $\overline{C}_x < \overline{C}_o$). The juvenile cod I studied exhibited distinct feeding cycles with clear-cut peaks in stomach fullness, patterns that are suitable for estimating gastric evacuation by this method. However, the validity of this method depends on the assumption that feeding does not take place over the series of time intervals where $\overline{C}_x$

$< \overline{C}_o$. I conclude that this factor had little influence on estimates of gastric evacuation for age 0 cod. For example, a gradual constriction of the anterior region of the stomach, formation of a distinct gastric bolus, and an increase in the percentage of individuals with empty stomachs, all of which were observed in the time series for the nocturnal collections only, provide evidence of zero food intake for age 0 cod at night (i.e., when $\overline{C}_x < \overline{C}_o$). However, "fresh" food items were found in the stomachs of age 1 cod throughout the 24-h surveys and there was no evidence of the formation of a gastric bolus. Additionally, in October and November there was a decrease in the percentage of fish with empty stomachs in the series of observations where $\overline{C}_x < \overline{C}_o$ (Fig. 2.4). Thus, there is a high likelihood that the field evacuation rates were underestimated for age 1 cod.

Stomach fullness at the beginning and end of a 24-h survey did not differ significantly for age 0 cod (September, $t_{12} = 2.05$, $p = 0.063$; November, $t_{12} = 0.84$, $p = 0.419$; December $t_{10} = 1.30$, $p = 0.223$) or age 1 cod (September, $t_{18} = 1.95$, $p = 0.067$; November, $t_{21} = 0.04$, $p = 0.967$; December $t_{15} = 0.71$, $p = 0.488$). Therefore equation 2.6 was used to estimate daily ration. The October diel survey only accounted for a 21-h period (16:00 to 13:00 hr). Since C_0 and C_{24} showed no significant difference during September, November, and December, I assumed these values were also equal during October and calculated daily ration using equation 2.6.

Even though age 0 cod were consuming considerably smaller zooplankters in September, mean daily ration was comparable to that observed in October when both age-classes increased their consumption of large calanoids. Consumption of planktonic Crustacea by both age-classes in September-October suggests that zooplankter abundance was relatively high early in the season. The October-November decrease in consumption of large calanoids by age 0 cod coincided with a 2.7 fold decrease in mean daily ration (Table 2.4). Ration size and the size of the zooplankters consumed continued to decline to December, suggesting a seasonal decline in the size and abundance of the zooplankton prey resource. The seasonal decline in daily ration also coincided with a decrease in water temperature (Table 2.4) and day length. There were no seasonal trends in the average daily ration of age 1 cod.

DISCUSSION

In this study, age 0 cod exhibited a distinct diurnal foraging cycle which contrasts with the nocturnal foraging cycle exhibited by pelagic juveniles of similar size in the North Sea (Robb 1981). In addition, a seasonal decline in day length and the size of planktonic Crustacea consumed contributed to a decrease in food intake, yet age 0 cod still maintained a strictly diurnal foraging cycle and zooplanktivory. This is surprising, as twilight consumption of benthos indicates that some of the benthos were within the size limits of prey that age 0 cod could successfully handle and consume, and the nocturnal consumption of benthos and small planktonic Crustacea by age 1 cod indicates these prey were available at night.

It is well documented that trade-offs between food availability and predation risk can affect where young fish decide to feed (Lima and Dill 1990) and studies show that fish can completely reverse their diel feeding behaviour in response to changes in food availability or predator distribution (Bowen and Allanson 1982). Helfman (1986) reviewed the diel behaviour of fish noting, "many fish appear to separate the day into an active, food gathering phase and a relatively inactive, resting phase that is ultimately linked to predator avoidance". I suggest that demersal age 0 cod move to protective bottom cover or into very shallow waters at night (Methven and Bajdik 1994; this study), cease feeding, and become relatively inactive in coastal regions of Newfoundland to reduce interactions with potential predators, in this case, older conspecifics. This interpretation of the results is supported by laboratory studies that have shown age 0 cod shift habitat and seek shelter to reduce predation mortality from actively foraging 1 to 3 year old conspecifics (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996; Gotceitas et al. 1997). Consumption of benthos by age 0 cod at dusk and dawn provides evidence of an increased benthic habit at night, which may be associated with seeking protective cover in eelgrass, and their nocturnal movement into very shallow water sites (<1.2 m; Methven and Bajdik 1994; this study) may also be in response to increased predation risk. Current findings indicate that a lack of nocturnal feeding by age 0 cod coincided with an increase in the catch of 2 and 3 year old conspecifics and increased foraging activity of 1 year old cod, suggesting that avoidance of older conspecifics is an important factor influencing the diel feeding behaviour and activity cycle of age 0 cod. Overall, it appears that prey availability is secondary to predator avoidance in explaining the diel feeding and activity patterns of age 0 cod in the study area.

Periodic influxes of high numbers of newly settled cod, which appear to remain localized within coastal areas for several weeks (Chapter 3), may be the stimulus that causes older conspecifics to move into shallow water regions at night (Clark and Green 1990; Keats 1990; Methven and Bajdik 1994; Cote et al. 1998). Pihl (1982), noted that twilight foraging by large juvenile cod may be more pronounced in coastal populations and increased activity at dusk and dawn by 2 and 3 year old cod appears to be associated with a migration into and out of shallow water regions (Clark and Green 1990; Cote et al. 1998). Intercohort cannibalism is common in cod and increases with predator length, density of young cod, and degree of overlap in distributions (Bogstad et al. 1994). In the north Atlantic, much of the cannibalism is upon age 0 cod and they are preyed upon by a wide size range of predators (Bogstad et al. 1994). Bogstad et al. (1994) documented that almost all cannibalism in cod was by fish that were at least twice the length of their prey and that most were more than three times longer. This study corroborates these findings as there was no evidence of cannibalism by 1 year old cod until they were approximately three times longer than their prey. Evidence, however, of intercohort cannibalism by cod that were twice the length of their prey (Bogstad et al. 1994) and the occurrence in the Goose Cove length-frequency distributions of age 1 cod that were at least twice the length of the average sized age 0 cod (Fig. 2.1) suggests that the age 0 cod studied were at risk of predation from age 1 cod.

Previous studies have shown that cod are opportunistic feeders, exhibiting a preference for larger prey as they increase in size (Powles 1958; Daan 1973; Hawkins et al. 1985; Keats et al. 1987; Lomond et al. 1998). In this study, cod within a size range of 8-10 cm shifted from feeding predominantly on small planktonic Crustacea by day to large benthic invertebrates at night. A similar size related shift to benthos has been reported at a nearby site in Trinity Bay (Lomond et al. 1998), and neighbouring Conception Bay, Newfoundland (Keats et al. 1987). However, this is the first documented case of a size-related shift to predominantly nocturnal foraging in juvenile cod. This size-related shift in feeding time and location suggests that larger fish accrue a size benefit in shallow nearshore waters of Newfoundland and are likely above the upper limit of prey size for nocturnal predators. Apart from the prevalence of older conspecifics and a closely related gadoid species (*G. ogac*), studies in nearshore regions of Newfoundland document low catch or general lack of potential predators on small juvenile cod (Gotceitas et al. 1997; this study). If cannibalism does play a major role in the survival of newly settled cod in nearshore regions of Newfoundland, then coastal nursery grounds may contribute little to the population in years/locations where abundance of older juveniles is high.

In this study, age 1 cod always exhibited an increase in feeding intensity at night, however, the feeding frequency and diet composition varied according to the time of day. As such, the appropriate point-in-time to collect stomachs over a 24-h period in order to maximize information gained per individual (i.e., peaks in stomach fullness) was not clear during autumnal sampling. Age 0 cod exhibited a consistent diel feeding pattern, suggesting that the best time to collect this age-class for diet studies would be late afternoon to dusk. However, this study shows that even point-in-time sampling when stomachs are fullest may influence the accuracy of dietary analysis. For example, evidence that diet composition of age 0 cod is related to the tidal cycle suggests that some prey species may be missed by point-in-time sampling when the stomach is fullest and the consumption of certain prey (i.e., fish) by age 1 cod may also be missed. Ultimately, the study objectives will dictate the best sampling frequency for diet analysis. However, if the feeding frequency and diet composition vary substantially during a 24-h cycle they may influence the accuracy of certain kinds of studies, particularly those that seek to estimate the level of predation on certain prey species or studies that investigate fish growth and (or) condition in relation to nutrient/energy (i.e., lipids) content of their prey (i.e., see Chapters 4&5). The possibility of missing important prey species may be relatively high in studies involving small fish, as they exhibit relatively high gastric evacuation rates, particularly when feeding on small prey items (Jobling 1986; 1987; Jobling et al. 1991; Bromley 1994).

Point-in-time dietary studies of fish are limited to reporting prey importance to the diet at one moment in time. As such, they provide little information on diel changes in diet composition, feeding frequency, and feeding intensity, behaviours that are ultimately linked to changes in the natural environment. Increased diversity (relative size and abundance) of available prey that accompanies an increase in body size of opportunistic feeders may increase diel variation in feeding frequency and diet composition, which may in turn influence the accuracy of dietary analysis and sampling frequency such that point-in-time sampling may miss daily and (or) seasonal feeding patterns (Hodgson et al. 1989). Diet composition, feeding frequency, and feeding intensity over a 24-h period may vary seasonally (Keast and Welsh 1968; Keast 1977; this study) and a recent study indicated that significant variation in feeding intensity may even occur from day-to-day in small juvenile fish (Grant and Kott 1999). Day-to-day variation in feeding intensity appears to be related to ontogenetic changes in prey size (Grant and Kott 1999). To obtain a clearer understanding of the ecological role of fish populations, particularly for opportunistic fish that exhibit ontogenetic shifts in prey size, I recommend that diet studies begin by establishing whether diet composition, feeding frequency, and feeding intensity varies during 24-h periods.

Current findings document a size related shift in foraging time and location by young juvenile cod, which may be explained by differential predation risk associated with an increase in shoreward movement (Clark and Green 1990; Keats 1990) and foraging by older conspecifics at night and (or) dusk and dawn (Arntz 1973; Pihl 1982). Clark and Green (1990) suggested that a seasonal shift to autumnal shoreward migrations at dusk and decreased activity at night by 2-3 year old cod in shallow coastal waters of Newfoundland were related to predator avoidance. However, the seasonal shift in migration patterns of 2-3 year old cod coincides with the nearshore settlement of age 0 cod, suggesting that the presence of age 0 cod should not be overlooked as a stimulus to this seasonal change in migration patterns. Autumnal shoreward movements by 2-3 year old cod at night appear to be common in coastal Newfoundland (Clark and Green 1990; Keats 1990; Cote et al. 1998), however, 2-3 year old cod may also be captured in shallow coastal waters during the day, particularly during the summer months (Clark and Green 1990; Methven 1997; Dietrich 1998). Therefore, I recommend that future studies seeking to determine the magnitude of juvenile cod predation mortality resulting from older conspecifics in shallow nearshore waters of Newfoundland sample at regular time intervals throughout the diel period.

Age 0 cod may be highly concentrated in nearshore regions of Newfoundland, maintain localized populations (Chapter 3), and the presence of eelgrass appears to be an important factor influencing their nearshore distribution throughout the north Atlantic (Tveite 1984; Tupper and Boutilier 1995; Gotceitas et al. 1997; Chapter 3). Studies suggest that small juvenile cod are associated with habitats that exhibit increased bottom structure due to the protection these areas provide from predators (Lough et al. 1989; Tupper and Boutilier

1995a; Gotceitas et al. 1997). However, suitable habitat must also provide an adequate supply of food. A recent study has identified strong (10 cm/sec) tidal currents in Goose Cove (S. Grant and B. de Young, unpubl. data), and results on diet composition presented here suggest a tidal related feeding pattern. I suggest that high concentrations of newly settled age 0 cod may also be associated with coastal areas that exhibit physical features that intensify water currents and serve to concentrate planktonic Crustacea. The use of food progression in the stomach to ascertain feeding time is not uncommon (Webster 1942), however, in the present study the importance of the tidal cycle to diet composition was not discovered until after sampling was completed. To test the hypothesis of tidal related feeding, additional data would have to be collected over more than one 24-h period and preferably on days when the change in tidal flood occurs at different times of the day.

Planktivorous fish are typically size selective, exhibiting a preference for larger prey items, and a decrease in zooplankton size and abundance may result in decreased growth (Brooks and Dodson 1965; Goodlad et al. 1974; Noble 1975). In neighbouring Conception Bay, Newfoundland, Davis (1982) documented a late summer-early autumn decrease in size and abundance of the same copepod species that dominated the diet of age 0 cod in this study. Current findings on diet composition and daily ration of age 0 cod were also indicative of an autumnal decrease in size and abundance of the copepod resource, suggesting that cod settling late in the season in coastal regions of Newfoundland may be food limited. Higher water temperature, increased day length, and evidence of increased size and abundance of planktonic Crustacea suggests age 0 cod that settle early may grow quicker and shift to feeding on larger prey, thereby increasing their growth efficiency (Kerr 1971a,

b) before winter. Many fish species in temperate climates overwinter on stored energy reserves and overwintering mortality is high for very small individuals (Henderson et al. 1988). Cod that settle early are likely in better condition for surviving the first winter and may reach a size where they prey on smaller cod that settle late (intracohort cannibalism). Intracohort cannibalism has been reported in age 0 cod in Icelandic waters (Bogstad et al. 1994). Small body size of age 0 cod results in cannibalism by age 1 cod and both age-classes overwinter in coastal regions of Newfoundland (Methven and Bajdik 1994; Chapter 3) suggesting that predation mortality may also contribute to a reduction in overwintering survival of age 0 cod that settle late.

Physical disturbance caused by sampling can affect habitat structure and the distribution and behaviour of mobile animals. Results presented in this study on the diel feeding of age 0 and age 1 cod indicate distinct diurnal and nocturnal peaks, respectively, in stomach content weight throughout the season and these peaks were each associated with the consumption of the same prey types (i.e., planktonic Crustacea and benthos, respectively) by each cohort. I conclude that repeat sampling at 3 or 4 h intervals at the same site had little influence on the diel behaviour and distribution of predators and their prey.

In Summary, current findings provide evidence that age 0 cod reduce potential interactions with larger 1 to 3 year old conspecifics through diel differences in foraging time and distribution in shallow nearshore waters. Nocturnal avoidance of older conspecifics may indirectly contribute to a seasonal decrease in foraging success (daily ration) and hence growth, condition, and overwintering survival, particularly for small age 0 cod that settle late in the season when day length and water temperatures are reduced. This study documents intercohort cannibalism by 1 year old cod and evidence of increased abundance of 2 and 3 year old cod in shallow coastal waters at night leads me to hypothesize that these shoreward movements into eelgrass habitat are, in part at least, related to high local densities of newly settled juveniles. The extent of cannibalism in shallow nearshore regions and its potential to directly or indirectly influence cod recruitment warrants further investigation.

Table 2.1. Variation in the catch (number/haul) of juvenile Atlantic cod over a 24-h period in a shallow water inlet in Goose Cove, Newfoundland, August 26-27, 1993.

Time	Age 0	Age 1
16:00	0	0
19:00	3	0
22:00*	13	7
01:00*	1	12
04:00*	0	5
07:00	0	11
10:00	0	0
13:00	0	0

*Denotes nocturnal collection

Table 2.2. Variation in the catch (number/haul) of juvenile Atlantic cod over 24-h periods in Goose Cove, Newfoundland, during September-December, 1993.

September				October				November				December			
Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1	Time	Age 0	Age 1	Age >1
08:00	393	16	0	16:00	106	5	2	09:00	379	13	1	16:00	181	13	0
11:00	803	17	0	19:30*	24	13	1	12:00	237	11	0	20:00*	30	16	3
14:00	418	12	0	22:00*	38	19	5	15:00	494	12	0	24:00*	18	13	4
17:00	569	15	0	01:00*	13	13	7	18:00*	76	20	1	04:00*	19	8	6
20:00*	75	21	2	04:30*	15	19	2	21:00*	48	18	4	08:00	437	17	0
23:00*	43	26	8	07:00*	35	7	3	24:00*	41	19	5	12:00	252	14	0
02:00*	47	29	3	10:00	200	38	2	03:00*	64	13	3	16:00	295	15	0
05:00*	59	24	5	13:00	146	20	1	06:00*	44	15	3				
08:00	287	20	0					09:00	346	21	0				

*Denotes nocturnal collection.

Table 2.3. Relative importance of dominant zooplankton taxa to the diurnal diet of age 0 Atlantic cod in Goose Cove, Newfoundland, during autumn 1993. Values >5% are shown.

Taxa	September	October	November	December
Cladocera	37.74	18.08	18.72	-
Pelecypod veligers	21.89	-	-	-
Acartia sp.	22.87	-	-	12.40
Calanus finmarchicus	-	21.47	5.83	-
Pseudocalanus sp.	-	7.11	29.63	14.98
Temora longicornis	-	41.38	37.96	48.26

Table 2.4. Field estimates of gastric evacuation rate (R; g dry · g wet^{-1} · h^{-1}) and average daily ration ($\overline{D}$; g dry · g wet^{-1} · day^{-1}) of age 0 and age 1 Atlantic cod in four months with different water temperatures (T; °C).

		Age 0		Age 1	
	T	R	$\overline{D}$	R	$\overline{D}$
September	12.8	0.248	1.65	0.191	1.82
October	9.1	0.095	1.56	0.114	1.54
November	6.0	0.132	0.57	0.258	2.36
December	3.7	0.095	0.26	0.164	1.32

Figure 2.1. Length-frequency distributions for each of age 0 and age 1 Atlantic cod in Goose Cove, Newfoundland, for a) September, b) October, c) November, and d) December, 1993. Total number (n) and average length (SL; cm) of each age-class is also presented.

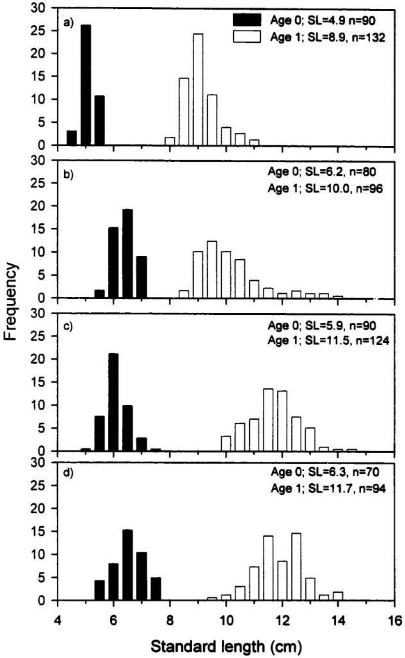

a)
Age 0; SL=4.9 n=90
Age 1; SL=8.9, n=132
b)
Age 0; SL=6.2, n=80
Age 1; SL=10.0, n=96
c)
Age 0; SL=5.9, n=90
Age 1; SL=11.5, n=124
d)
Age 0; SL=6.3, n=70
Age 1; SL=11.7, n=94
Frequency
0
5
10
15
20
25
30
4
6
8
10
12
14
16
Standard length (cm)

Figure 2.2. Diel variation in mean gut fullness of age 0 Atlantic cod sampled in Goose Cove, Newfoundland, during a) September, b) October, c) November, and d) December, 1993. Error bars represent the 95% CI for ten cod. Note, left vertical axes are not equal. Solid horizontal bars indicate night.

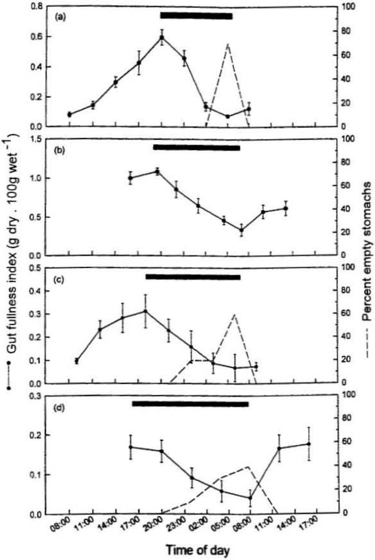

(a)
(b)
(c)
(d)
0.8
0.6
0.4
0.2
0.0
1.5
1.0
0.5
0.0
0.5
0.4
0.3
0.2
0.1
0.0
0.3
0.2
0.1
0.0
100
80
60
40
20
0
Gut fullness index (g dry . 100g wet $^{-1}$)
Percent empty stomachs
08:00
11:00
14:00
17:00
20:00
23:00
02:00
05:00
08:00
11:00
14:00
17:00
Time of day

Figure 2.3. Diel variation in the relative importance of prey taxa in the diet of age 0 Atlantic cod sampled in Goose Cove, Newfoundland, September-December, 1993. The number of prey taxa identified at each sampling event is indicated above each bar and high (H) and low (L) tide are also shown.

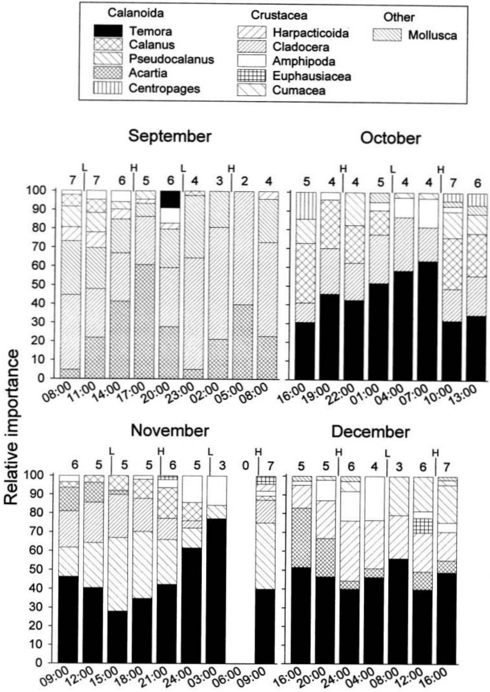
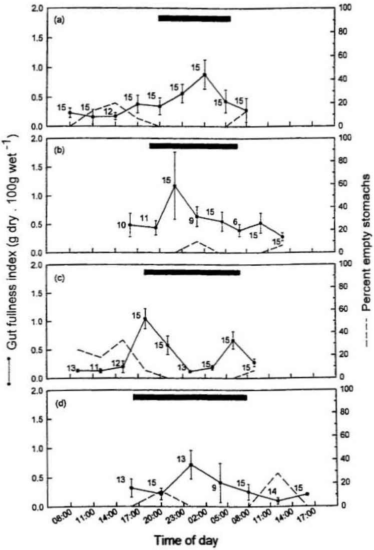
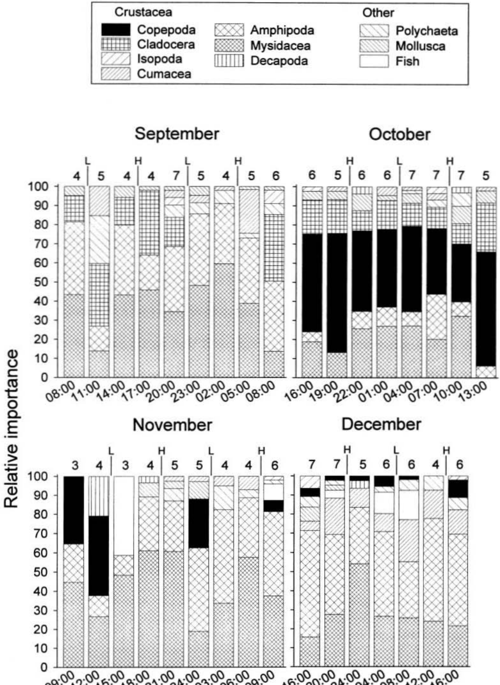

Calanoida
Temora
Calanus
Pseudocalanus
Acartia
Centropages
Crustacea
Harpacticoida
Cladocera
Amphipoda
Euphausiacea
Cumacea
Other
Mollusca
September
October
November
December
Relative importance
0
10
20
30
40
50
60
70
80
90
100
L
H
L
H
7 7 6 5 6 4 3 2 4
08:00 11:00 14:00 17:00 20:00 23:00 02:00 05:00 08:00
H
L
H
5 4 4 5 4 4 7 6
16:00 19:00 22:00 01:00 04:00 07:00 10:00 13:00
L
H
L
H
6 5 5 5 6 5 3 0 7
09:00 12:00 15:00 18:00 21:00 24:00 03:00 06:00 09:00
H
L
H
5 5 6 4 3 6 7
16:00 20:00 24:00 04:00 08:00 12:00 16:00

Figure 2.4. Diel variation in mean gut fullness of age 1 Atlantic cod sampled at Goose Cove, Newfoundland, during a) September, b) October, c) November, and d) December, 1993. Values left of each symbol represent the number of cod sampled and error bars represent the 95% CI. Solid horizontal bars indicate night.



(a)
(b)
(c)
(d)
Gut fullness index (g dry . 100g wet $^{-1}$)
Percent empty stomachs
Time of day
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
100
08:00
11:00
14:00
17:00
20:00
23:00
02:00
05:00
08:00
11:00
14:00
17:00
15
15
12
15
15
15
15
15
15
10
11
15
9
15
6
15
15
13
11
12
15
15
13
15
15
15
13
15
13
9
15
14
15

Figure 2.5. Diel variation in the relative importance of prey taxa in the diet of age 1 Atlantic cod sampled in Goose Cove, Newfoundland, September-December, 1993. The number of prey taxa identified at each sampling event is indicated above each bar and high (H) and low (L) tide are also indicated.


Crustacea
Copepoda
Cladocera
Isopoda
Cumacea
Amphipoda
Mysidacea
Decapoda
Other
Polychaeta
Mollusca
Fish
Relative importance
September
L H L H
4 5 4 4 7 5 4 5 6
08:00 11:00 14:00 17:00 20:00 23:00 02:00 05:00 08:00
October
H L H
6 5 6 6 7 7 7 5
16:00 19:00 22:00 01:00 04:00 07:00 10:00 13:00
November
L H L H
3 4 3 4 5 5 4 4 6
09:00 12:00 15:00 18:00 21:00 24:00 03:00 06:00 09:00
December
H L H
7 7 5 6 6 4 6
16:00 20:00 24:00 04:00 08:00 12:00 16:00
0
10
20
30
40
50
60
70
80
90
100

CHAPTER 3: Nearshore settlement and site fidelity of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland

ABSTRACT

Capture-mark-recapture experiments and standardized beach seine samples were conducted to examine the level of movement, spatial distribution, behaviour, and abundance of demersal age 0 Atlantic cod (*Gadus morhua*) in shallow (<8 m) water eelgrass (*Zostera marina*) and no-eelgrass habitat in Trinity Bay, Newfoundland during 1994 and 1995. Cod remained localized for several weeks (September-December) after settling from a pelagic habit. Marked cod did not appear to move further than a few hundred metres in eelgrass habitat, but moved at least 1.2 km in no-eelgrass habitat. Recapture results suggest cod may also remain localized during their first winter. Slope values for variance-mean density relationships of replicate samples taken at four closely spaced eelgrass sites indicate that age 0 cod aggregate during the day, while high within and between site variation in diurnal catch rates at the scale of hours and weeks at eelgrass and no-eelgrass sites provide evidence of localized lateral movement. These patterns in the catch rates are interpreted to reflect social behaviour in the form of mobile shoaling aggregations during the day. Day-night comparisons of ratios of variance to mean density at a single eelgrass site were also indicative of aggregative behaviour during the day. Not only did age 0 cod appear to aggregate in relatively lower numbers at night, but lack of a significant divergence from unity (i.e., variance = mean) in three of seven day-night comparisons suggests that age 0 cod commonly disaggregate at night, at which time they may be randomly distributed. These day-night patterns in the catch rates are interpreted to be due to a decrease in activity and

local dispersal of shoaling aggregations at night. A significant increase in abundance of age 0 cod in less suitable habitat (no-eelgrass cover) when settlement strength was high, is consistent with the hypothesis of density-dependent habitat selection. Behaviour patterns exhibited by age 0 cod, i.e., restricted movements in shallow nearshore waters, diurnal shoaling, and preference for structurally complex habitat, are mechanisms for predator avoidance, suggesting that predation risk is high in coastal Newfoundland.

INTRODUCTION

It is well established that trade-offs between food availability and predation risk influence fish distribution and activity; alterations in behaviour may occur at various life history stages and reflect a balance between food intake and the need to be vigilant (Lima and Dill 1990). Helfman (1986) reviewed the diel behaviour of fish, noting, "many fish appear to separate the day into an active, food gathering phase and a relatively inactive, resting phase that is ultimately linked to predator avoidance". For example, on coral reefs, where predation risk is high (Hixon 1991), small zooplanktivorous fish generally feed in large relatively stationary aggregations over refuge sites during the day and seek cover in structurally complex bottom habitats during increased activity of nocturnal fish (Helfman 1986). Diel behaviour patterns are well established for fish inhabiting coral reefs, however, Helfman (1986) suggested that convergent patterns in fundamental activities can be expected in almost any fish assemblage; behaviour patterns that successfully reduce predation risk while maintaining adequate food intake may transcend geographic and taxonomic boundaries.

Coastal settlement of age 0 Atlantic cod (*Gadus morhua*) may result in movement into regions occupied by older conspecifics and cannibalism is common when large and small cod occur together (Bogstad et al.1994). Age 0 cod appear to reduce encounter rates with larger conspecifics by moving into shallower waters containing protective bottom cover (Riley and Parnell 1984; Gotceitas et al. 1997; Chapter 2). However, larger nocturnally active conspecifics may be more abundant in shallow coastal waters at night (Pihl 1982; Clark and Green 1990; Keats 1990; Cote et al. 1998; Chapter 2) and as potential prey, age 0 cod appear to assess this increased predation risk by adjusting their behaviour. For example, although age 0 cod of similar size were zooplanktivorous during both the pelagic (Robb 1981) and nearshore demersal phase (Olsen and Soldal 1989; Lomond et al. 1998; Chapter 2), they exhibited contrasting nocturnal (Robb 1981) and diurnal (Chapter 2) activity cycles, respectively, while cod that settle in offshore waters maintain a nocturnal activity cycle (Lough et al. 1989). Echo-sounder studies in Norway document a diurnal activity cycle and shoaling behaviour by demersal zooplanktivorous age 0 cod in coastal environments (Olsen and Soldal 1989) and a diurnal activity cycle and zooplanktivory has also been reported for demersal age 0 cod occurring in a shallow cove of coastal Newfoundland (Chapter 2). Although site fidelity and crypsis in structurally complex habitats has been reported for demersal age 0 cod (Lough et al. 1989; Tupper and Boutilier 1995b), the cited literature suggests behaviour patterns that coastal populations of demersal age 0 cod use to reduce predation may parallel those observed for zooplanktivorous fish on coral reefs.

Laboratory and field studies provide evidence that the distribution and survival of small juvenile cod are dependent on habitat type (Lough et al. 1989; Gotceitas et al. 1995;

Tupper and Boutilier 1995b; Fraser et al. 1996; Gotceitas et al. 1997) and shoaling near protective bottom cover provides prey fish with a means of evading predator attacks (Pitcher 1986). Eelgrass (*Zostera marina*) habitat appears to influence the distribution of small juvenile cod in coastal waters throughout the north Atlantic (Tveite 1984; Støttrup et al. 1994; Tupper and Boutilier 1995b) and a recent study on habitat use by age 0 cod in coastal Newfoundland showed that age 0 cod are found primarily in eelgrass (Gotceitas et al. 1997). If fish select habitats due to differing levels of density-dependent resources, such as food and shelter, then as density increases and habitat suitability declines, distribution should expand to include the use of previously less suitable habitats (MacCall 1990). Density-dependent habitat selection has been used to explain positive correlations between abundance and area occupied by large juvenile and adult cod (Swain 1993).

Our current understanding of the movement levels, distribution, and behaviour of demersal age 0 cod in coastal Newfoundland is limited to underwater observations and capture rate studies that can only describe occurrence or absence at specific sites at one moment in time. Consequently these studies cannot distinguish between small or large scale movements and tell us little about the mechanisms that influence movements, distribution, and behaviour in space and time. Recent evidence suggests that day-night differences in behaviour of age 0 cod may be related to varying levels of predation risk (Chapter 2) and degree of predation risk and movement rates of animals vary inversely (Perry and Pianka 1997). In this study, I used capture-mark-recapture experiments to determine whether post-settled age 0 cod exhibit site fidelity at two nearshore locations that differed in habitat type (eelgrass vs no-eelgrass) in Trinity Bay, Newfoundland, during the autumn of 1994 and 1995.

Implications of the movement levels, spatial distribution, and behaviour of demersal age 0 cod in shallow (<8 m) nearshore regions of Newfoundland are derived from variance-mean density relationships of weekly standardized beach seine samples, day-night comparisons of the ratio of variance to mean density, and site specific catch versus cumulative catch curves.

The juvenile cod studied are an inshore component of the northern cod stock which has been under moratorium since 1992 (Taggart et al. 1994). Anticipating year-to-year variation in abundance of the 0-group cohort, I also tested the hypothesis of density-dependent habitat selection. If age 0 cod are site attached and territorial (i.e., Tupper and Boutilier 1995a), than density-dependent habitat selection at relatively small spatial scales (i.e., between closely spaced sites) may be appropriate. However, evidence of frequent (i.e., daily and/or weekly) and repeated movements between closely spaced sampling sites would preclude a valid comparison of density-dependent habitat selection at the scale of individual sites. In the current study, I evaluated density-dependent habitat selection by age 0 cod at two nearshore locations that differed in habitat type, were separated by approximately 2.6 km of coastline, and for which there was no evidence of inter-location migration by post-settled age 0 cod.

Annual beach seine assessments of juvenile cod populations in shallow nearshore regions of Newfoundland have recently been revisited (Ings et al. 1997), and these data have been used to test geographic contraction of juvenile cod at the scale of individual beach seine sites and bays (Schneider et al. 1997). The variability and relative precision surrounding weekly density estimates of juvenile cod in nearshore regions currently remain uncertain. The current study presents an opportunity to evaluate sampling time (i.e., weekly intervals) as a factor affecting catch rates and precision (i.e., coefficient of variation) of mean density estimates obtained from standardized beach seine samples. Evaluating the variation of mean density estimates obtained from weekly sampling with a beach seine in the coastal marine environment is important. For example, recent studies have identified two to three temporally spaced settlement pulses of age 0 cod in coastal Newfoundland (Methven and Bajdik 1994; Methven 1997; Chapter 2) and it is not clear how sampling time (before, during, or after a settlement pulse) influences the precision of density estimates. High precision is desirable since low variability is a prerequisite for meaningful interpretation of among-year patterns. In this study, I also evaluated the relative precision of weekly density estimates of age 0 cod in Goose Cove.

MATERIALS AND METHODS

Study area

A description of the movement levels, spatial distribution, behaviour, and abundance of demersal age 0 cod in the nearshore environment was obtained from capture-mark-recapture experiments and seasonal sampling carried out at Goose Cove (Sites 1-4, Fig. 3.1; 47°51' N, 53°54' W) and across from the community of Sunnyside (Sites 5-7, Fig. 3.1; 47°51' N, 53°55' W). Both study areas are located in Bull Arm of Trinity Bay, Newfoundland.

The shoreline of Bull Arm is typical of the northeast coast of Newfoundland, consisting largely of steep cut banks with narrow beach areas, where present. Bull Arm is protected from the open ocean, and has a mean tidal amplitude of approximately 1.2 m. The nearshore zone at the Sunnyside study location is dominated by a relatively flat and gradual sloping bottom. Bottom depth in the nearshore zone increases gradually to 5-10 m, forming a ledge that extends 100-500 m from shore, at which point depth increases sharply (20-50 m). Substrate type within the 5-10 m depth zone was largely comprised of sand/gravel (0.1-2.0 cm) and cobble (2.0-25 cm), with sparse patches of vegetation. There were also various sized clusters of rocks (25-100 cm) and boulders (>100 cm) that formed narrow (20-50 m) rocky reefs extending 20-50 m from shore.

Goose Cove is a shallow, well protected cove with a surface area of about 24.5 hectares. Differences in overall depth allow a separation of the cove into two distinct regions. The first region is located at the head of the cove (shaded area, Fig. 3.1), where the maximum low tide depth is about 0.7 m. The bottom type in this area is comprised of sand and silt (≤0.1 cm) deposited by a stream entering from the east. Cod were not observed in this region during the day. The remainder of the cove forms a large basin that can be separated into two distinct habitat types. A substrate of mainly sand/gravel extends to a distance of 30 to 60 m from shore, and eelgrass is distributed throughout this zone at varying degrees of bottom cover to a depth of about 5.0 m. The substrate in the central region of the cove is comprised of sand, silt, and mud (≤0.1 cm). Rocks and boulders are deposited along the north shore at the entrance to the cove. This rocky reef extends 20-50 m from shore and continues for about 1 km along the northwest shore of Bull Arm toward Site 5 (Figure 3.1). The bottom type at the south shore entrance to the cove is largely of sand, gravel, and cobble, and this substrate type continues to dominate for at least 1 km along the southwest shore of Bull Arm.

All sample sites were marked on shore (i.e., metal stakes and flagging tape) and the bottom area sampled at each site was standardized to cover approximately 800 m^2 (16 m × 50 m). To reduce the affect of tidal phase on habitat types sampled at each site the sample series at each location (i.e., Sites 1-4 and Sites 5-7) was conducted within 1-2 h of mid-flood or mid-ebb tide. In Goose Cove, low tide depth at 50 m from shore was 3.0 to 8.0 m and eelgrass cover was 25 to 75% for Sites 1 to 4 (Fig. 3.1). The maximum low tide depth 50 m from shore at the Sunnyside sampling sites was 3.0 to 8.5 m (Fig. 3.1). There was no vegetative cover at Site 5, macro algae (*Fucus* spp.) cover at Site 6 was low (<5%) and Site 7 had approximately 5% eelgrass cover. Vegetative cover was similar at all sampling sites in 1994 and 1995.

Juvenile cod sampling

A beach seine with headrope and footrope lengths of 24.4 and 26.2 m, respectively, was used to collect cod. The seine was made from a knotless nylon netting with a stretched mesh size of 19 mm in the wings and belly, 13 mm in the codend, and a 1.5 m length of 9 mm mesh was attached to the codend. A 75 cm aluminum pole was attached to each wing to aid in keeping the wings vertical while hauling the net to shore and a 55 m tow-rope was attached to each pole.

The net was deployed from a small (6 m) motorized boat at a distance of 50 m from shore, then retrieved at a constant and even rate by two individuals standing 16 m apart on the shore. During each set, the tow-ropes were located in the same marked locations on shore, thereby keeping the position sampled at each site fairly constant. The seine sampled the lower 2 m of the water column. Fish were placed in a large tub filled with seawater and sorted by age-class and settlement phase (i.e., recently settled and post-settled).

Nearshore studies on the northeast coast of Newfoundland indicate that there are two to three temporally spaced autumnal influxes of recently settled cod (Methven and Bajdik 1994; Methven 1997; Chapter 2). In coastal regions, recently settled cod typically lose their pelagic pigmentation within 1-2 weeks post-settlement (Tupper and Boutilier 1995a). In the current study, recently settled cod (3.8 to 6.5 cm standard length; SL) were distinguished by a barred or checkerboard pigmentation pattern on a pale background and a silvery underbelly. Post-settled juveniles (>5.0 to 7.0 cm SL) are mottled, heavily pigmented with a white underbelly, and may also be identified by the presence of encysted metacercaria of the digenean *Cryptocotyle lingua*.

Capture-mark-recapture experiments

Two capture-mark-recapture experiments were conducted in Goose Cove during 1994. The first experiment began on September 24 when 667 post-settled age 0 cod were marked by clipping the dorsal and ventral lobe of the caudal fin. A second experiment was initiated on November 13, when 654 post-settled age 0 cod were marked by clipping the dorsal lobe of the caudal fin. Both marking programs were conducted on cod from the first settlement pulse (see results) and were restricted to cod captured at a single site (Site 2; Fig. 3.1). Once captured, cod were held in 150 litre tanks that allowed a free flow of seawater. Cod were marked, placed in recovery tanks, and monitored for at least one hour before being released at Site 2.

A single capture-mark-recapture experiment was conducted in Goose Cove during 1995. A total of 1188 age 0 cod from the first settlement were marked on September 16, by clipping the dorsal lobe of the caudal fin. This marking program was conducted in the same manner to that outlined for 1994.

Age 0 cod were counted weekly from September to December, in 1994 and 1995, from a series of samples conducted at four haphazardly chosen sites in Goose Cove (Sites 1-4; Fig. 3.1). Each sample series was conducted during the day and completed quickly, always within 2.5-h. The weekly sample series in Goose Cove produced four replicate capture rate estimates. The variation among these capture rate estimates is expected to be high if the degree of aggregation is high in the Goose Cove population (Downing 1979; 1986; Pinel-Alloul et al. 1988; Rasmussen and Downing 1988). That is, if on any given date the sample sites in Goose Cove contain very few or very many individuals the variance of the age 0 cod population will be greater than the mean. I tested for aggregated spatial distributions of age 0 cod by fitting the function $\log_{10}S^2 = a + b \log_{10}M$ by method of least squares regression, where S^2 and M are variance and mean density, and a and b are fitted coefficients for this relationship (Taylor 1984; Downing 1986; Rasmussen and Downing 1988; Johannes 1993). I considered age 0 cod to be aggregated when $b > 1$, uniformly distributed when $b < 1$, and randomly distributed when $b = a = 1$ (Elliott 1977; Downing 1979; 1986; Rasmussen and Downing 1988; Johannes 1993).

The weekly sample series in Goose Cove produced 13 and 10 estimates of the relative abundance of age 0 cod in 1994 and 1995, respectively. Relative precision of the abundance estimates was compared between the weekly sample series by calculating the sample series coefficient of variation (CV = 100 × SD/mean, where SD [standard deviation] and mean refer to untransformed catch rate data).

At Sunnyside, a single capture-mark-recapture experiment was conducted on cod from the first settlement pulse in 1994. This area was identified as a suitable sampling location on October 22, at which time 624 age 0 cod were marked at Site 6 (Fig. 3.1) by clipping the ventral lobe of the caudal fin. Pre- and post-marking procedures were the same as those outlined for the Goose Cove experiments. In 1995, there were too few age 0 cod captured at Sunnyside to conduct capture-mark-recapture experiments.

Limited beach areas required a modification of the sampling design at Sunnyside. Cod were sampled at Site 6 for eight consecutive weeks (October 22 to December 10) during 1994. Each weekly sampling program consisted of a series of five consecutive hauls conducted during the day at Site 6. Each sample series was completed quickly, always within 2-h. Cod collected during each haul were held in separate 150 litre tanks until all hauls were completed. Cod were counted then released at Site 6. Secondary sample sites at Sunnyside (i.e., Site 5 and Site 7; Fig. 3.1) were sampled approximately fortnightly (i.e., October 30, November 13, November 26 and December 10) during the day in 1994.

In 1995, all Sunnyside sites were sampled during the day from September to December. Sampling at Site 6 was the same as in 1994, and Sites 5 and 7 were sampled throughout the study.

Data obtained during the capture-mark-recapture experiments were used to estimate the population size of cod from the August-September settlement pulse for Goose Cove and the shallow water ledge at the Sunnyside study area. Population size was estimated using the simple single-census Petersen type capture-mark-recapture formula (Ricker 1975) which states $N=MC/R$, where N is the estimate of population size, M is the number of marked fish in the population, C is the total number of fish in the recapture sample, and R is the number of marked fish recaptured in the sample, C. Bias associated with estimates of N are negligible when MC exceeds $4N$ or if R is at least 7 (Robson and Regier 1964). These criteria were met during the capture-mark-recapture experiments at Goose Cove and Sunnyside. Differential mortality among marked and unmarked cod and immigration of newly settled cod that are not detected in the samples may also bias estimates of N. In an attempt to reduce the influence of these factors, N was estimated 6-8 days after the initial release of marked post-settled cod.

Fifty age 0 cod were haphazardly removed from the weekly catches at Site 2 in 1994 and 1995 and at Site 6 in 1994. These samples included both recently settled and post-settled cod. When present in high numbers, an additional sub-sample of up to 25 recently settled cod were also taken from the samples. Cod were killed (MS 222), frozen (dry ice), and later thawed for measurement of standard length (± 1.0 mm).

Depletion sampling

Depletion sampling, involving consecutive standardized beach seine hauls at a single site, can be used to estimate fish density (Raleigh and Short 1981). However, if movements of fish onto or through the site being sampled are substantial, then two or more peaks may occur in the catch versus cumulative catch curves, precluding a valid density estimate. In the current study, I used plots of the catch versus the cumulative catch during consecutive standardized beach seine samples at a single site, conducted as quickly as physically possible, as an indirect measure of lateral movements of age 0 cod. High sampling efficiency of the beach seine used in this study (Gotceitas et al. 1997; Methven 1997), suggests that catchability contributes little to the variation in catch between consecutive hauls at the same site. The sample series of five consecutive hauls conducted at Site 6 (Sunnyside) throughout the 1994 sampling season and a series of 12 consecutive hauls conducted within a 4-h period (10:00 - 14:00 h) at Site 2 (Goose Cove) during the 1995 marking program were used for plots of the catch of age 0 cod versus cumulative catch.

Diel sampling

Diel beach seine surveys were conducted at Site 2 to determine: 1) whether marked individuals remain within the study area at night, 2) day-night differences in the mean catch of age 0 and age 1 cod, and 3) day-night differences in the spatial distribution patterns of age 0 cod. In this study, the terms "day" and "night" are defined as the periods from dawn to dusk and dusk to dawn. Samples were conducted at 3-h intervals over three 24-h periods, two in September and one in October, 1994. Low beam flash-lights, directed away from the water (i.e., placed on and directed onto the ground or directed into the bottom of the boat), were used during night sampling. Thus, effects of the artificial light source on the distribution and movement of fish at night was considered to be negligible.

Repeat samples at the same site within a short period of time (i.e., immediately after one another) are not true replicates, as the distribution and movement patterns of fish in the immediate vicinity of the site may be disrupted for a short period of time after the seining activity. I consider a three hour time period between samples to be adequate time to allow distribution and movement patterns to return to pre-sampling conditions.

Day-night differences in capture rates (i.e., number of fish per haul) of age 0 and age 1 cod were assessed using the Mann-Whitney *U* test (Siegel 1956). Day-night differences in the spatial distribution patterns of the age 0 cod populations in Goose Cove were assessed using the ratio of variance to mean density (i.e., S^2/M). The variance to mean ratio is an index of dispersion, whereby organisms are considered randomly distributed when $S^2 = M$, uniformly distributed when $S^2 < M$, and aggregated when $S^2 > M$ (Elliott 1977). The significance of the departure of the variance to mean ratio from unity (i.e., when $S^2 \neq M$) can be assessed by reference to a table of chi-squared (Elliott 1977). The following expression:

3.1) $$\chi^2 = \frac{S^2(n-1)}{M},$$

which is a good approximation to the chi-squared statistic with n-1 degrees of freedom (Elliott 1977), was used to test whether the variance to mean ratios differed significantly from unity for each light period. Because the 1993 age 0 cod catch data (also conducted at Site 2; Chapter 2) showed similar day-night patterns to those described in the current study (see results), I also utilized these data to test for day-night differences in the spatial distribution patterns of age 0 cod.

Additional sampling

Winter sampling was conducted to determine if marked cod were present at the study sites. Both study locations were resampled on February 19 and March 26, 1995. All sampling was conducted using the same gear and methodology outlined above.

RESULTS

Autumnal influxes of recently settled cod

A total of 9,522 and 3,779 age 0 cod were captured in Goose Cove during autumn of 1994 and 1995, respectively (Table 3.1). There were three temporally spaced influxes of recently settled cod in Goose Cove during 1994 and 1995 (Table 3.1, Fig. 3.2, and Fig. 3.3) In both years, the first settlement pulse began before sampling commenced. During 1994, recently settled (see definition, Chapter 2) cod represented the highest proportion of the total catch (Site 1-4 combined) on September 16. The decrease in percentage of recently settled cod on September 24 indicates that the first settlement pulse was largely complete by this time. The second settlement pulse occurred in mid-October, and coincided with the autumnal peak in total catch in 1994 (Table 3.1). Apparently, the first two settlement pulses were approximately 2 weeks earlier in 1995. For example, when sampling began in September, 1995, the proportion of recently settled cod from the first settlement was considerably lower than that observed on the same day in 1994 and the proportion of recently settled cod from the second pulse peaked 2 weeks earlier (September 30) in 1995 (Table 3.1).

The timing of the third influx was similar in both years (i.e., late November-December; Table 3.1).

Length-frequency distributions for cod sampled in Goose Cove indicate a clear size separation between cod from the first and second settlement pulses in 1994 and 1995 (Fig. 3.2 and Fig 3.3). By mid-October, 1994, both the total catch and the proportion of recently settled cod from the second settlement declined abruptly (Table 3.1). Length-frequency distributions after the decline indicate that juveniles from the first settlement pulse dominated in Goose Cove (Fig. 3.2). During 1994, smaller juveniles from the second settlement pulse were not well represented in the Goose Cove catches again until late November (Fig. 3.2). In contrast, cod from the second settlement pulse were well represented in the Goose Cove length-frequency distributions throughout the autumn of 1995 (Fig. 3.3), a year of seasonally lower total catch rates (Table 3.1) and lower estimates of abundance (*N*; see capture-mark-recapture experiments) of cod from the first settlement pulse. The third settlement pulse resulted in a clear tri-modal length-frequency distribution in Goose Cove in 1994 and 1995 (Fig.3.2 and Fig. 3.3).

Variance-mean density relationships in Goose Cove exhibited slope values >2, indicating that age 0 cod formed aggregations during the day in 1994 and 1995 (Fig. 3.4). On any given date, each sample site contained very few or very many individuals (Table 3.2), and therefore the variance of the age 0 cod populations in Goose Cove was always greater than the mean.

Peaks in the CV for the weekly sample series in Goose Cove coincided with the influxes of smaller recently settled cod in 1994 and 1995 (Table 3.1; 3.2). From these results, I conclude that the most variable estimates of relative abundance of age 0 cod, i.e., highest CV, will be obtained during the settlement pulses.

A total of 2302 age 0 cod were captured at Sunnyside from October to December, 1994 (Table 3.1). Most (92.2%) of these cod were captured at Site 6 in 1994. Tri-modal length-frequency distributions at Sunnyside (Fig. 3.5) in December were similar to those observed in Goose Cove (Fig. 3.2), indicating that all three settlement pulses were wide spread in Bull Arm in 1994. However, bimodal length distributions in October-November contrasted with the length distributions for Goose Cove (Fig. 3.2 and 3.5), indicating that cod from the second settlement pulse were well represented at the no-eelgrass site at Sunnyside in 1994. The seasonal catch of age 0 cod was considerably lower at Sunnyside in 1995 (Table 3.1). In 1995, the highest catches were in eelgrass at Site 7, which is where most (79.4%) of the cod were captured.

Capture-mark-recapture experiments

Marked post-settled cod from the first settlement pulse were recaptured in Goose Cove over a 12 week period in 1994 and 1995 (Fig. 3.6). Post-settled cod marked in Goose Cove were not recaptured at Sunnyside in 1994 or 1995 and cod marked at Sunnyside were not recaptured in Goose Cove. Thus, there was no evidence of migration between study locations that were separated by approximately 2.6 km of coastline.

The weekly catch of age 0 cod at each site within Goose Cove was expressed as a percentage of the total weekly catch of age 0 cod in a sample series (i.e., Sites 1-4) in 1994 (Fig. 3.7a) and 1995 (Fig. 3.7c), and the weekly catch of marked cod at each site was expressed as a percentage of the total weekly catch of marked cod in a sample series in 1994 (Fig. 3.7b) and 1995 (Fig. 3.7d). Comparable weekly shifts in distribution of marked and unmarked cod and the recapture of marked cod at all sample sites in 1994 and 1995 indicates mixing among marked and unmarked cod and frequent movement between sites. On September 24 1994, all marked cod were released at Site 2 at 11:00 hours and within two to three hours marked individuals were captured at all four sites sampled in Goose Cove. Sites 1 and 3 had relatively low eelgrass cover (25 and 30%, respectively) and seemed to represent peripherally used eelgrass habitat in Goose Cove, generally supporting a relatively small proportion of the total weekly catch in both years (Fig. 3.7; 14.3 to 32.3% in 1994; 7.9 to 23.3% in 1995). Cod appeared to be more highly concentrated in the vicinity of sites that exhibited the highest eelgrass cover (i.e., Site 2, 75% and Site 4, 65%) and distribution among these sites changed in a converse manner in both years (Fig. 3.7).

At Sunnyside, one age 0 cod (unmarked) was captured at Site 5 during the fortnightly collections conducted in 1994. Age 0 cod were captured at Site 7 during all of the fortnightly collections (October 30, 4 cod; November 13. 62 cod; November 26, 17 cod; December 10, 95 cod). Cod were captured at Site 6 throughout the Sunnyside capture-mark-recapture experiment in 1994 (Table 3.2). There was high temporal variation in the catch at Site 6 at the scale of hours (haul 1 through 5) and weeks, a result comparable to that observed in Goose Cove.

Two cod previously marked at Site 6 were recaptured at Site 7 on November 13, and one marked cod was recaptured at Site 7 on December 10. Marked cod were recaptured at Site 6 over a period of seven weeks (Table 3.3). The percent recapture of marked cod, averaged over all five hauls at Site 6, showed little change from October 30 to November 05, 1994 (Table 3.3), however, the total catch of age 0 cod almost doubled over the same time period. Marked cod were recaptured in all five hauls on October 30, November 05, and November 26, and two seasonal peaks in the total catch (November 05 and November 26) coincided with peaks in the total number of marked cod recaptured (Table 3.3). Overall, these results indicate frequent movements and mixing of marked and unmarked cod at Sunnyside.

Capture-mark-recapture abundance estimates indicate that cod from the first settlement pulse were 4.9 times more abundant in Goose Cove in September 1994 than September 1995 (Table 3.4). This difference was significant, as the 95% CI's did not overlap between years. The abundance estimates for cod from the first settlement pulse depict a decline of approximately 50% in Goose Cove by mid-November of 1994. However, overlap in the 95% CI's indicates that the September-November abundance estimates did not differ significantly. During 1994, cod from the first settlement pulse were significantly more abundant in Goose Cove than at Sunnyside as the 95% CI's did not overlap between locations (Table 3.4).

Significant (i.e., non-overlapping 95% CI) year-to-year differences in seasonal mean density were also apparent within the study locations. Relative indices of abundance (catch per unit area; Sites 1-4), calculated as the seasonal mean (± 95% CI) of both recently settled and post-settled cod, were 2.1 times higher in 1994 (0.230 ± 0.039) compared to 1995 (0.112 ± 0.020). Fish per unit area of habitat sampled at Sunnyside from October 22 to December 10, were 32 times higher in 1994 (0.064±0.040) than 1995 (0.002±0.002).

The general assumption underlying capture-mark-recapture methods of estimating fish population size by netting is that initially all individuals in the population have the same probability of being captured, and that this probability remains unchanged between sampling periods (Hamersley 1953). Hamersley (1953) states this as: "The catch is considered as a random sample of individuals from the population, i.e., each individual in the population has an equal chance of being captured on any given occasion irrespective of age, health, type, etc., and of any previous captures it may have suffered". As noted by Dice (1941), emigration, immigration, and reproduction will influence errors in estimates of population size even if the above premises are met. If individuals are being tagged, there should be no loss of tags, for this would inflate the estimate of population size and a lost tag would be equivalent to immigration or reproduction.

Two specific assumptions underlying the Petersen method of estimating population size are: 1) the proportion of tagged individuals is constant (this means that no new individuals are added to the population due to immigration or reproduction) and 2) the sampling may be by live-netting or by dead-netting (De Lury 1951). The Petersen estimate is not affected by natural mortality (De Lury 1951). If mortality occurs, and the mortality rate for the marked and unmarked individuals is the same then the ratio N/M (population size/number of marked individuals previously released) would not change. If reproduction or immigration occur or the mortality rate of the tagged individuals is greater than for the untagged individuals the ratio C/R (number in census sample/number of marked individuals in the census sample) will be too large. This will lead to over estimating the population.

In this study, only post-settled cod were marked and newly settled cod can be distinguished from the former for up to two weeks after settling (Tupper and Boutilier 1995a). Hence, bias associated with immigration was likely minimal for abundance estimates obtained for Goose Cove as the marking and census sampling took place between the first and second influx of newly settled cod in September 1994 and 1995 (Table 3.2) and cod marked in November, 1994 were from the first influx (Fig. 3.2; see also Fig. 3.10 in section on additional sampling). In 1994, cod were marked at Sunnyside during the second influx of newly settled cod, which may have resulted in an overestimate of abundance as it appears that some newly settled cod had acquired post-settled characteristics by the time the census sample was carried out (i.e., October 30; Fig. 3.5).

In an attempt to reduce the possibility of over estimating abundance due to unrealized mortality and trauma of being released at a different location, marked cod were monitored for at least 1 hour and released at the capture site during all capture-mark-recapture experiments. Two mortalities (2/669 = 0.3%) occurred during the September, 1994 marking program in Goose Cove. These fish were apparently killed by shifting rocks used to stabilize the recovery tanks held *in situ*. There were no mortalities discovered during the remaining marking programs conducted at Goose Cove or Sunnyside. All fish appeared healthy when released; they maintained equilibrium and did not hesitate to move into deeper water at the release site. Further, no mortalities were recorded during laboratory marking experiments that involved fin clipping (caudal, anal, and dorsal) and holding similar sized age 0 cod for periods of 2-4 weeks. Thus, it appears that the mortality of marked individuals was not greater than unmarked individuals. The relatively high proportion of marked cod recaptured at Site 2 shortly after marking on September 24 (see Table 3.5, section on diel sampling) suggests that some of the marked fish may have undergone a period of decreased activity for a short time after release. For this reason, all capture-mark-recapture abundance estimates were obtained from catch data conducted approximately one week (6-8 days) after the release of marked fish. A period of decreased activity is not uncommon for fish that have undergone marking procedures (Ricker 1975). Decreased activity of marked fish may reduce their risk to predation, which may result in underestimates of abundance.

Depletion sampling

A substantial peak (i.e., representing over 75% of catch in first haul) in the plot of catch versus cumulative catch at Site 2 during the 1995 marking program indicates lateral movement in eelgrass habitat during day-light hours (Fig. 3.8). Substantial peaks (i.e., catch always greater than the first haul) in seasonal plots of the catch versus the cumulative catch illustrate that substantial lateral movement also occurred in no-eelgrass habitat during day-light hours (Fig. 3.9). Each plot of catch versus cumulative catch exhibited at least one substantial increase in catch after the first haul, and a second, smaller increase, was observed in three of the eight plots (Fig. 3.8 and Fig. 3.9). The sudden increases in catch did not occur until the third (two sample series), fourth (three sample series), or seventh haul (one sample series) and a substantial period of time (1-2 h) had elapsed since the first haul. Given the high capture efficiency of the seine (Gotceitas et al. 1995; Methven 1997) and the relatively high catches during the sudden increases in catch, which did not occur until the third, fourth, or seventh haul, I interpret these peaks in catch to represent clumped lateral movements of age 0 cod. This interpretation is supported by evidence of aggregated spatial distributions (Fig. 3.4).

Diel sampling

Marked age 0 cod were recaptured in Goose Cove throughout the diel period, indicating that they occupy the same general areas at night that they occupy during the day (Table 3.5). The catch of age 0 cod was always higher during the day, declined after sunset, remained low throughout the night, then increased sharply at dawn (Table 3.5). Conversely, the catch of age 1 cod increased at night. The Mann-Whitney U test revealed a significant difference in capture rates between light periods for age 0 cod (September 24, $U = 0$, $p = 0.008$; September 30, $U = 0$, $p = 0.008$; October 08, $U = 0$, $p = 0.018$) and age 1 cod (September 24, $U = 0$, $p = 0.008$; September 30, $U = 0$, $p = 0.008$; October 08, $U = 0.018$, $p = 0.008$).

Day-night comparisons of the variance to mean ratios (S^2/M) for age 0 cod populations sampled during diel surveys at Site 2 in 1993 and 1994 show a greater departure from unity during the day (Table 3.6). High chi-square values (i.e., significantly >1) indicate that age 0 cod formed aggregations in Goose Cove during both light periods on three of four diel surveys conducted in 1993 and one of three diel surveys conducted in 1994 (Table 3.6). High chi-square values (i.e., >1) during the day on December 13, 1993 and September 24 and 30, 1994 are indicative of aggregated spatial distributions during the day, however, chi-square values for samples conducted at night indicate that the variance to mean ratios did not differ significantly from unity (i.e., 1.0; Table 3.6). The consistently higher mean catch rates, sudden increases in catch, and higher variance to mean ratios observed during the day-light period for all diel surveys considered (i.e., 1993-94) suggest that age 0 cod in Goose Cove occurred in relatively larger more active groups during the day. Conversely, consistently lower mean catch rates, lack of sudden increases in catch, and comparatively lower variance to mean ratios suggest that age 0 cod form relatively smaller less active groups in Goose Cove at night. Variance to mean ratios not significantly different from unity during three of seven (43%) of the diel surveys suggest that it is not uncommon for individual age 0 cod to be randomly distributed at night. Overall, the combined results from the diel surveys in eelgrass habitat provide evidence of a local nocturnal dispersal by age 0 cod.

Additional sampling

Landward ice precluded collections at Sites 1-4 (Goose Cove) and Sites 5 and 6 (Sunnyside) during February, 1995. Fifteen age 1 and five age 2 cod (formerly age 0 and age 1, respectively) were captured at Site 7 at a water temperature of −1.2°C in February. In March, 1995, a total of 131 age 1 and twelve age 2 cod were captured at Site 4 in Goose Cove at a water temperature of 0.5°C. The length-frequency distribution of age 1 cod was tri-modal (Fig. 3.10) and similar to that observed on December 10, 1994 (Fig. 3.2). A shift in length for all three size-classes suggests that growth occurred between the sampling interval December to March. Eight (6.1%) of the age 1 cod captured in March were initially marked at Site 2 on November 13, 1994. The length-frequency distribution of marked cod indicates that these fish were from the first settlement pulse (Fig. 3.10).

DISCUSSION

This study documents localized movements of post-settled age 0 cod within shallow (<8 m) nearshore waters of Newfoundland. The age 0 cod studied did not appear to be site attached as reported in coastal waters of Nova Scotia (Tupper and Boutilier 1995a). Movements of post-settled age 0 cod in nearshore waters of Newfoundland were, however, somewhat restricted in both eelgrass and no-eelgrass habitat as marked cod remained in the vicinity of the initial capture site for several weeks after release. In Goose Cove, post-settled age 0 cod moved frequently between eelgrass sites that were a few hundred metres apart, while the recapture of marked cod approximately 1.2 km from the no-eelgrass release site at Sunnyside indicates that post-settled age 0 cod may move several hundred metres in shallow coastal waters of Newfoundland. There was no evidence of movement of post-settled age 0 cod between the Goose Cove and Sunnyside study areas which were separated by approximately 2.6 km of coastline.

The fact that some post-settled age 0 cod move several hundred metres in shallow coastal waters suggests that factors other than the distance between study areas, such as greater risk of predation in deeper coastal waters, may influence their distribution and movement in the coastal environment. Post-settled age 0 cod appear to be concentrated at depths of 4-7 m in coastal Newfoundland (Methven and Schneider 1998), and there is likely a greater risk of predation in deeper coastal waters, particularly from older conspecifics which prey on yearling cod (Bogstad et al. 1994; Dietrich 1998; Chapter 2) and tend to be more prevalent at greater depths (Keats et al. 1987; Clark and Green 1990; Keats 1990; Cote et al. 1998). This study corroborates recent findings (Methven and Schneider 1998) on limited depth distribution of age 0 cod within coastal waters of Newfoundland, as the cod studied remained in the vicinity of sites that lie within the 5 m depth contour for several weeks after settling. The recapture of marked cod in March suggests juveniles may also remain in these shallow water regions over their first winter. Post-settled juvenile cod also remained localized over their first winter in coastal waters of the northeast Atlantic; Loch Torridon, Scotland (Hawkins et al. 1985) and Masfjorden, Norway, (Smedstad et al. 1994).

It has been suggested that the use of shallower waters by age 0 cod reduces predation by older conspecifics (Riley and Parnell 1984). In this study, there was no evidence of along-shore movement by post-settled age 0 cod between sites where the water depth away from shore increased relatively sharply to 5-20 m. It is possible that limited shoreline access for sampling with the beach seine affected the results. Nevertheless, in coastal areas where potential predators are more prevalent in deeper waters, it is conceivable that shallow water coves (i.e., Goose Cove) and shallow water ledges (i.e., Sunnyside) act as refuge areas for age 0 cod settling in coastal waters. Larger conspecifics may generally avoid these shallow water areas during the day because they are at greater risk from their own diurnal predators (i.e., piscivorous birds). The initial marking programs in Bull Arm were conducted at beach sites where age 0 cod could be captured in high numbers with a beach seine (i.e., Site 2 and Site 6). Subsequent recapture sampling was conducted at these sites and shoreline locations that also provided adequate physical conditions for sampling with the beach seine (i.e., beaches and lack of physical obstructions in the water and on shore). Unfortunately, determination of movement outside of the relatively shallow waters of Goose Cove was restricted to the closest beach site to the north entrance of the cove, which was Site 5 (~1.5

km away), while the closest suitable beach site to the south entrance was over 4 km away. Similarly, at Sunnyside, sampling was largely restricted to shallow water sites. Additional data would have to be collected on age 0 cod and potential predators, not only by beach seine, but possibly by studies that combine diel diet analysis of potential predators with SCUBA observations, ultrasonic tagging, small mesh cod traps, and (or) echo-sounder location in order to test the hypothesis that along-shore movements of post-settled age 0 cod are restricted by water depth and presence of potential predators.

Slope values for the 1994 and 1995 variance-mean density relationships of replicate samples conducted at four sites in Goose Cove indicate that age 0 cod form aggregations in shallow nearshore waters during the day. Aggregated spatial distributions, high within and between site variation in catch at the scale of hours and weeks, and two or more peaks in the catch versus cumulative catch curves provide evidence of clumped lateral movements of age 0 cod. Independent observations of shoals of age 0 cod in coastal Newfoundland (see below) lead me to interpret these patterns in the catch rates to reflect social behaviour by age 0 cod in the form of mobile shoaling aggregations.

A shoal, which by definition is comprised of three or more fish, is generally considered a relatively unorganized form of social behaviour while highly organized and polarized swimming behaviour defines a school (Pitcher 1983). By convention, some social attraction among individuals is required for a group to be considered a shoal or a school, whereas fish that are mutually attracted to food or other resources are an aggregation (Freeman and Grossman 1992). Aggregations may also simply be a species-specific function related to density, as suggested for many other animal species (Taylor 1984). Unfortunately, without direct observation, shoaling behaviour can only be inferred from beach seine sampling and variance-mean density relationships. However, shoals of demersal age 0 cod have been reported in coastal waters of the north Atlantic (Olsen and Soldal 1989; Tupper and Boutilier 1995a), and more importantly, SCUBA divers conducting juvenile cod distribution studies in Goose Cove and environmental affects monitoring in Goose Cove and numerous other small coves within Bull Arm have observed shoals of demersal age 0 cod (pers. comm., Dr. V. Gotceitas, J. Christian, and E. Lee). These shoals were observed in shallow (<6 m) water, either swimming away from the observer or as stationary and mobile groups approximately 1-2 m up in the water column. Laboratory investigations on predation risk of cod collected in the nearshore environment of Newfoundland (Gotceitas and Brown 1993) report the formation of loose groups of age 0 cod up in the water column in the absence of a predator and subsequent movement out of the water column when a predator (older conspecific) was introduced. The decision to either shoal or seek refuge in the presence of a potential predator may be related to a number of factors including, local cohort abundance, predator abundance, size of the predator, and in laboratory experiments, size and depth of the experimental tank. For example, in the presence of few similar sized conspecifics, Cyprinids seek refuge from a predator, but shoal when enough conspecifics are present and studies suggest that small shoal size provides less protection from predators (Magurran and Pitcher 1983; Pitcher 1986).

Age 0 cod remained localized after settling in coastal regions of St. Margaret's Bay, Nova Scotia (Tupper and Boutilier 1995a). In Nova Scotia, the age 0 cod studied exhibited a uniform pattern of settlement among habitats and locations and they also exhibited relatively high site fidelity, being site attached and territorial (Tupper and Boutilier 1995a; 1995b). Differences in the movement levels, spatial distribution patterns, and behaviour between age 0 cod examined in my study area and the study area in Nova Scotia may be related to the prevalence of certain predators and how differing foraging behaviours of dominate predators influence the ability of age 0 cod to detect predation risk. For example, studies indicate that the behaviour of prey species is flexible in response to the magnitude of perceived risk from predators (Milinski 1986; Gilliam and Fraser 1987; Johnson and Dropkin 1993; Lima and Dill 1990). Unlike this study, there was no mention of older age-classes of cod inhabiting the study area examined by Tupper and Boutilier (1995a; 1995b). Sculpins, which rely on crypsis and are generally lie-in-wait ambush predators, appeared to be the major predator influencing age 0 cod survival in Nova Scotia (Tupper and Boutilier 1995a; 1995b). Two gadids, *G. morhua* and *G. ogac*, which are generally actively swimming and relatively visible while foraging, were the most prevalent potential predators of age 0 cod in my study area (i.e., Chapter 2) and older juveniles of both species consume yearling cod (Bogstad et al. 1994; Fraser et al. 1996; Dietrich 1998; Chapter 2). Cannibalism is common when distributions of small and large cod overlap (Bogstad et al. 1994) and age 0 cod and older (larger) conspecifics are commonly captured together in beach seine hauls in shallow coastal waters of Newfoundland (Gotceitas et al. 1997; Ings et al. 1997; Schneider et al. 1997; Dietrich 1998; Chapter 2; this study). In coastal Norway, where age 0 cod form large shoaling aggregations that appear to limit their movements to 1-2 km of the coastline, older age-classes of cod (i.e., age 1-2) are also frequently captured together with age 0 cod (Olsen and Soldal 1989). As noted above, shoaling in prey fish has been shown to be related to density of prey fish and their predators (Magurran and Pitcher 1987; Lima and Dill 1990; Johannes 1993). I suggest that high local densities of demersal age 0 cod and overlapping distributions with older conspecifics in coastal areas leads to social behaviour by age 0 cod and somewhat limited spatial movements (e.g., Goose Cove or along shallow water ledge at Sunnyside) in shoals while in search of food. Contrasting habitat preferences of demersal age 0 cod in coastal Newfoundland and Nova Scotia have also been attributed to greater predation risk from older conspecifics in coastal Newfoundland (Gotceitas et al. 1997). If movement levels and behaviour of age 0 cod are related to the prevalence of certain predators then it is conceivable that both social and territorial behaviour may be observed over relatively small spatial scales. That is, in coastal areas where older year-classes of cod or other actively swimming predators are generally absent and structurally complex habitat is present, age 0 cod may be site attached and territorial (Tupper and Boutilier 1995a). However, sympatry with older conspecifics may result in social behaviour and frequent, yet localized movements as suggested by this and other studies (Olsen and Soldal 1989) on the distribution and abundance of age 0 cod in coastal waters.

Laboratory experiments indicate that the presence or absence of older year-classes of cod can affect the habitat type selected by age 0 cod (Gotceitas and Brown 1993; Gotceitas et al. 1995; Fraser et al. 1996) and the prevalence of older year-classes of cod may give rise to social behaviour and shoaling aggregations of sympatric age 0 cod (i.e., Olsen and Soldal 1989; this study). If individual age 0 cod are typically solitary and site attached (Tupper and Boutilier 1995a), then they should only shoal when it is advantageous to do so (Pitcher 1986). Most fish shoals are unstable, even throughout the day (Freeman and Grossman 1992;

Noda et al 1994), and the decision to join a shoal will depend on local biotic factors such as cohort abundance, prey availability, and predation risk. Circumstances that lead to shoaling, shoal size, and the level of movement (i.e., few hundred metres vs 1-2 km) in nearshore waters by age 0 cod may vary with the strength of each settlement pulse, which may vary from one location to another within and between years. As a result, in areas where age 0 cod are locally abundant and shoaling is prevalent, abundance estimates at a given sampling site may vary substantially over relatively short periods of time (i.e., hours and days). However, in areas where age 0 cod are effectively sessile and uniformly distributed (Tupper and Boutilier 1995a; 1995b) abundance estimates may be less variable. Juvenile fish exhibit increased exploratory behaviour in poor habitats (Sale 1969) and failure to account for local variation in movements and behaviour during sampling may introduce uncertainty in age 0 cod abundance estimates. However, whether these kinds of behavioral differences bias estimates of the mean is unknown. If shoaling is widespread in coastal Newfoundland, where the shoreline consists largely of steep cut banks with narrow beach areas, then beach seine surveys on the distribution and abundance of age 0 cod may benefit when a relatively large number of sites are sampled within a given region/habitat.

The beach seine used in this study was an effective gear for capturing age 0 cod in shallow nearshore waters, however, the variability (i.e., coefficient of variation) in the mean catch rates over four eelgrass sites in Goose Cove was high throughout the weekly sample series in 1994 and 1995. In Goose Cove, the highest variability in catch between sites was observed during the autumnal influxes of recently settled cod, which I interpret to be the result of comparatively larger shoaling aggregations of age 0 cod during settlement pulses.

This interpretation is not unreasonable, as studies document decreased risk of predation mortality of smaller fish when they shoal with larger individuals (Peuhkuri 1997). This may explain the higher variation in catch of age 0 cod during influxes of smaller recently settled cod. Increased variability in beach seine catch rates during the settlement pulses of age 0 cod may increase the uncertainty of relative abundance estimates made at this time. Large aggregations and frequent movements within nearshore habitats may, in part at least, explain why studies that use the same gear (i.e.. Schneider et al. 1997) have observed that widely spaced beach seine sites with high age 0 cod densities in some years can have low densities in years with high abundance.

Most fish shoals are relatively unstable and few species maintain groups throughout an entire 24-hour period (Helfman 1986; Freeman and Grossman 1992). A comparison of the ratios of variance to mean density for seven paired day-night samples conducted at a single eelgrass site in Goose Cove indicate that age 0 cod were aggregated during the day, while substantial peaks in catch versus cumulative catch curves and weekly shifts in distribution among closely spaced sampling sites indicate that they are mobile. Ratios of variance to mean density indicate that age 0 cod were also aggregated at night on four of seven day-night comparisons. However, mean catch rates were lower at night over all day-night comparisons tested and there was a lack of a significant divergence from unity in the ratios of variance to mean density during three of the nocturnal sample series. Given that marked age 0 cod were recaptured in Goose Cove throughout the night and the catch of both marked and non-marked cod increased at dawn, I interpret these day-night patterns in the mean catch rates and variance to mean ratios to be due to reduced activity and a local dispersal by shoaling aggregations of age 0 cod at night.

The hypothesis of a nocturnal dispersal by age 0 cod is consistent with echo-sounder studies that document diurnal shoaling aggregations of age 0 cod in coastal regions of Norway (Olsen and Soldal 1989) and increased catch of age 0 cod in very shallow (1.2 m) waters at night (Methven and Bajdik 1994; Chapter 2). The hypothesis of a nocturnal dispersal by demersal age 0 cod in nearshore regions of Newfoundland is also supported by recent documentation of a strictly diurnal foraging cycle (Chapter 2). The diurnal foraging cycle appears to be an avoidance strategy related to increased abundance and foraging activity of 1 to 3 year old conspecifics in shallow coastal waters at night. However, both age 0 and age 1 cod are commonly captured over the same habitat during the day in shallow coastal waters of Newfoundland (Gotceitas et al. 1997; Chapter 2; this study). Given that intercohort cannibalism has been documented for 1 to 3 year old cod in the wild (Bogstad et al. 1994; Dietrich 1998; Chapter 2), I suggest that age 0 cod shoal near refuge sites in nearshore regions of Newfoundland during the day to increase detection of age 1 cod and enhance foraging success and move out of the water column and cease foraging at night due to increased shoreward movement of older conspecifics and reduced visual ability to coordinate in groups. Limiting shoal movements to relatively shallow water refuge sites (i.e., eelgrass in Goose Cove and rocky reefs at Sunnyside) would provide a means of evading predator attacks and may also reduce predator encounter rates. Lower light levels and reduced visual ability to coordinate in groups can cause prey fish to reduce levels of aggregation at night (Whitney 1969; Hunter and Nicholl 1985; Glass et al. 1986). Studies show that prey fish may experience difficulty adjusting to the changing photic environment (Munz and McFarland 1977; McFarland et al. 1979) and increased activity of older year-classes of cod that move into shallow waters at dusk (Clark and Green 1990; Keats 1990; Cote et al. 1998) may be related to increased foraging success of piscivorous cod at this time. Large juvenile cod also exhibit shoreward migrations into shallow waters at dusk in coastal Sweden, and these movements are associated with increased foraging (Pihl 1982). These factors may account for a nocturnal dispersal of age 0 cod in coastal waters of the north Atlantic.

Beach seine and small bottom trawl surveys in coastal Newfoundland document increased catch of age 0 cod at night (Methven and Bajdik 1994; Methven and Schneider 1998), a result that I interpret to be consistent with a nocturnal movement out of the water column (i.e., Chapter 2) and dispersal of this age-class. Beach seine and bottom trawl surveys, based on blind random spot samples, are likely to provide less variable capture rate estimates when age 0 cod are effectively sessile and uniformly distributed (i.e., Tupper and Boutilier 1995a; 1995b). Patchy distributions and mobile concentrations of age 0 cod that are up in the water column may increase uncertainty in beach seine and bottom trawl capture rates in certain habitats, as a single change in swimming direction by a group of fish can result in large differences in catch. Demersal age 0 cod exhibit a diurnal foraging cycle and zooplanktivory in coastal waters of Newfoundland (Chapter 2), which provides evidence of a more pelagic habit and greater activity during the day, and the current findings indicate aggregative behaviour and frequent yet, localized movements of this age-class during the day. Bottom trawl studies show that the height of the vertical opening and diel movements into the water column by fish may affect the catch rates (Atkinson 1989). Diel vertical migrations have been documented for adult cod with relatively higher bottom trawl catches occurring during the day when adults are on the bottom and lower catches occurring at night when they are off the bottom (Beamish 1966; Shepherd and Forrester 1987). These patterns are not consistent, however, and the diel vertical migration pattern can be totally reversed (Casey and Myers 1998). Evidence of a converse pattern in day-night bottom trawl catch rates of age 0 cod (Methven and Schneider 1998) may in fact be related to the more demersal habit of sympatric older conspecifics during the day. Age 0 cod may avoid older conspecifics by feeding in the water column during the day and the formation of large foraging shoals (Olsen and Soldal 1989) would improve detection of patchy prey (i.e., zooplankton) and potential predators (Pitcher 1986; Magurran and Higham 1988; Lima and Dill 1990).

If the distribution of age 0 cod in the nearshore environment of Newfoundland is currently centred at depths of 4-7 m (Methven and Schneider 1998), then beach seine collections taken at very shallow water sampling sites (i.e., 1.2 m; Methven and Bajdik 1994) may not be representative of the typical daytime densities in the nearshore. However, increased abundance of age 0 cod in very shallow water at night (Methven and Bajdik 1994; Chapter 2) is consistent with the hypothesis of a dispersal and settling out of the water column in response to increased predation risk by vertically and (or) shoreward migrating older conspecifics (Beamish 1966; Pihl 1982; Shepherd and Forrester 1987; Clark and Green 1990; Keats 1990; Cote et al. 1998; Chapter 2).

Although based on small temporal and spatial scales, current results on variation in settlement strength and the distribution and abundance of age 0 cod in eelgrass and no-eelgrass habitat are consistent with the hypothesis of density-dependent habitat selection. In the present study, the presence of eelgrass was an important factor influencing the nearshore distribution of age 0 cod, a result that is consistent with findings in coastal waters throughout the north Atlantic (Tveite 1984: Støttrup et al. 1994; Tupper and Boutilier 1995b; Gotceitas et al. 1997). High settlement in eelgrass (i.e., Goose Cove) in years of high and low abundance is consistent with the hypothesis that the most suitable nearshore habitats are generally always fully utilized by age 0 cod regardless of year-class strength (Olsen and Soldal 1989). Year to year variation in abundance in no-eelgrass (i.e., Sunnyside) suggests that this habitat is less suitable, only supporting high densities of age 0 cod when more suitable nearby habitats are fully utilized.

In a year of relatively low abundance (i.e., 1995), three distinct settlement pulses of age 0 cod were apparent from length-frequency distributions in eelgrass habitat in Goose Cove during the autumnal sampling. During a year of relatively high abundance (i.e., 1994) smaller cod from the second settlement gradually disappeared from the length-frequency distributions. A density-dependent resource that is likely to be an important determinant of cod distribution is prey abundance. As such, the relatively higher local densities of age 0 cod in 1994 and competitive interactions during feeding between recently settled and post-settled cod may have caused smaller cod from the second settlement pulse to move out of Goose Cove, which would be consistent with the hypothesis of density-dependent habitat selection. However, their decline in abundance may also be explained by differential predation mortality associated with the shoreward movement of larger conspecifics at night and competition among smaller recently settled and relatively larger post-settled age 0 cod for limited shelter/resting sites at night. Evidence of a nocturnal dispersal (Olsen and Soldal 1989; Methven and Bajdik 1994; Chapter 2; this study) by age 0 cod in the nearshore and greater predation risk from older conspecifics in nearshore environments at night (Pihl 1982; Clark and Green 1990; Keats 1990; Cote et al. 1998; Chapter 2) suggests that competitive processes associated with availability of suitable shelter/resting sites may be highest for age 0 cod at night. Competition for available resting sites has been documented for diurnal fish (Robertson and Sheldon 1979), suggesting that nocturnal shelter sites may constitute resting territories. It has been suggested that when the most suitable shelter sites are already saturated age 0 cod may be forced to occupy less suitable refuge sites (Tupper and Boutilier 1995a) and as a result they may suffer higher predation mortality. Studies show that increased body size may result in a competitive advantage for age 0 cod (Tupper and Boutilier 1995a). Subsequently, in coastal regions of Newfoundland where adequate shelter sites are limited, post-settlement processes may influence the contribution of smaller cod from the later settlement pulses to the population in years/locations where strength of the first settlement pulse is high.

Studies of juvenile fish are increasingly supplying evidence that specific habitat requirements must be met in order to attain high recruitment. Current findings suggest that in coastal waters, age 0 cod shoal and feed locally during the day on or near structurally complex bottom habitat and settle on these habitats at night for protection from predators. These diel behaviour patterns appear to parallel those described for small zooplanktivorous fish inhabiting coral reefs (Helfman 1986), where predation risk is high (Hixon 1991). Behaviour patterns exhibited by age 0 cod, i.e., restricted movements in shallow nearshore waters, diurnal shoaling, and preference for structurally complex habitat, are mechanisms for predator avoidance, suggesting that predation risk is also high in coastal Newfoundland. Additional information is needed on the extent of age 0 cod predation mortality in coastal regions of the north Atlantic, such as effects of year-to-year variation in strength of autumnal settlement pulses of age 0 cod on the movement rates and extent of cannibalism by older juveniles in shallow water habitats.

The importance of cannibalism of age 0 cod by 1 to 3 year old cod may be tested by examining whether the abundance of age 0 cod follows a two or three year cycle or by simply examining whether a strong year-class will depress a following year-class. Evidence that this kind of pattern exists across numerous nearshore sites would suggest that the current (chapters 2 and 3) inferences on high predation risk from older conspecifics is representative of coastal Newfoundland and not simply site specific (i.e., Bull Arm). In fact, beach seine catches of age 0, 1, and 2 year old cod from 1959-1964 at a series of coastal sites extending over 1500 km of the Newfoundland coastline provide evidence of a strong year-class depressing the abundance of a following year-class (i.e., see results presented in Table 2 of Schneider et al. 1997). Results presented by Schneider et al. (1997) show a strong 1959 year-class of cod that remained relatively strong as age 1 cod in 1960 and as age 2 cod in 1961. The relatively strong 1959 year-class coincided with a weak 1961 year-class suggesting that a high abundance of age 2 cod may depress the abundance of age 0 cod. In addition, a relatively high and similar mean count of age 2 cod in catches conducted in 1964 coincided with a weak 1964 year-class (see Table 2 in Schneider et al. 1997). Thus, a high abundance of age 2 cod coincided with a low abundance of age 0 cod at the spatial scale of numerous sites extending over 1500 km of coastline in Newfoundland in two separate years suggesting that an extrapolation of my conclusions with regard to high predation risk of age 0 cod by older conspecifics to other coastal regions of Newfoundland may be valid.

Table 3.1. Total beach seine catches (n) of age 0 Atlantic cod and percentage of recently settled cod (%RS) at Goose Cove (Site 1-4) and Sunnyside (Site 5-7), Newfoundland from September to December, 1994 and 1995 (ns = no sample).

	Goose Cove		Sunnyside			Goose Cove		Sunnyside	
1994	n	%RS	n	%RS	1995	n	%RS	n	%RS
Sep. 16	381	33.1	ns	ns	Sep. 16	251	8.4	11	0
Sep. 24	779	3.9	ns	ns	Sep. 24	194	4.6	10	10.0
Sep. 30	890	1.1	ns	ns	Sep. 30	465	48.0	2	0
Oct. 08	1001	8.9	ns	ns	Oct. 06	442	31.0	0	0
Oct. 15	1206	21.4	ns	ns	Oct. 14	356	23.0	6	0
Oct. 22	780	4.2	716	5.9	Oct. 22	366	12.3	18	11.0
Oct. 30	789	2.5	165	18.2	Oct. 28	357	4.5	4	0
Nov. 05	716	1.3	257	3.1	Nov. 12	336	0	11	0
Nov. 13	721	0.5	114	0.9	Nov. 26	522	40.0	2	0
Nov. 19	361	0	56	0	Dec. 10	490	35.3	33	12.1
Nov. 26	545	6.4	477	1.5	Total	3779		97	
Dec. 03	680	2.6	415	5.3					
Dec. 10	718	2.4	102	1.0					
Total	9522		2302						

Table 3.2. Beach seine catches of age 0 Atlantic cod by sample date and sampling site in Goose Cove, Newfoundland, during 1994 and 1995. The seasonal mean catch and coefficient of variation (CV) for the daily mean catch across all sample sites (i.e., Site 1-4) are presented.

1994	Site 1	Site 2	Site 3	Site 4	Mean	CV	1995	Site 1	Site 2	Site 3	Site 4	Mean	CV
Sept.16	47	267	38	29	95.3	120.5	Sept.16	19	174	21	37	62.8	118.9
Sept.24	98	416	74	191	194.8	80.0	Sept.24	27	100	18	49	48.5	75.7
Sept.30	145	479	86	180	222.5	78.8	Sept.30	13	100	23	323	116.3	125.6
Oct.08	76	762	156	7	250.3	138.5	Oct.06	24	273	36	109	110.5	103.8
Oct.15	119	870	123	94	301.5	125.8	Oct.14	53	166	28	109	89.0	69.1
Oct.22	109	213	57	401	195.0	78.9	Oct.22	43	122	37	164	91.5	67.7
Oct.30	63	210	127	389	197.3	71.6	Oct.28	32	78	35	212	89.3	94.7
Nov.05	99	126	96	395	179.0	80.8	Nov.12	48	93	26	169	84.0	75.2
Nov.13	56	347	85	233	180.3	75.2	Nov.26	35	72	61	354	130.5	114.8
Nov.14	31	172	40	73	79.0	81.7	Dec.10	36	117	35	302	122.5	102.6
Nov.26	40	414	38	53	136.3	136.0							
Dec.03	64	422	74	120	170.0	99.9							
Dec.10	69	138	163	348	179.5	66.4							

Table 3.3. Beach seine catches (number/haul) of age 0 Atlantic cod during 5 consecutive hauls at Site 6 (see Fig. 3.1) in Sunnyside, Newfoundland from October to December, 1994. Values in parenthesis are percentage in catch of marked cod and ns = no sample.

Sample	October 22		October 30		November 05		November 13		November 19		November 26		December 03		December 10	
1	181	ns	27	(22.2)	66	(30.3)	7	(28.6)	2	(0)	14	(7.1)	26	(3.8)	1	(0)
2	327	ns	6	(16.6)	24	(12.5)	1	(0)	38	(7.9)	127	(9.4)	3	(0)	3	(33.3)
3	24	ns	17	(23.5)	11	(27.3)	34	(11.8)	0	(0)	17	(5.9)	325	(5.2)	1	(0)
4	70	ns	79	(21.5)	98	(23.5)	9	(22.2)	14	(14.3)	164	(6.1)	14	(7.1)	0	(0)
5	114	ns	5	(20.0)	50	(10.0)	0	(0)	2	(0)	131	(6.1)	15	(6.7)	2	(0)
Total catch	716		134	(21.6)	249	(21.7)	51	(15.7)	56	(8.9)	453	(7.1)	393	(5.1)	7	(14.3)

Table 3.4. Capture-mark-recapture abundance estimates for post-settled age 0 Atlantic cod in Goose Cove during September (GC-1994-1) and November (GC-1994-2) 1994, September 1995 (GC-1995), and at Sunnyside in October 1994 (SS-1994). *N* is the population estimate, *M* is number of cod marked in the population, *C* is the number of cod in the recapture sample and *R* is the number of marked cod in the recapture sample. The 95% confidence intervals (in parenthesis) were calculated from a Poisson frequency distribution.

Location	*R*	*C*	*M*	*N*
GC-1994-1	24	880	667	24457 (16488-38114)
GC-1994-2	17	316	654	12157 (7598-20875)
GC-1995	44	185	1188	4995 (3725-6868)
SS-1994	29	135	624	2905 (2025-4342)

Table 3.5. Beach seine catches (number/haul) of age 0 and age 1 Atlantic cod during diel sampling at Site 2 in Goose Cove, Newfoundland, September and October, 1994. Values in parentheses are the number of marked age 0 cod recaptured in the sample. Note, 667 cod were marked and released at Site 2 by 11:00 hrs on 24 September, 1994.

	September 24			September 30			October 08		
Time	Age 0		Age 1	Age 0		Age 1	Age 0		Age 1
09:00	302	ns	18	77	(11)	26	364	(20)	20
12:00	416	(79)	21	191	(13)	19	762	(25)	15
15:00	445	(75)	19	479	(13)	15	278	(14)	16
18:00	325	(22)	18	187	(5)	26	393	(7)	10
21:00*	94	(7)	35	49	(0)	27	66	(2)	33
24:00*	71	(7)	38	42	(2)	35	ns	ns	ns
03:00*	74	(2)	52	49	(2)	47	42	(1)	28
06:00*	61	(2)	39	29	(1)	38	26	(0)	32
09:00	368	(42)	29	316	(10)	20	1028	(42)	11

*Denotes nocturnal sample; ns = no sample.

Table 3.6. Mean catch (M), coefficient of variation (CV), and variance to mean rations (S^2/M) for day and night samples of age 0 cod at Site 2 in Goose Cove during 1993 and 1994. Results of chi-square (χ^2) tests of significant divergence of the of the index of dispersion (S^2/M) from unity are also presented (*df* = degrees of freedom, p = probability level, i.e., that the null hypothesis is true).

	1993								1994					
	Sep 13		Oct 04		Nov 13		Dec 13		Sep 24		Sep 30		Oct 08	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
M	494.0	56.0	150.7	25.0	364.0	54.6	291.3	22.3	371.2	75.0	250.0	42.3	565.0	44.7
CV	40.5	25.7	31.3	45.4	29.1	18.5	37.1	29.8	16.2	18.4	61.4	22.3	56.4	45.1
S^2/M	80.9	3.7	14.8	5.1	30.7	4.3	40.0	2.0*	9.7	2.6*	94.2	2.1*	179.3	9.1
χ^2	323.7	11.1	29.5	20.6	92.2	16.2	119.6	3.97	38.8	7.65	376.7	6.31	717.8	18.1
df	4	2	2	4	3	4	3	2	4	3	4	3	4	2
p	0.001	0.004	0.001	0.001	0.001	0.004	0.001	0.152	0.001	0.055	0.001	0.098	0.001	0.001

* index of dispersion (S^2/M) does not differ significantly from unity (i.e., 1.0).

Figure 3.1. Study area in Bull Arm of Trinity Bay, Newfoundland, indicating depth (m) contours and study site locations. GC = Goose Cove.

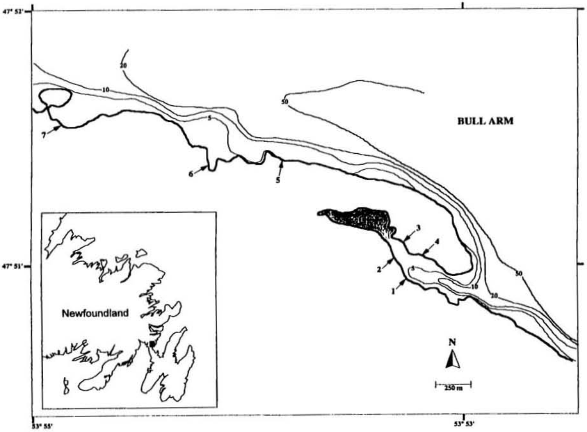

47° 52'
47° 51'
53° 55'
53° 53'
BULL ARM
Newfoundland
N
250 m
1
2
3
4
5
6
7
5
10
20
50

Figure 3.2. Length-frequency distributions for each of recently settled (hatched bars) and post-settled (solid bars) age 0 Atlantic cod in Goose Cove, Newfoundland, September-December, 1994.

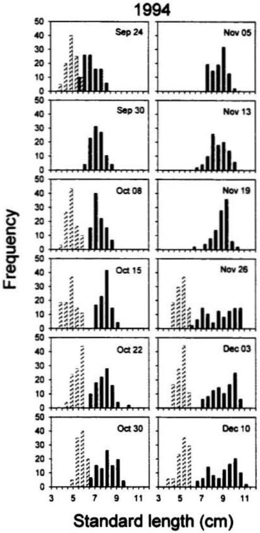

1994
Frequency
Sep 24
Sep 30
Oct 08
Oct 15
Oct 22
Oct 30
Nov 05
Nov 13
Nov 19
Nov 26
Dec 03
Dec 10
0
10
20
30
40
50
3
5
7
9
11
Standard length (cm)

Figure 3.3. Length-frequency distributions for each of recently settled (hatched bars) and post-settled (solid bars) age 0 Atlantic cod in Goose Cove, Newfoundland, September-December, 1995.

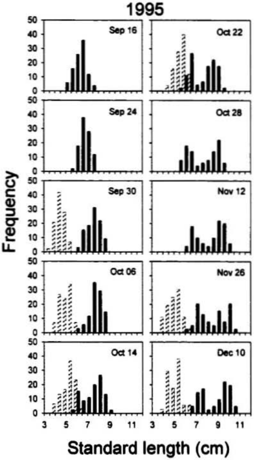

1995
Frequency
50
40
30
20
10
0
Sep 16
Sep 24
Sep 30
Oct 06
Oct 14
Oct 22
Oct 28
Nov 12
Nov 26
Dec 10
3
5
7
9
11
Standard length (cm)

Figure 3.4. Variance-mean density relationships with least squares regression line for age 0 cod sampled at four eelgrass sites in Goose Cove in a) 1994 and b) 1995. Linear regressions describing the relationships are presented. A 1:1 line illustrates the variance-mean relationship suggestive of random spatial distribution: all variances above this line indicate aggregated spatial distributions.

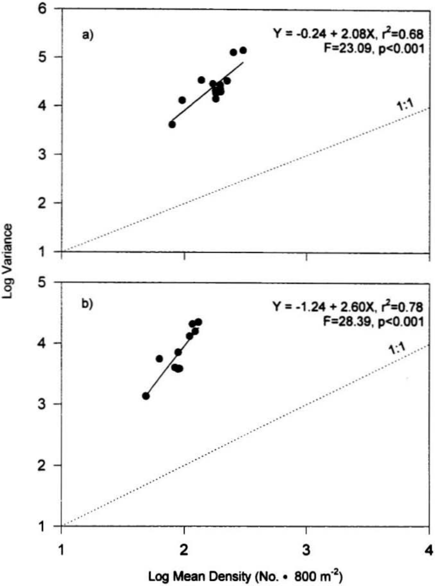

Log Variance
a)
Y = -0.24 + 2.08X, r²=0.68
F=23.09, p<0.001
1:1
6
5
4
3
2
1
b)
Y = -1.24 + 2.60X, r²=0.78
F=28.39, p<0.001
1:1
5
4
3
2
1
1
2
3
4
Log Mean Density (No. • 800 m⁻²)

Figure 3.5. Length-frequency distributions for each of recently settled (hatched bars) and post-settled (solid bars) age 0 Atlantic cod at Sunnyside, Newfoundland, October-December, 1994.

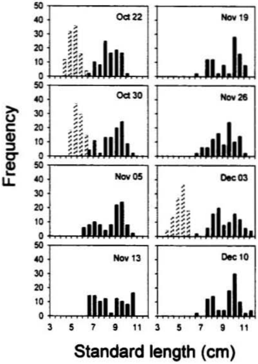

Oct 22
Nov 19
Oct 30
Nov 26
Nov 05
Dec 03
Nov 13
Dec 10
Frequency
0
10
20
30
40
50
3
5
7
9
11
Standard length (cm)

Figure 3.6. Total catch (•) of post-settled age 0 Atlantic cod and percent recapture of cod marked on (a) September 24 (◦) and November 13 (▵), 1994 and (b) September 16, 1995, (◦) in Goose Cove, Newfoundland. E1, E2, and the arrow indicate when marked cod were released into the population.

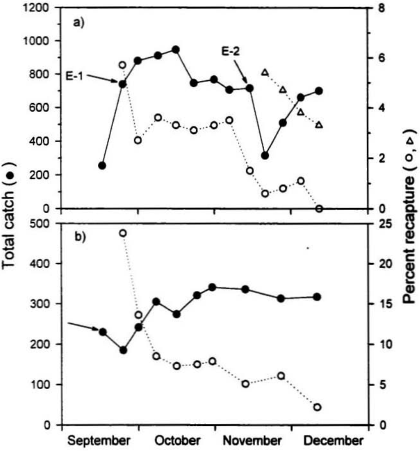
a)
b)
E-1
E-2
Total catch (●)
Percent recapture (○, △)
1200
1000
800
600
400
200
0
500
400
300
200
100
0
8
6
4
2
0
25
20
15
10
5
0
September
October
November
December

Figure 3.7. Seasonal variation in frequency of occurrence of age 0 Atlantic cod (a and c) at Sites 1 to 4 in Goose Cove, Newfoundland, and frequence of occurrence of marked cod (b and d) during 1994 and 1995, respectively. Values are expressed as percent of the total number of cod captured at all sites in 1994 (a) and 1995 (c) and percentage of the total number of marked cod recaptured at all sites in 1994 (b) and 1995 (d).

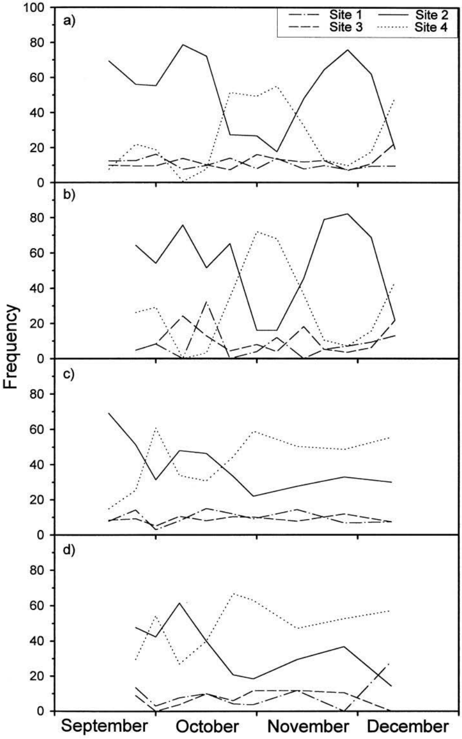

a)
b)
c)
d)
Site 1
Site 2
Site 3
Site 4
Frequency
0
20
40
60
80
100
September
October
November
December

Figure 3.8. Catch versus cumulative catch for age 0 Atlantic cod sampled over a 4-h period at Site 2 in 1995.

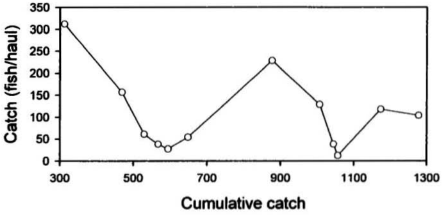

Catch (fish/haul)
350
300
250
200
150
100
50
0
300
500
700
900
1100
1300
Cumulative catch

Figure 3.9. Catch versus cumulative catch for age 0 Atlantic cod sampled at Site 6 over 2-h periods. October-December. 1994. Note. axes are not equal.

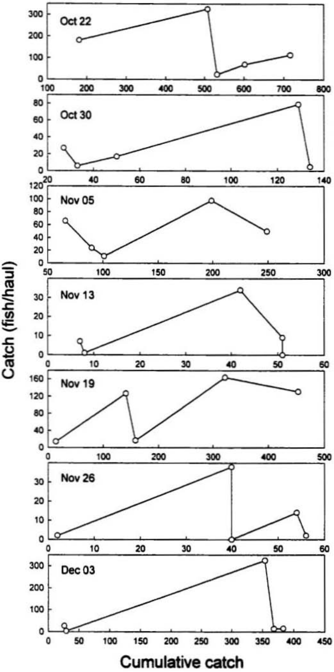
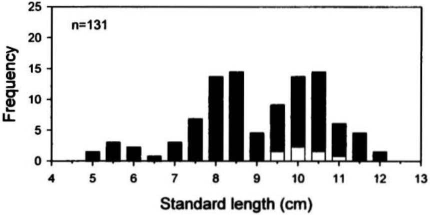

Oct 22
0
100
200
300
100
200
300
400
500
600
700
800
Oct 30
0
20
40
60
80
20
40
60
80
100
120
140
Nov 05
0
20
40
60
80
100
120
50
100
150
200
250
300
Nov 13
0
10
20
30
0
10
20
30
40
50
60
Nov 19
0
40
80
120
160
0
100
200
300
400
500
Nov 26
0
10
20
30
0
10
20
30
40
50
60
Dec 03
0
100
200
300
0
50
100
150
200
250
300
350
400
450
Catch (fish/haul)
Cumulative catch

Figure 3.10. Length-frequency distribution of post-settled age 0 Atlantic cod captured in Goose Cove, Newfoundland in March, 1995. Open bars represent the length-frequency distribution of marked cod in each bar.


n=131
Frequency
0
5
10
15
20
25
4
5
6
7
8
9
10
11
12
13
Standard length (cm)

CHAPTER 4. Variation in condition of coastal Newfoundland age 0 Atlantic cod (*Gadus morhua*): field and laboratory analysis using simple condition indices

ABSTRACT

Diet composition and simple indices of condition (hepato-somatic index, condition factors, and body ash content) were determined for age 0 Atlantic cod (*Gadus morhua*) captured in a small cove of insular Newfoundland, between August 1993 and January 1994. Laboratory experiments were also conducted to determine whether simple indices of condition reflect differences in energy intake (ration level) and to determine minimum index of condition values assessed from age 0 cod that died due to exhaustion of their energy reserves. Determination of lower, critical indices of condition provided a meaningful criterion for interpreting field data on feeding, condition, and survival of age 0 cod. In the wild, indices of condition representing variation in liver and muscle energy reserves of cod increased rapidly with the consumption of *Calanus finmarchicus*, which exhibited a high incidence of oil sacs, and declined abruptly when this lipid-rich prey was no longer consumed. Liver and muscle energy reserves of wild age 0 cod varied seasonally, however, their condition was well above that of cod which died in the laboratory. Laboratory studies revealed that condition of cod differed significantly over time as well as between ration levels. Indices of condition representing variation in muscle energy reserves exhibited a steady decline once the hepto-somatic index fell below a value of about 2.0, which I interpret as evidence of a pattern of depletion of lipids and then proteins, similar to that observed for

larger juveniles and adults. I conclude that as long as age 0 cod are above a "safe" level of condition their body length may still increase despite a decline in condition.

INTRODUCTION

The recent decline of Atlantic cod stocks in offshore waters of the northwest Atlantic has increased interest in the ecology of juveniles settling in coastal regions. Several studies (Gotceitas and Brown 1993; Methven and Bajdik 1994; Gotceitas et al. 1995; Tupper and Boutilier 1995a; 1995b; Fraser et al. 1996; Gotceitas et al. 1997; Ings et al. 1997; Schneider et al. 1997; Grant and Brown 1998a; 1998b; Lomond et al. 1998) suggest that availability of prey and suitable habitat may influence survival of age 0 cod settling in shallow nearshore areas, and that the shift from a pelagic to demersal habit may represent a limitation to the successful recruitment of cod.

Cod settling in coastal regions appear to prefer nearshore areas that provide both protection from predators and an adequate supply of suitable prey (Tupper and Boutilier 1995b; Chapter 2; Chapter 3). Once settled, age 0 cod may become either solitary, site attached, and territorial (Tupper and Boutilier 1995a) or under certain conditions they may form shoals (Olsen and Soldal 1989; Tupper and Boutilier 1995a; Chapter 3) which appear to exhibit restricted movements in coastal waters (Olsen and Soldal 1989; Chapter 3). Young cod are largely zooplanktivorous for several weeks after settling in nearshore waters (Chapter 2; Lomond et al. 1998), and evidence of spatial and temporal variation in zooplankton composition and abundance in coastal regions (Davis 1982; 1986) suggests that newly settled cod may experience periods of limited food resources. The carrying capacity of age 0 cod in coastal regions appears to be related to the advection of zooplankton (Smedstad et al. 1994) and a seasonal decrease in prey size may contribute to a decrease in average daily ration (Chapter 2) and hence growth and condition of demersal age 0 cod. Documentation of settlement pulses of age 0 cod in coastal regions of the northwest Atlantic (Methven and Bajdik 1994; Tupper and Boutilier 1995a; 1995b; Chapter 2; Chapter 3), suggest that if food resources are limited, competition may intensify with each temporal influx of age 0 cod. Species composition and abundance of zooplankton vary seasonally and annually in coastal regions, but whether short-term variation in food supply affects the condition and survival of age 0 cod during the first several weeks post-settlement is not fully understood.

Variation in fish condition is viewed as a consequence of fish storing excess energy under conditions of optimal food intake and conversely, drawing on these energy reserves during periods of reduced food intake or food limitation. Methods for estimating the condition of fish are many and varied. These include what are commonly referred to as crude or simple measures of condition such as morphological indices incorporating length and weight (Fulton's condition factor), the hepato-somatic index, and percent body ash (Phillips et al. 1960; Oliver et al. 1979; Hawkins et al. 1985; Dos Santos et al. 1993; Foster et al. 1993), and more sophisticated laboratory analyses in which biochemical constituents of various tissues are analysed (Black and Love 1986; Foster et al. 1993; Lambert and Dutil 1997). It is generally the extreme values that are of interest as once the upper and lower limits of condition have been established they can be used to provide a meaningful interpretation of field data regarding condition and survival.

Lipids are the major form of storage of usable energy in fish (Shul'man 1974), and in cod the liver is of great utility when assessing energy reserves, as the majority of the lipids are stored in this organ (Love 1970; Lambert and Dutil 1997). The contractile muscle of cod is comprised largely of proteins (Love 1970; Lambert and Dutil 1997) and food deprivation studies conducted on large juvenile and adult cod show that cod do not begin to deplete protein reserves in the body musculature below "normal" condition until lipid reserves within the liver have been exhausted (Love 1970; Black and Love 1986; Hemre et al. 1993). Together, the liver and body musculature represent the bulk of the energy reserves in cod (Love 1970; Holdway and Beamish 1984; Hemre et al. 1993; Lambert and Dutil 1997).

In the present study, I used simple indices of condition, reflecting changes in energy reserves of the liver (hepato-somatic index) and body musculature (condition factors and body ash content) to assess seasonal variation in physical condition of age 0 cod. These indices were assessed in relation to seasonal variation in daily ration (Chapter 2) and diet composition of age 0 cod settling in Bull Arm of Trinity Bay, Newfoundland from late summer to early winter of 1993-94.

Field data pertaining to condition and survival can only be interpreted meaningfully when minimum index of condition values have been assessed for fish that have exhausted their energy reserves. A decline in condition is generally attributed to reduced food intake, usually as a consequence of poor feeding conditions (Pedersen and Jobling 1989). However, seasonal variation in food quality (lipid content) alone may affect condition (Black and Love 1986; Jobling 1988), yet fish may still be at a "normal" level of condition, that is, capable of surviving various environmental stresses. I therefore also carried out a laboratory experiment on wild age 0 cod to determine: 1) the relationship between simple indices of condition and differences in energy intake (i.e., three ration levels), and 2) minimum values of these condition indices in age 0 cod that died due to exhaustion of their energy reserves (starvation).

MATERIALS AND METHODS

Field studies

Demersal age 0 cod were captured at 1-2 week intervals by beach seine in Goose Cove, Newfoundland (47°51' N, 53°54' W), from August 1993 to January 1994. To maximize the amount of dietary information obtained per individual age 0 cod collected (i.e., see Chapter 2), the point-in- time samples were conducted during late afternoon (i.e., 15:50-20:00). A complete description of the study location and methods of collection are given in Chapters 2 and 3 (Site 2). Random samples of 50 and 10 cod from the 0-group age-class were removed for condition and dietary analysis, respectively. Fish were killed (MS-222), placed on dry ice, returned to the laboratory and stored at -20°C for 2-3 weeks, then analysed. Following each collection, water temperature was measured 50 m from shore, within 1.0 m of the bottom.

In the laboratory, cod were thawed, blotted, measured for standard length (SL; ±1.0 mm) and wet weight (±0.01 g). To assess seasonal changes in condition, the viscera were removed and the liver and alimentary tract dissected. The alimentary tract was discarded. The eviscerated body and total liver were dried separately to a constant weight (±0.001 g) at 60°C. Ash content (±0.001 g) of the eviscerated body was determined after burning for 72 h at 550°C as recommended by the Association of Official Analytical Chemists (1965). Five condition indices were calculated. Condition factor was expressed as Fulton's condition factor (Ricker 1975):

4.1) $$K = 100W/L^3.$$

Studies show that a loss of body lipids and proteins results in an increase in water content of the body, such that wet weight is conserved (Love 1970; Shul'man 1974). Therefore, in this study, K was derived using three different measures of body weight (W; grams); these included wet (K_{WET}), eviscerated dry (less liver; K_{DRY}), and ash free eviscerated dry (less liver; $K_{ASH\ FREE}$) body weight. In this study, L represents standard length (cm) and the various condition factors were scaled through multiplication by 100 (wet body weight), or 1000 (dry body weights). Since the majority of the lipid reserves of cod are stored in the liver, changes in the dry weight of this organ in relation to dry body weight will provide an indication of changes in lipid reserves. Energy reserves of the liver were assessed using the hepato-somatic index (HSI), expressed as:

4.2) $$HSI = (LW/W) \times 100,$$

where LW and W represent dry liver weight and dry body weight (less alimentary tract), respectively. Cod used in this study were immature (age 0), therefore the hepato-somatic index, first introduced by Heidinger and Crawford (1977; liver-somatic index), is valid.

Changes in percent body ash can provide a measure of changes in muscle mass at length. For example, a relative decrease in ash content of the eviscerated body is indicative of an increase in the proportion of flesh in relation to bone. In this study, percent body ash (ASH) was calculated for the eviscerated dry body weight as follows:

$$\text{ASH} = (\text{ash content of eviscerated dry body weight}/\text{eviscerated dry body weight}) \times 100. \tag{4.3}$$

Food items in the stomach of individual cod were identified, counted, and dried to constant weight at 60°C. A complete description of the methods used to assess the various prey types in the diet of age 0 cod is given in Chapter 2. The contribution of various prey types to the diet were assessed by an index of relative importance (IRI; George and Hadley 1979), also summarized in Chapter 2.

Laboratory experiment

On January 01, 1994, 520 age 0 cod were captured at Goose Cove (0.5°C water temperature), transported to the laboratory at the Ocean Sciences Centre, Logy Bay, Newfoundland, then evenly distributed among eight circular (1 m × 0.5 m deep) flow through (2.0 ± 0.2 litres/min) tanks at a water temperature of 0.1°C. Water temperature was gradually lowered in all tanks and maintained at -0.5°C (range ±0.5°C) from January 04 to April 04, 1994.

These eight tanks of cod were haphazardly assigned to one of four ration regimes. Each regime was replicated once. The first regime was a starvation treatment, which was intended to determine indices of condition at time of death due to the exhaustion of energy reserves. Cod were starved from the day of capture onwards, and as mortality occurred, fish were removed and stored at -20° C for 2-3 weeks, then analysed. This component of the experiment was carried out until all fish in both tanks died. In order to compare the magnitude of the initial response of various condition indices for fasting cod, groups of cod (ten per sample) were sampled from each of these two tanks on January 14 and 26. The last sample was taken (i.e. January 26) when the first mortality was discovered.

Regimes two through four were different feeding regimes. These cod were held at constant temperatures and sampled over 82 days. From January 04 to 09, cod in regimes two through four were fed freeze-dried krill twice a day until feeding ceased (i.e., apparent satiation). On January 12, two tanks were randomly assigned to each of the following feeding rations: 0.1 (regime II), 0.2 (regime III), and 0.4 (regime IV) grams dry · grams wet fish weight $^{-1}$ · day $^{-1}$. Cod were fed every other day. The highest ration coincided with the average of the November and December field estimates of daily ration (i.e., 0.42 grams dry · grams wet fish weight $^{-1}$ ·day^{-1}; Table 2.1). To determine quantities of food to be supplied to each tank, cod were wet weighed (±0.01 g) after anaesthetization in seawater containing MS 222 at 30 mg/l on Day 1 (January 12), Day 14, Day 42, and Day 70. A haphazard sample of ten cod was removed from each of the fed tanks prior to weighing. Cod sampled from all tanks were killed (MS 222) and stored at -20°C for 2-3 weeks then analysed. Cod dying in the fed treatments were also stored at -20°C, for 2-3 weeks.

Once thawed, cod were analysed in the same manner as the field study, except all dry weights were measured to the nearest 0.0001 grams.

Data analyses

Fulton's condition factor, K, is a meaningful measure of condition, provided the assumption of isometric growth is verified and the condition index is not correlated with body size (Bolger and Connolly 1989). Weight-length regression equations were derived for wet, eviscerated dry, ash free eviscerated dry, and ash body weight by the method of least squares. All data were $\log_{10}$ transformed. Growth was considered isometric when the 95% confidence intervals of the regression slope estimates (b) encompassed a value of 3.0. Relationships between condition factors and body length were tested for significance (i.e., $p < 0.05$).

Seasonal differences in condition indices were determined using simple one-way Analysis of Variance (Proc GLM, SAS 1988). Data transformation was not required to satisfy the assumptions of the test (i.e., normality).

Paired t-tests (Proc TTEST, Cochran and Cox approximation, SAS 1988) were used to determine between tank differences in condition indices within treatments at time of death due to exhaustion of energy reserves. Indices of condition analysed for samples collected from feeding regimes two through four were compared between feeding regimes and over time using a two-way Analysis of Variance (Proc GLM, SAS 1988). All data were transformed ($\log_e$) to meet the assumptions of the test. For a two-way ANOVA, a significant interaction term precludes interpretation of a main effect. Under such conditions, I proceeded to test for differences in the temporal response of each condition index to the feeding regimes. This was accomplished by performing t-tests to compare regression slopes of semilogarithmic relationships of the average of each condition index against time between consecutive ration levels (i.e., 0.4% vs. 0.2%, 0.2% vs. 0.1%) using the methodology described by Zar (1984). The assumption of normality concerning the residuals (i.e., residual plots) of each relationship appeared to be met by the $\log_e$ transformation.

RESULTS

Field studies

Although field sampling commenced in mid-August, 1993, age 0 cod were not captured in appreciable numbers ($n > 60$) until late August. Box plots of seasonal variation in the size of age 0 cod in Goose Cove (Fig. 4.1), confirm three temporal influxes of recently settled Atlantic cod documented for coastal Newfoundland (Methven 1997; Grant and Brown 1998a; 1998b). In 1993, the first influx occurred when age 0 cod were first captured in high numbers in late August-September, the second, during late October-early November, and the third, during December-January. Both the second and third influxes were preceded by periods of growth by cod that had already settled (Fig. 4.1). Water temperature declined from 12.8 to 0.5°C over the sampling period (Fig. 4.1).

Weight-length regressions for the various body weights analysed did not exhibit appreciable seasonal variation (Table 4.1). The 95% confidence intervals for the slope estimates (b) encompassed a value of 3.0 for all measures of dry body weight, indicating that growth was isometric for the various dry weight-length increments analysed. Significant relationships between condition factors and length were only observed for estimates of K_{WET} on December 07 and 20, which coincided with samples that exhibited non-isometric growth based on wet body weight ($b \neq 3$). Thus, only two (i.e., <5%) of the forty-eight condition factor-length relationships tested were significant at the 5% significance level. Additionally, there were no significant relationships within the samples when percent body ash or the HSI was regressed on length (%ASH, F_{48} ranged from 0.001 - 1.94, p ranged from 0.971 - 0.170; HSI, F_{48} ranged from 0.001 - 3.23, p ranged from 0.959 - 0.079).

Analysis indicated a significant seasonal change in the HSI ($F_{11,588} = 65.3, p \ll 0.001$), percent body ash ($F_{11,588} = 49.8, p \ll 0.001$), and condition factors (K_{DRY}, $F_{11,588} = 7.0, p \ll 0.001$; $K_{ASH\ FREE}$, $F_{11,588} = 14.2, p \ll 0.001$; K_{WET}, $F_{9,490} = 41.5, p \ll 0.001$). There was a rapid increase in both liver and muscle energy reserves during late September (Fig. 4.2). Indices of liver and muscle energy reserves remained relatively high to late November, declined abruptly, and then appeared to stabilize by late December-early January, as the 95% CI's for all condition indices overlapped values observed prior to the September increase. For indices reflecting variation in muscle energy reserves, percent body ash was the most responsive throughout the seasonal sampling (Fig.4.2). Fulton's condition factors most representative of variation in muscle energy reserves (i.e., K_{DRY} and $K_{ASH\ FREE}$) showed similar seasonal responses, while condition factor based on wet body weight responded in a converse manner to the dry body weight condition factors over six of the eleven sampling intervals (Fig 4.2b).

When indices of condition that were most representative of variation in muscle energy reserves (i.e., percent body ash, K_{DRY} , and $K_{ASH\ FREE}$) were plotted on HSI for each sample, the relationships were rarely significant ($p > 0.05$), and relationships that did exist showed a very low coefficient of determination ($r^2<0.11$). This was apparently due to high individual variation in muscle and liver energy reserves. Seasonal means, however, showed strong correlations (Fig. 4.3), indicating that indices describing changes in liver and muscle energy reserves responded in a similar manner throughout the season.

Lack of a correlation between the condition indices and body length within the samples indicates that the seasonal variation in condition of age 0 cod was not caused by the intermittent influxes of smaller recently settled cod into Goose Cove. Both liver and muscle energy reserves remained high during the second influx indicating a similar condition for both post-settled and smaller, recently settled cod (Fig. 4.2). Liver and muscle energy reserves declined prior to the third influx of recently settled cod, indicating that the late November-early December decline in condition was associated with fish that had already settled. Both small cod from the third influx and larger post-settled cod exhibited relatively low liver and muscle energy reserves in December-January. Overall, these results provide evidence that factors affecting the condition of age 0 cod were consistent throughout the pelagic and nearshore zones within the local area during this study.

Planktonic Crustacea dominated the diet of age 0 cod in Goose Cove (Table 4.2). Cladocerans (*Evadne* spp. and *Podon* spp.) dominated the diet when age 0 cod first appeared in nearshore catches in late August (Table 4.2) and condition was relatively low (Fig. 4.2). Copepodite stages of *Acartia* spp. were the dominant prey by mid-September, at which time condition of age 0 cod still remained relatively low, despite a high daily ration (i.e., Chapter 2, Table 2.1). The consumption of copepodites of *Calanus finmarchicus* with a high incidence of oil-sacs (87-96%) and *Temora longicornis* (Table 4.2) coincided with a sudden increase in condition of age 0 cod in late September, and condition remained high to late November (Fig. 4.2). Daily ration declined over the same time period (Table 2.1). A sudden increase in consumption of *Pseudocalanus* spp. copepodites in mid-November (Table 4.2) coincided with an increased proportion of smaller copepodite stages of *T. longicornis* in the diet of age 0 cod, and small copepodites continued to dominate the diet to January. Increased consumption of small copepodites also coincided with an abrupt decrease in daily ration (Table 2.1) and a slight decrease in condition in November. Nevertheless, it was the complete disappearance of lipid-rich *C. finmarchicus* in the diet of age 0 cod that corresponded with an abrupt decrease in condition during late November-early December. Lack of *C. finmarchicus* in the December diel survey of the stomach contents (Chapter 2; Fig. 2.3) suggests that the disappearance of this lipid-rich prey was not an artifact of the point-in-time sampling program.

Laboratory experiment

Relationships between the condition indices and body length were tested for significance by replicate and by date sampled for feeding regimes one through four. Analysis revealed that the condition indices were not correlated with body length (i.e., $p > 0.05$: HSI, F_s ranged from 0.01 - 1.66, p ranged from 0.916 - 0.234; ASH, F_s ranged from 0.001 - 0.75, p ranged from 0.977 - 0.413; K_{WET}, F_s ranged from 0.001 - 5.11, p ranged from 0.980 - 0.054; K_{DRY}, F_s ranged from 0.001 - 5.11, p ranged from 0.991 - 0.053; $K_{ASH\ FREE}$, F_s ranged from 0.05 - 5.19, p ranged from 0.825 - 0.052).

Cod with larger body size survived longer without food then small cod. Plots of the length of dying cod against days without food indicated positive and significant relationships (Fig. 4.4). Between replicate comparisons of individual condition indices for cod that died due to starvation indicated that only two of the five indices analysed (HSI and K_{WET}) differed significantly between replicates (Table 4.3).

Average body length and means of individual condition indices did not differ between replicate samples taken on January 14 and 26 from the two tanks in which cod were starved (i.e., Jan. 14, Length, $t_{18} = 1.10$, $p = 0.284$; HSI, $t_{18} = 1.24$, $p = 0.231$; ASH, $t_{18} = 0.49$, $p = 0.627$; K_{WET} $t_{18} = 0.14$, $p = 0.891$; K_{DRY}, $t_{18} = 0.23$, $p = 0.822$; $K_{ASH\ FREE}$, $t_{18} = 0.23$, $p = 0.820$; Jan 26, Length, $t_{18} = 0.03$, $p = 0.975$; HSI, $t_{18} = 2.05$, $p = 0.056$; ASH, $t_{18} = 1.86$, $p = 0.079$; K_{WET} $t_{18} = 0.56$, $p = 0.584$; K_{DRY}, $t_{18} = 0.43$, $p = 0.675$; $K_{ASH\ FREE}$, $t_{18} = 0.12$, $p = 0.904$), so the replicates were combined for each sample date (Table 4.4). The HSI showed the greatest initial response, differing significantly from the mean observed on January 1 after 13 days (i.e., 95% CI did not overlap). Overlap of the 95% CI's for the remaining indices after 13 days provides evidence of a delayed response in the depletion of energy reserves of the body musculature (Table 4.4).

Results of nested analysis of tank effect within feeding regimes two through four revealed that there was no significant difference in body length or condition indices analysed (Length, $F_{2,3} = 0.32$, $p = 0.841$; HSI, $F_{2,3} = 0.89$, $p = 0.454$; ASH, $F_{2,3} = 0.43$, $p = 0.782$; K_{WET} $F_{2,3} = 0.24$, $p = 0.904$; K_{DRY}, $F_{2,3} = 1.20$, $p = 0.301$; $K_{ASH\ FREE}$, $F_{2,3} = 1.18$, $p = 0.368$), so the replicates were combined by date for each treatment. Comparison of the condition indices of cod held in feeding regimes two through four revealed a significant date-by-ration interaction (HSI, $F_{4,8} = 13.27$, $p \ll 0.001$; ASH, $F_{4,8} = 15.03$, $p \ll 0.001$; K_{WET} $F_{4,8} = 7.02$, $p \ll 0.001$; K_{DRY}, $F_{4,8} = 11.49$, $p \ll 0.001$; $K_{ASH\ FREE}$, $F_{4,8} = 12.77$, $p \ll 0.001$). Therefore, t-tests were used to test for differences in the rate of change between feeding regimes. These tests revealed that the rate of change for the condition factors and body ash content differed significantly between feeding regimes (Table 4.5 and Fig. 4.5). The rate of decline in the liver energy reserves (HSI) differed between the 0.4% and 0.2% ration levels, but did not differ between rations of 0.2% and 0.1% (Table 4.5 and Fig. 4.5).

Dead individuals were recovered from the two replicate tanks at the 0.1% ration after 60 and 64 days, respectively. By Day 82, a total of 18 dead cod (8 and 10 per replicate) were removed from the two tanks held at this ration. T-tests revealed that comparisons within indices of condition for cod that died at the 0.1% ration level did not differ significantly between replicates ($t_{16} = 0.41, p = 0.690$), so these data were combined. A comparison of the mean and 95% CI's for all cod (n=18) that died in the 0.1% ration (i.e., HSI = 1.02 ± 0.06; ASH = 21.30 ± 0.38; $K_{DRY} = 0.91 \pm 0.03$; $K_{ASH\ FREE} = 0.71 \pm 0.02$; $K_{WET} = 0.64 \pm 0.02$) with cod that died in the starvation treatment (Table 4.3) revealed an overlap in these values. Thus, it appears that cod died due to exhaustion of energy reserves whether they were starved or maintained on the lowest ration.

The HSI and body ash content responded in a converse manner to feeding regimes two through four (Fig. 4.5a), which was similar to the responses observed in the wild (Fig. 4.2a). The nature of the curves indicates a decline in liver and muscle reserves at each experimental ration level. The degree of the responses, however, and within treatment overlap of the 95% CI's after Day 42 and Day 70 for cod held at rations of 0.4% and 0.2%, respectively, suggests that these curves were approaching a ration related asymptote (Fig. 4.5a). Unfortunately, the experiments were not of sufficient duration to establish whether the condition of cod held at these rations had in fact stabilized. Nonetheless, the rate of the response of the liver and muscle condition indices was related to ration level (Table 4.5) and the varying time (42 vs 70 days) required to attain overlap in the 95% CI's within each treatment suggests an initial ration related period of adjustment in condition and a subsequent period of relatively stable condition. The mean HSI of cod held at the 0.1% ration appeared to stabilize just above the lower limit for cod that died due to exhaustion of their energy reserves while indices of muscle energy reserves declined steadily to Day 82 (Fig. 4.5a). By day 82, only cod held at the 0.1% ration exhibited means with 95% CI's for the condition factors and ash body weight that overlapped values obtained for cod that died in the starvation treatment. Mortalities at this treatment suggest that the HSI stabilized prior to Day 70 and the mortalities positively biased the HSI value thereafter.

Curves describing the response of the condition factors based on dry body weight showed a similar ration related pattern to that outlined above (Fig. 4.5b, c). Although the condition factor based on wet body weight exhibited a similar tendency towards a reduction in condition, the nature of the curves appeared somewhat reversed, with a relatively stable period followed by an increased reduction in condition (Fig. 4.5c). In the present study, cod were pre-frozen then thawed before analysis, and additional laboratory studies indicated that variable amounts of water (0 - 3.4% initial wet body weight) are lost from small cod due to this procedure. These results suggest K_{WET} estimates based on pre-frozen small juvenile cod were a less reliable index of short-term changes in condition than K_{DRY} and $K_{ASH\ FREE}$.

When indices of liver and muscle energy reserves were considered in relation to one another, there was clear evidence of a delayed response in the latter (Fig. 4.6). Indices of muscle energy reserves declined steadily once the HSI fell below a value of approximately

2.0%. To determine whether cod captured in Goose Cove were at risk of dying due to the depletion of energy reserves, similar plots were produced for individual cod when the sample mean HSI was <5.0 (i.e., August 26, September 13, December 14, 20, and January 01; Fig. 4.7). A small proportion of cod in Goose Cove exhibited HSI values <2.0%, but when the HSI was considered in relation to indices representing variation in muscle energy reserves, it was apparent that very few cod in Goose Cove were approaching the condition at which cod of similar size died due to exhaustion of their energy reserves in the laboratory experiments.

DISCUSSION

This study shows that simple indices of condition such as the condition factor (based on dry body weight), hepato-somatic index, and percent body ash can be used to assess long- and short-term changes in energy intake of small juvenile cod, responding rapidly (1-2 weeks) to changes in food quality and quantity. These results agree with previous studies on the use of simple indices to assess the condition of larger juveniles and adult cod (Holdway and Beamish 1984; Lambert and Dutil 1997). This study also indicates the importance of establishing lower limits for indices of condition, which provide a standard for interpreting field studies on condition and survival. In this study, age 0 cod exhibited considerable variation in condition during the first several weeks post-settlement and a diel feeding study on this cod population (Chapter 2) revealed an abrupt seasonal decrease in prey size and average daily ration. Condition indices analysed were, however, well above the minimum values at which cod died due to exhaustion of their energy reserves during food deprivation treatments, suggesting that age 0 cod survival is generally not limited by the seasonal variation in size, abundance, or availability of prey. Goose Cove supports a large number of age 0 cod from year to year (Chapter 2 and 3) and results presented in this study show that these fish were in good condition throughout the autumnal settlement indicating that shallow nearshore regions in coastal Newfoundland may serve as trophically adequate nursery and rearing grounds for age 0 cod for the first several weeks post-settlement.

The indices of condition analysed in this study were selected because once inherent assumptions have been met they provide a quick and simple means of measuring the condition of fish. For example, valid use of Fulton's condition factor hinges on the assumption of isometric growth (b=3), since correlations between the condition factor and length could arise if this assumption is violated (Bolger and Connolly 1989). With the exception of K_{WET} (two out of twelve field samples), all indices analysed in this study were independent of body length. In the present study, the K_{WET} estimates did not account for the seasonal variation in whole body weight caused by the digestive tract contents. Stomach contents alone can comprise >1% body weight (grams dry · grams wet^{-1}) of small juvenile cod (Chapter 2), indicating the importance of accounting for variation in consumption. A loss of body lipids and proteins results in an increase in water content of the body (Love 1970; Shul'man 1974), and variable individual water-loss during freezing and thawing may have contributed to the varying response of K_{WET} during the present study. Nevertheless, K_{WET} exhibited similar long-term responses to the other indices analysed, particularly during abrupt changes in condition, indicating that this index also represents a reliable means of monitoring condition of small juvenile cod. Overall, these observations justify using these condition indices to assess seasonal variation in condition of juvenile cod within a size range of 4.2 to 7.9 cm SL.

The present study suggests that an HSI value of 2.0 to 4.0% represents the "normal" and "safe" condition for juvenile cod within the size range studied. I suspect that the concomitant responses of liver and muscle energy reserves to seasonal changes in prey quality (lipid content) were indicative of a whole body condition above that of the "safe" state, and a consequence of increased prey quality which resulted in a nutritional surplus in the form of lipids. When lipid-rich prey were no longer consumed, indices of liver and muscle energy reserves exhibited a rapid decline and stabilized at levels not significantly different (i.e., overlapping 95% CI's) from values observed prior to the consumption of lipid-rich prey. In the wild, indices of liver and muscle condition were not correlated within the samples, a result that supports the hypothesis of a nutritional surplus. In the laboratory, however, cod held at reduced rations showed strong relationships between indices of liver and muscle energy reserves once the HSI fell below about 2.0%. The food deprivation study revealed that the greatest initial response was by the HSI, and liver energy reserves also exhibited a rapid initial decline at all laboratory ration levels, while indices representing changes in muscle energy reserves showed a somewhat delayed response. It appears that only when small juvenile cod are below what may be considered the "safe" body condition does the depletion pattern of lipids first and proteins second follow a pattern similar to that described for larger juveniles and adult cod (Love 1970; Black and Love 1986). Results from studies on larger cod suggest that the HSI may be the most useful indicator of short-term changes in nutritional intake (Black and Love 1986; Foster et al. 1993). Given the rapid response of indices of both liver and muscle energy reserves of age 0 cod to changes in nutrient intake, I recommend that similar future studies on condition of small juvenile cod assess the energy reserves of both tissue components.

The present field results on feeding, condition, and growth of age 0 cod support the hypothesis of a time lag in the readjustment of the metabolic rate in response to abrupt changes in nutrient intake (review by Jobling 1994). It has been demonstrated that juvenile fish can partition growth energy between increases in body length or energy stores (Booth and Keast 1986). This study provides evidence of an increase in average body length during a decline in indices of both liver and muscle energy reserves, suggesting that a high metabolic expenditure associated with high nutrient intake (i.e., lipid-rich *C. finmarchicus*) was maintained for a short time after a decline in nutrient intake. It is conceivable that a metabolic time lag will also be accompanied by a time lag in the reduction of the production and secretion of growth hormones. I suggest that the combined effect of a high metabolic demand and high production of growth hormone in the absence of adequate nutrient intake resulted in the reallocation and (or) mobilization of lipid and protein reserves in order to increase body length. The metabolic time lag may also have contributed to the rapid initial decrease in the HSI during the feeding experiments, where the degree of the response was associated with ration level.

The current field results also suggest that as long as liver and muscle energy reserves of small juvenile cod are above a "safe" level, body length increases can still occur, even though condition is declining. These results contrast with the strong positive relationship between the HSI and whole body growth rate exhibited by larger juvenile cod (~300 g as reported by Foster et al. 1993 vs ~1-4 g in this study). The effect of life stage and (or) body size on the partitioning of growth energy may explain this difference, but the liver is a component of growth based on whole body weight. As such, correlations between the HSI and whole body growth rates in captive cod may also be related to the development of enlarged fatty livers, which is well documented for cod that are fed lipid-rich food (Lie et al. 1986; Jobling 1988; Chapter 5).

A late autumn decline in liver energy reserves suggests that it may not be important for age 0 cod to store large amounts of lipids prior to overwintering. Many fish in northern climates build-up lipid reserves prior to overwintering (Foltz and Norden 1977; Booth and Keast 1986: Henderson et al. 1988; Miranda and Hubbard 1994) and increased overwintering survival of young-of-the-year fish in temperate regions is generally associated with larger body size (Lindroth 1965; Oliver et al. 1979; Shuter et al. 1980; MacLean et al. 1981; Henderson et al. 1988; Post and Evans 1989; Malloy and Targett 1991; Miranda and Hubbard 1994). It has recently been suggested, based on evidence of decreased rations (Chapter 2) and lower growth (Tupper and Boutilier 1995a) of age 0 cod settling late in the season in coastal regions of the northwest Atlantic, that overwintering mortality may be high for smaller cod which settle late in the season. This study shows that the condition of small age 0 cod responded rapidly to the consumption of lipid-rich *C. finmarchicus* and condition remained high even when daily ration was low and lipid-rich prey comprised only a small proportion of the diet. The lipid storage of comparatively smaller calanoids in genera such as *Acartia*, *Temora*, and *Pseudocalanus* is limited by body size (Norrbin et al. 1990), which may account for the relatively lower condition of age 0 cod in August-early September when daily ration was high, yet prey size small. At high latitudes, large calanoid copepods lay down relatively large lipid reserves in their oil sacs (Lee 1974; Sargent 1976; Sargent and Falk-Petersen 1988) and for *Calanus* species, total lipids of copepodite stages IV and V often exceed 50% dry body weight during the winter (Gatten et al. 1980; Sargent et al. 1977; Sargent and Falk-Petersen 1988). Sub-zero winter water temperatures are common on the northeast coast of Newfoundland and juvenile cod inhabit these waters over winter (Methven and Bajdik 1994; Chapter 3; Chapter 5). Previous studies on the effect of energy reserves and body size on overwintering survival of young juvenile fish have largely focused on temperate freshwater systems, where food is limiting over the winter (Post and Evans 1989). Recent work on condition and over winter survival in herring in relatively warmer coastal waters of Alaska have shown that winter condition does decline to levels that risk survival and that fall condition may predict spring survival (Paul and Norcross 1999). Temperature experience over the winter would influence the rate of depletion of energy reserves during periods of low food availability. I speculate that a build-up of energy reserves in small juvenile marine fish that feed largely on planktonic Crustacea may not be necessary in areas of the north Atlantic where temperatures fall below zero over the winter and *Calanus* species overwinter as lipid-rich copepodites. Results presented here on age 0 cod suggest that zooplanktivorous juveniles may only require a very small proportion of lipid-rich zooplankton in the diet, even if available at irregular intervals, in order to maintain a "safe" condition over the winter.

In Chapter 2, I documented cannibalism on small age 0 cod by age 1 cod, and both age classes have been shown to occur in shallow coastal regions of Newfoundland over the winter (Methven and Bajdik 1994; Chapter 3). Increased body size may reduce the threat of cannibalism by larger co-occurring juveniles (Bogstad et al. 1994; Chapter 2). Conversely, a build-up of lipid stores would divert surplus energy away from further length increases. Although it remains unclear which strategy is more advantageous for young-of-the-year fish, results presented here suggest that cod take advantage of the seasonal build-up of large lipid stores in the oil sacs of calanoid copepods, a strategy that apparently allows them to increase body length prior to overwintering. Laboratory studies at temperatures of 0.6 to 8.3 °C showed that conversion efficiency increases with decreasing temperature (Brown et al. 1989) and recent evidence that growth may occur over the first winter (Chapter 3), also suggests that age 0 cod exploit this high-energy prey resource over the winter.

This study shows that simple indices of condition can provide reference values to aid in interpreting variation in condition both within and between populations. Results presented in this study suggest that the "normal" condition for cod is best assessed when indices describing variation in liver and muscle energy reserves are considered in relation to one another. This is apparently related to the compartmentalization of lipids and proteins in the liver and muscle, respectively, and the hierarchical manner in which lipids are depleted first when condition is below "normal". I suspect that age 0 cod in the northern northwest Atlantic exploit seasonally abundant lipid-rich copepodites, reducing the need for a seasonal build up of lipid stores and possibly enhancing survival. Cod may be localized in shallow coastal waters during their first winter, however (Chapter 3), and if overwinter survival depends on the periodic advection of lipid-rich prey then nearshore recruitment may be strongly affected by spatial and temporal variability in abundance and availability of this prey resource. Results presented in this study support the hypothesis of a time lag in adjustment of the metabolic rate in response to abrupt changes in nutritional intake in fish. Because the metabolic expenditure of fish is size related (Winberg 1956), that is, higher metabolic rates are associated with small body size, a time lag may be more pronounced in small juveniles. Until this issue is more clearly resolved, however, laboratory investigations on the response of growth and condition to varying nutritional intake in small juvenile cod should be interpreted with caution.

Table 4.1. Regression statistics of wet, eviscerated dry, ash free eviscerated dry and ash body weight on length for age 0 Atlantic cod in Goose Cove, Newfoundland, August, 1993 to January, 1994. The regression equation is $\log_{10}$ weight = a + b $\log_{10}$ length (n=50).

	Wet body weight			Eviscerated dry body weight			Ash free eviscerated dry body weight			Ash body weight		
Date	**a**	**b ± 95% CI**	**r^2**	**a**	**b ± 95% CI**	**r^2**	**a**	**b ± 95% CI**	**r^2**	**a**	**b ± 95% CI**	**r^2**
Aug 26	-2.06	3.08 ± 0.30	90.1	-2.81	2.98 ± 0.28	90.3	-2.92	2.99 ± 0.34	86.8	-3.58	2.96 ±0.21	94.4
Sep 13	-1.94	2.91 ± 0.21	94.1	-2.95	3.15 ± 0.20	95.8	-3.04	3.16 ± 0.22	94.2	-3.67	3.09 ± 0.17	96.5
Sep 28	-1.95	2.97 ± 0.23	93.3	-2.93	3.17 ± 0.30	90.5	-2.97	3.09 ± 0.34	87.7	-3.78	3.15 ± 0.38	85.4
Oct 19	-2.00	3.03 ± 0.19	95.4	-2.76	2.95 ± 0.34	86.2	-2.87	2.96 ± 0.35	85.9	-3.61	2.93 ± 0.40	81.9
Nov 02	-1.92	2.91 ± 0.12	97.9	-2.84	3.07 ± 0.14	97.5	-2.95	3.07 ± 0.12	98.2	-3.63	2.97 ± 0.18	96.0
Nov 13	-1.94	2.95 ± 0.22	94.0	-2.67	2.82 ± 0.20	94.6	-2.77	2.83 ± 0.19	94.8	-3.48	2.77 ± 0.25	91.1
Nov 24	-1.84	2.81 ± 0.21	93.8	-2.86	3.05 ± 0.19	95.7	-2.93	3.05 ± 0.18	95.9	-3.70	3.07 ± 0.26	92.3
Nov 30	-2.02	3.00 ± 0.15	97.3	-2.93	3.14 ± 0.16	96.8	-3.01	3.15 ± 0.18	96.1	-3.69	3.07 ± 0.14	97.6
Dec 07	-1.89	2.83 ± 0.14*	97.2	-2.74	2.88 ± 0.17	96.0	-2.80	2.85 ± 0.19	95.6	-3.65	3.03 ± 0.25	92.7
Dec 14	-2.03	2.99 ± 0.16	96.6	-2.92	3.08 ± 0.17	96.5	-2.99	3.08 ± 0.17	96.4	-3.69	3.08 ± 0.27	91.9
Dec 20	-1.87	2.79 ± 0.16*	96.3	-2.82	2.99 ± 0.20	95.0	-2.89	2.95 ± 0.19	95.4	-3.63	3.02 ± 0.31	89.0
Jan 01	-1.97	2.95 ± 0.13	98.0	-2.79	2.92 ± 0.15	97.3	-2.89	2.94 ± 0.14	97.2	-3.50	2.84 ± 0.18	95.4

***non-isometric growth (i.e., 95% CI of slope estimate, b, do not encompass a value of 3.0).**

Table 4.2. Seasonal variation in relative importance of various prey types present in the diet of demersal age 0 Atlantic cod in Goose Cove, Newfoundland, August 1993 to January 1994. Ten cod were analysed on each date.

Prey type	Aug 26	Sep 13	Sep 28	Oct 19	Nov 02	Nov 13	Nov 24	Nov 30	Dec 07	Dec 14	Dec 20	Jan 01
Calanoida												
Temora longicornis			34.41	38.48	42.91	34.93	27.19	56.98	47.88	43.05	60.09	48.15
Calanus finmarchicus			22.52	19.64	13.55	10.16	7.64					
Pseudocalanus sp.	7.27	6.01	5.00	16.07	26.16	35.29	18.04	4.99	2.26	11.00	7.14	6.79
Acartia sp.	22.42	48.59					6.19	7.02	31.72	27.61	8.17	7.48
Metridia sp.							14.06					19.76
Centropages sp.			4.99				8.55					
Other												
Harpacticoida			3.29	4.65			2.43	14.84	9.32	14.45	10.49	6.46
Cladocera	43.59	27.02	20.83	18.05	18.32	17.68	12.23					
Amphipoda	5.40		4.95	3.11		1.94		2.41	2.28	3.90	8.72	6.87
Mollusca	21.32	18.34					3.68	13.77	6.54		5.40	4.50

Table 4.3. Results of paired t-tests (p-value in parenthesis) comparing mean length (cm) and indices of condition (95% CI in parentheses) between replicate tanks (A and B) at time of death of age 0 Atlantic cod due to starvation.

Variable	A	B	t_{88}	Variable	A	B	t_{88}
Length	6.10 (0.16)	6.07 (0.16)	0.30 (0.763)	K_{WET}	0.64 (0.01)	0.62 (0.01)	2.42* (0.017)
HSI	1.10 (0.03)	1.04 (0.03)	2.97* (0.004)	K_{DRY}	0.93 (0.02)	0.91 (0.02)	1.82 (0.073)
ASH	21.54 (0.36)	21.50 (0.35)	0.17 (0.865)	$K_{ASH\ FREE}$	0.73 (0.02)	0.71 (0.01)	1.48 (0.143)

*significant difference ($p < 0.05$).

Table 4.4. Mean (±95% CI) of condition indices analysed for age 0 Atlantic cod starved from date of capture (January 01, 1994). Percent change, based on initial values, is given in parentheses. The number of cod analysed is also shown (n).

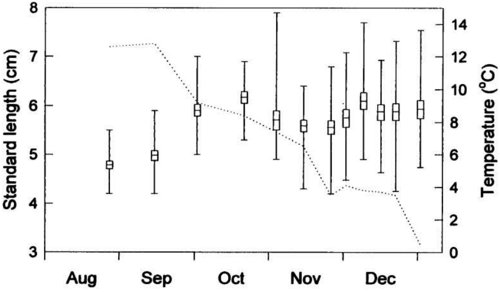
Date	n	HSI	ASH	K_{WET}	K_{DRY}	$K_{ASH\ FREE}$
Jan 01	50	4.11±0.25	17.05±0.35	0.91±0.02	1.40±0.02	1.16±0.03
Jan 14	20	1.75±0.09 (-57.4)	17.65±0.43 (+3.5)	0.88±0.04 (-3.3)	1.36±0.04 (-2.9)	1.10±0.04 (-5.2)
Jan 26	20	1.46±0.08 (-64.5)	18.18±0.34 (+6.6)	0.84±0.03 (-7.6)	1.18±0.03 (-15.7)	0.95±0.03 (-18.1)

Table 4.5. Results of paired t-tests, t and p-values, testing for difference between regression coefficients (slopes) derived from semilogarithmic relationships of various condition indices against time for age 0 Atlantic cod fed daily rations of 0.4, 0.2 and 0.1% body weight (g dry $\cdot$ g wet^{-1} $\cdot$ day^{-1}).

	0.4% vs. 0.2%		0.2% vs. 0.1%	
Variable	t_6	p	t_6	p
HSI	11.01	«0.001*	0.70	0.509
ASH	9.71	«0.001*	4.69	0.004*
K_{WET}	3.53	0.013*	3.45	0.015*
K_{DRY}	5.25	0.002*	2.73	0.038*
$K_{ASH\ FREE}$	7.42	«0.001*	4.69	0.004*

*significant difference between ration levels ($p < 0.05$).

Figure 4.1. Box plots of seasonal variation in length of age 0 Atlantic cod in Goose Cove, Newfoundland, August 1993 to January 1994. Mean (n=60), 95% CI's and range are shown. Seasonal change in water temperature is also shown (broken line).



Standard length (cm)
8
7
6
5
4
3
Temperature (°C)
14
12
10
8
6
4
2
0
Aug
Sep
Oct
Nov
Dec

Figure 4.2. Seasonal variation in a) the hepato-somatic index (HSI; •), percent body ash (◦) and b) condition factors for dry eviscerated (▲), ash free dry eviscerated (□), and wet (■) body weight of age 0 Atlantic cod in Goose Cove, Newfoundland, August 1993 to January 1994. Mean (n=50) and 95% CI's are shown.

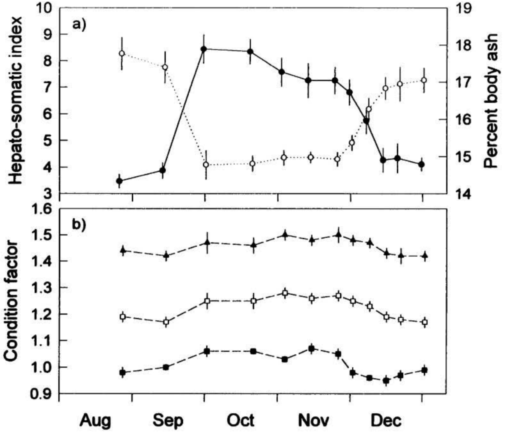

a)
Hepato-somatic index
10
9
8
7
6
5
4
3
Percent body ash
19
18
17
16
15
14
b)
Condition factor
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
Aug
Sep
Oct
Nov
Dec

Figure 4.3. Relationships between averages of a) percent body ash and b) condition factors for dry eviscerated (☐) and ash free dry eviscerated (○) body weight on hepato-somatic index for age 0 Atlantic cod in Goose Cove, Newfoundland, August 1993 to January 1994. Mean (n=50) and 95% CI's are shown. Linear equations describing the relationships are presented.

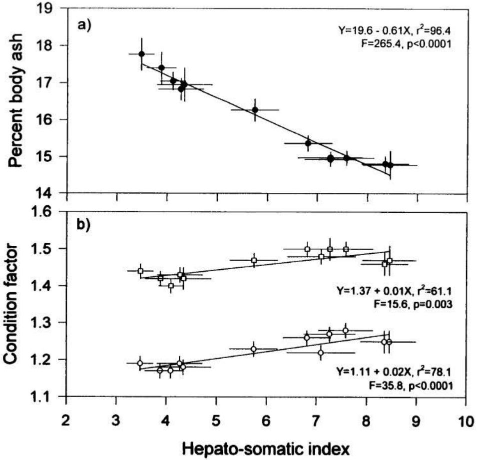

a)
Y=19.6 - 0.61X, r^2=96.4
F=265.4, p<0.0001
Percent body ash
19
18
17
16
15
14
b)
Y=1.37 + 0.01X, r^2=61.1
F=15.6, p=0.003
Y=1.11 + 0.02X, r^2=78.1
F=35.8, p<0.0001
Condition factor
1.6
1.5
1.4
1.3
1.2
1.1
2
3
4
5
6
7
8
9
10
Hepato-somatic index

Figure 4.4. Length of dying age 0 Atlantic cod obtained from two replicate tanks (◦, •) in starvation regime. Linear equations describing the relationships are presented.

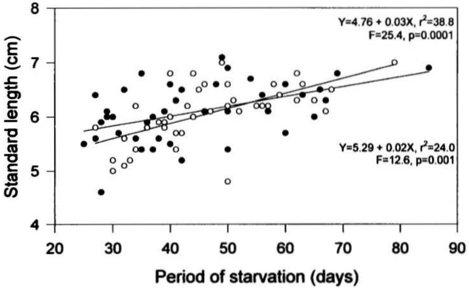
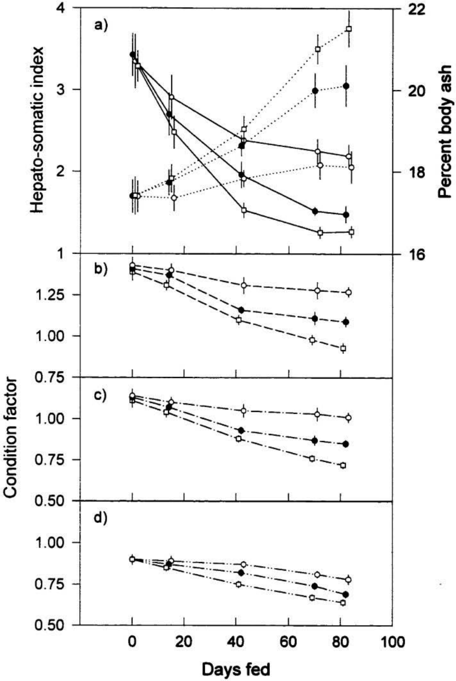

Y=4.76 + 0.03X, r2=38.8
F=25.4, p=0.0001
Y=5.29 + 0.02X, r2=24.0
F=12.6, p=0.001
Standard length (cm)
8
7
6
5
4
20
30
40
50
60
70
80
90
Period of starvation (days)

Figure 4.5. Changes in a) hepato-somatic index (solid lines), percent body ash (broken lines) and condition factors for b) dry eviscerated, c) ash free dry eviscerated and d) wet body weight of age 0 Atlantic cod fed 0.4 (◦), 0.2 (•) and 0.1% (☐) body weight per day (grams dry ·grams wet^{-1}) over a period of 82 days.



a)
b)
c)
d)
Hepato-somatic index
Percent body ash
Condition factor
Days fed
4
3
2
1
22
20
18
16
1.25
1.00
0.75
1.00
0.75
0.50
1.00
0.75
0.50
0
20
40
60
80
100

Figure 4.6. Plots of a) percent body ash and condition factors for b) dry eviscerated and c) ash free dry eviscerated body weight on the hepato-somatic index for age 0 Atlantic cod sampled from feeding regimes two through four (○) and for cod dying in the food deprivation treatment (●).

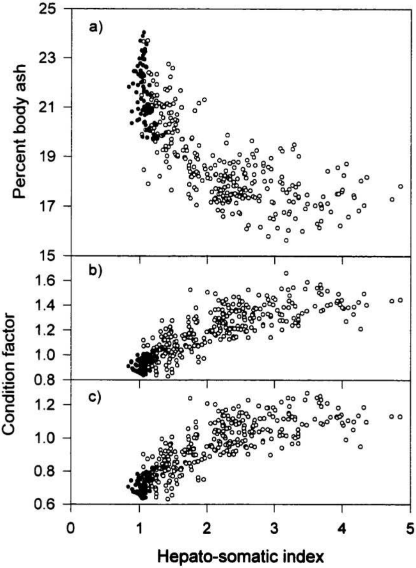
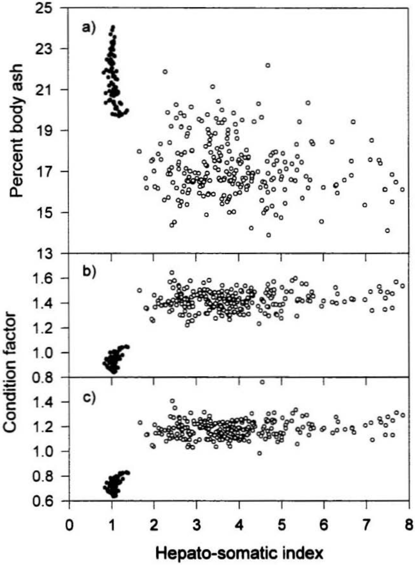

a)
b)
c)
Percent body ash
25
23
21
19
17
15
Condition factor
1.6
1.4
1.2
1.0
0.8
1.2
1.0
0.8
0.6
0
1
2
3
4
5
Hepato-somatic index

Figure 4.7. Plots of a) percent body ash and condition factors for b) dry eviscerated and c) ash free dry eviscerated body weight on the hepato-somatic index for age 0 Atlantic cod collected in Goose Cove, Newfoundland, on August 26, September 13, December 14 and 20, 1993 and January 01, 1994, (○) and for cod dying in the food deprivation treatment (●).

Percent body ash
Condition factor
Hepato-somatic index
a)
b)
c)
25
23
21
19
17
15
13
1.6
1.4
1.2
1.0
0.8
1.4
1.2
1.0
0.8
0.6
0
1
2
3
4
5
6
7
8

CHAPTER 5. Enlarged fatty livers of small juvenile cod (*Gadus morhua*): a comparison of laboratory cultured and wild juveniles

ABSTRACT

Large juveniles and adult cod (*Gadus morhua* L.) develop enlarged fatty livers when fed high-energy lipid-rich diets in captivity, however, little is known of the partitioning of growth energy of small juveniles. Indices of liver and contractile muscle condition were compared for laboratory cultured and a population of wild juvenile cod of similar size from coastal Newfoundland to determine whether small juveniles develop enlarged fatty livers in captivity. Cultured cod developed enlarged fatty livers, exhibiting significantly higher liver and contractile muscle energy reserves than wild cod. Cultured cod of similar age exhibited a high divergence in body size over time and indices of liver energy reserves were positively correlated with body size suggesting that a size-selective social hierarchy had developed in the laboratory. In contrast, indices of liver energy reserves of wild cod were negatively correlated with body size, providing evidence of high utilization of dietary lipids by larger juveniles in association with increased metabolic expenditure when feeding on small prey items. I conclude, from analysis of condition in relation to diet, that shallow nearshore regions of Newfoundland may serve as trophically adequate rearing grounds for age 0 cod during the first several months post-settlement.

INTRODUCTION

The recent decline in stocks of Atlantic cod in the northwest Atlantic has increased interest in cod aquaculture in this region. Current aquaculture approaches include hatchery operations to raise cod from eggs and grow out of undersized wild juveniles. The development of cod aquaculture in this region may prove beneficial to cod farming and may also aid in the recovery of cod stocks by supplying juveniles for stocking programs. One area which will determine the success of cod farming in the northwest Atlantic is the development of cost effective feeding programs aimed at maximizing food conversion efficiencies and growth in body length. In cod, the majority of the lipids are stored in the liver (Love 1970; Jobling et al. 1991; Hemre et al. 1993; Lambert and Dutil 1997) and when high-energy lipid-rich food is consumed in captivity, cod tend to build up excess lipids which may result in the development of corpulent livers (Lie et al. 1986; Jobling 1988; Jobling et al. 1991). This excessive build-up of lipids is undesirable as it may divert growth energy away from optimal body length increases. Although the presence of enlarged fatty livers is well documented for captive large juvenile and adult cod fed high fatty food, little is known about the partitioning of growth energy in captive small juvenile cod.

Contractile muscle protein and liver lipid represent the bulk of the energy reserves in cod (Love 1970; Hemre et al. 1993; Lambert and Dutil 1997). Lipids are largely responsible for variation in the biochemical composition of the liver, accounting for as much as 70% wet weight, while the biochemical composition of contractile muscle is almost entirely comprised of proteins (ca. 79-88% as reported by Lambert and Dutil 1997). Water content of contractile muscle and liver are highly correlated with biochemical composition and the relative energy content of these tissues (Love 1970; Holdway and Beamish 1984; Lambert and Dutil 1997).

The primary objective of this study was to advance our knowledge on the effect of lipid-rich food on deposition of energy stores in cultured juvenile cod by comparing condition indices of the liver and contractile muscle to wild juveniles. In this study, cod were cultured from artificially fertilized eggs and wild juveniles were collected during a monthly sampling program conducted in coastal Newfoundland during the autumn and winter of 1994-95. In Chapter 4, I demonstrated that wild zooplanktivorous age 0 cod were well above the condition of cod that died due to exhaustion of their energy reserves and concluded that nearshore regions of Newfoundland may serve as trophically adequate rearing grounds for the first several weeks post-settlement. Results presented in Chapter 4 provided evidence of a positive correlation between condition and the consumption of lipid-rich prey, and results on condition and diet led me to hypothesize that the periodic consumption of lipid-rich prey reduces the need for age 0 cod to build up lipid reserves prior to overwintering. Secondary objectives of this study included: 1) determining whether juvenile cod do in fact consume lipid-rich zooplankton during their first winter and 2) testing the hypothesis that nearshore regions of Newfoundland are trophically adequate for age 0 cod during their first winter.

MATERIALS AND METHODS

Atlantic cod were raised in the laboratory from naturally-spawned, fertilized eggs produced by brood stock of wild-caught fish held at the Ocean Sciences Centre, Logy Bay, Newfoundland. Eggs hatched from June 26 to July 10, 1994, and first feeding larvae were supplied wild and cultured zooplankton. Following metamorphosis, juveniles were transferred to circular (1 m × 0.5 m deep) tanks and fed finely chopped capelin (spring-summer) and herring (summer-autumn) muscle over a 10 to 15 minute period (apparent satiation), twice daily. Contractile muscle of capelin and herring is high in lipids (Love 1970). On October 12, the feeding schedule was adjusted to once every second day. At this time artificial seagrass was placed in the bottom of the tanks and stocking densities were adjusted to 50 fish per tank (0.13 fish per litre). On January 12, 1995 all cod (size range of 5.4 to 11.3 cm) within a single tank were killed (MS 222) and stored at -20°C for 2-3 weeks, and then analysed. From October to January, cod were held at about 2°C above ambient water temperature in Logy Bay, experiencing a low of 1.0°C (range of 0-2.0°C) by mid-January.

A monthly sampling program was conducted during the autumn and winter of 1994-95 to monitor diet and condition of juvenile cod settling in Goose Cove, a small cove located in Trinity Bay, Newfoundland. All samples were collected during late afternoon (i.e., 15:00-20:00 h). A complete description of the study location and method of collection (i.e., beach seine) is given in Chapter 3. Cod were killed (MS 222), placed on dry-ice, returned to the laboratory, and stored at -20°C for 2-3 weeks, then analysed.

In the laboratory, cod were thawed, blotted, measured for standard length (SL; ±1.0 mm), and wet weight (±0.01 g). Tissue water content was estimated from a standardized sample of epaxial muscle (M_{H2O}) and the whole liver (L_{H2O}), which were each blotted, weighed wet (±0.001 g), and dried to constant weight (±0.0001 g) at 60°C. Condition was also assessed by calculating Fulton's condition factor (Ricker 1975; see equation 4.1). As in Chapter 4, three separate Fulton's K values were calculated for each fish using whole wet, eviscerated dry, and ash free eviscerated dry body weight. The hepato-somatic index (HSI), was calculated as in equation 4.2. Two estimates of the HSI were calculated for each fish, using wet (HSI_{WET}) and dry (HSI_{DRY}) liver and body weights. The alimentary tract was removed for estimates of the HSI based on dry weight. Ash content (±0.0001 g) of the eviscerated body was obtained by burning in a muffle furnace for 72 h at 550°C, as recommended by the Association of Official Analytical Chemists (1965).

Cod collected in March showed a tri-modal length distribution (see Fig. 3.8). Cod from each length mode represent three intermittent settlement pulses of small recently settled age 0 cod within the nearshore waters of Newfoundland (Chapter 2 and 3). Dietary analysis was conducted on a sample of ten cod from each settlement class (i.e., August-September, October, and November-December) on a monthly basis throughout the study. Prey items in the stomach of each fish were analysed in the same manner outlined in Chapter 2. Prey importance for each settlement class was assessed using an index of relative importance (IRI; George and Hadley 1979), also outlined in Chapter 2.

Data analysis

Regression equations calculated for wild and cultured cod populations included: the various condition indices on body length, liver weight on body weight, ash body weight on length, and eviscerated dry body weight on ash body weight. When the condition indices were not corelated with body length (i.e., $p > 0.05$), I used paired t-tests (Proc TTEST, Cochran and Cox approximation, SAS 1988) to determine whether the condition indices differed significantly between populations. Regressions were fitted by the method of least squares, then the residuals were plotted against the explanatory variable to determine whether they were evenly distributed above and below zero (i.e., homoscedasticity). The residuals were also examined to determine whether a normal error structure could be assumed for each regression. When homoscedasticity and a normal error structure of the residuals could be assumed for two complimentary regression equations (i.e., liver weight-body weight for the wild and cultured cod populations) a t-test (Zar 1984) was conducted to determine whether the regression slopes differed significantly. When regression slopes did not differ, a t-test (Zar 1984) was used to determine whether the regression elevations differed significantly.

RESULTS

Condition indices that represent liver energy reserves of wild cod (HSI_{DRY}, HSI_{WET}, and liver water content) were correlated with body length throughout the study (Table 5.1). K_{WET} was correlated with body length in September and December, while condition indices that were most representative of energy reserves of the contractile muscle, specifically, K_{DRY}, $K_{ASH\ FREE}$, body ash content, and muscle water content, were correlated with body length in September, October and December. Analysis for cultured cod indicated that all condition indices representing liver energy reserves were correlated with body length (Table 5.1). When condition indices representing contractile muscle energy reserves were considered in relation to body size for cultured cod, only K_{DRY} and $K_{ASH\ FREE}$ were correlated with body length (Table 5.1).

Liver and muscle energy reserves were compared between laboratory cultured and wild cod from the March, 1995 sample. Justification for this comparison is based on the following: 1) comparable range in body size, 2) number of wild cod collected was sufficiently high, 3) lipid-rich prey dominated the diet of wild cod (see results; Table 5.3), 4) overall condition was higher than that of similar sized cod collected earlier in the season, and 5) bottom water temperature in March was comparable to that experienced by cultured cod prior to sampling (Table 5.1).

Paired t-tests (Proc TTEST, Cochran and Cox approximation, SAS 1988), comparing indices that were not correlated with body length showed that muscle condition differed significantly (K_{WET}, $t_{67} = 14.8$, $p \ll 0.001$; body ash content, $t_{69} = 9.2$, $p \ll 0.001$; muscle water content, $t_{148} = 6.24$, $p \ll 0.001$), indicating that cultured cod had relatively higher muscle mass and hence higher protein content than wild cod collected in March (Table 5.1).

Liver weight and body weight relationships were highly significant for cultured and wild cod collected in March ($p \ll 0.001$; Fig. 5.1). Comparison by t-tests revealed that the regression slopes for the cultured and wild cod population regression equations of wet ($t_{146} = 17.91$; $p \ll 0.001$) and dry ($t_{146} = 30.86$; $p \ll 0.001$) liver weight on body weight differed significantly. These results indicate that cod in the cultured population had larger livers in relation to body weight and hence higher lipid reserves.

Estimates of the condition factor based on eviscerated dry and ash free eviscerated dry body weight were positively correlated with body length for the cultured population (Table 5.1). However, analysis of the data, which consisted of a two-step process, revealed that differences in muscle mass could be assessed when eviscerated dry body weight and ash body weight were considered in relation to one another. For the first step, I considered the ash body weight to provide a reasonable measure of the skeletal weight and proceeded to test for isometric skeletal growth (b=3) in cultured and wild cod populations. The 95% CI's for the slope estimates of ash body weight on length encompassed a value of 3.0 for cultured cod and wild cod collected in March (Table 5.2). Comparison by t-tests revealed that neither the regression slopes ($t_{146} = 0.69$, $p = 0.493$) nor the elevations ($t_{145} = 0.11$, $p = 0.919$) of the regression equations differed significantly between populations. These results provide evidence of isometric skeletal growth for both populations and indicate that ash body weight at length did not differ. The second step involved examining and comparing relationships between eviscerated dry body weight and ash body weight. These regression equations were highly significant for the cultured and wild cod populations (Fig. 5.2) and t-tests indicated that the regression slopes differed significantly ($t_{146} = 13.33$, $p \ll 0.001$). This analysis indicates that higher dry body weight of cultured cod was associated with significantly higher muscle mass. However, plots of the data were observed to exhibit a high degree of overlap between the smallest individuals from both populations (Fig. 5.2). Plots of the liver weight on body weight also overlapped (Fig. 5.1) and re-analysis of the data indicated that overlap for all relationships was associated with cod <0.8 g dry body weight.

To determine whether differences in the energy reserves were significant for the smaller cod, analysis were conducted on cod <0.8 g dry body weight from both populations. Indices of muscle condition for the cultured and wild cod population were significantly different (K_{WET}, $t_{55} = 12.3$, $p \ll 0.001$; body ash content, $t_{65} = 5.9$, $p \ll 0.001$; muscle water content. $t_{42} = 4.19$, $p \ll 0.001$). Regression equations for liver weight and body weight were highly significant for both populations (cultured population, wet weights, $F_{35} = 81.65$ p $\ll$ 0.001, dry weights, $F_{35} = 81.65$ p $\ll$ 0.001; wild population, wet weights, $F_{32} = 30.54$ p $\ll$ 0.001, dry weights, $F_{32} = 21.86$ p $\ll$ 0.001) and t-tests indicated that the regression slopes were significantly different between populations for both the wet ($t_{65} = 3.8$, p $\ll$ 0.001) and dry ($t_{65} = 5.6$, p $\ll$ 0.001) weight regression equations. Eviscerated dry-ash body weight regression equations were also highly significant for both populations (cultured, $F_{35} = 421.45$, p $\ll$ 0.001; wild, $F_{32} = 1206.36$, p $\ll$ 0.001) and t-tests revealed that the regression slopes were significantly different ($t_{65} = 64.0$, p $\ll$ 0.001). Overall, these results indicate that small cod from the cultured population also had significantly larger livers and higher muscle mass than wild cod of similar body length.

Analysis of diet composition of wild cod indicated that upon settlement, all settlement classes fed predominantly on small crustacean zooplankton, specifically members of the order Calanoida (Table 5.3). All cod analysed throughout the field study had food in their stomachs. A late autumn increase in the consumption of large benthos (Mysidacea and Amphipoda) and larger planktonic Crustacea (krill) was observed for cod settling in September (Table 5.3), which coincided with an increase in body length (i.e., 8-10 cm) of this settlement class (see Fig. 3.2). Cod from the October settlement class also began to feed at higher trophic levels by late autumn. Although diet composition of the September and October settlement classes indicated a size related shift to large benthos, there was still strong evidence of a pelagic habit. In fact, all settlement classes consumed small planktonic Crustacea during the winter months sampled.

Temora longicornis and *Calanus finmarchicus* were the dominant zooplankters in the diet throughout autumn and late winter (Table 5.3). Seasonal peaks in liver energy reserves (Table 5.1) coincided with increased importance of *C. finmarchicus* in the diet of all settlement classes (Table 5.3). A high proportion of *C. finmarchicus* identified in the diets contained oil sacs indicating that increased condition of wild cod was associated with the consumption of this high-energy lipid-rich prey. Analysis revealed that 71, 86, 84 and 96% of the individuals of this species consumed by all settlement classes possessed oil sacs in September, October, February, and March, respectively.

DISCUSSION

Results presented in this study show that when small juvenile cod are fed high-energy lipid-rich diets to satiation in captivity they develop enlarged fatty livers. Cultured cod had larger livers in relation to body length and when expressed on a dry weight basis, liver weight represented as much as 27.6% of body weight compared to a high of 15.9% in wild cod. The liver weight-body weight relationships were indicative of a higher liver lipid content, while condition factor, body ash content, and muscle water content indicated that energy reserves (i.e., protein content) of the contractile muscle, were also higher in cultured cod. When eviscerated dry and ash body weight were considered in relation to one another they also provided a good indicator of differences in muscle mass. When the organic content of the body is burned-off at high temperatures, the inorganic content (ash) that remains is largely representative of bone. Thus, when skeletal growth is isometric (i.e., $b = 3$) and similar among populations, differences in eviscerated dry body weight can largely be attributed to differences in muscle mass. Regression slopes for the eviscerated dry-ash body weight equations differed significantly between cultured and wild cod of similar body length indicating that satiation feeding of lipid-rich food in captivity resulted in significantly higher muscle mass.

Laboratory studies of whole body growth and condition of cod have documented a positive correlation between the HSI and growth (Holdway and Beamish 1984; Foster et al. 1993). However, the liver is an integral component of measures of growth based on whole body weight. It is not clear whether the diets used in previous laboratory studies prevent over-excessive lipid deposition in the liver of cod as reported here and elsewhere (Lie et al. 1986; Jobling 1988; Jobling et al. 1991). These studies show that lipids in excess of immediate requirements will be stored, leading to the accumulation of lipids in the liver (Jobling 1988; Jobling et al. 1991). If cod develop corpulent livers in captivity but not in the wild, then laboratory derived relationships between the HSI and growth should be interpreted with caution. In fact, studies outlined in Chapter 4 provide evidence of an increase in body length during a decline in the HSI for a wild population of small juvenile cod. Excessive storage of lipids may reflect an "overweight" condition in small juvenile cod and reduce their ability to evade predators, which may explain the lack of evidence for the development of corpulent livers in the wild.

In this study, the population of cultured cod had a long history of lipid-rich food. Knowledge of the previous nutritional history of the wild cod population is limited to inferences that can be drawn from temperature experience and single point-in-time estimates of dietary contents and condition. Cod do not show a substantial depletion in muscle protein until the lipid reserves of the liver have been exhausted (Love 1970; Black and Love 1986; Hemre et al. 1993) and muscle protein is preferentially repleted following periods of under nutrition (Black and Love 1986). Results of a laboratory study on condition of small juvenile cod suggest that lipids are largely depleted at an HSI of about 2.0% (based on dry liver and body weight), as this value coincided with a substantial decline in indices representing variation in muscle mass (Chapter 4). Studies on cod in the northeast Atlantic suggest that a muscle water content of about 80.5% represents the "normal" condition (Love 1960). However, in the current study, wild individuals having the highest muscle water content (83.9% and 83.8%) also exhibited relatively high liver energy reserves (HSI of 13.1 and 11.9%, based on dry weights). Furthermore, high individual HSI values (>10%) were commonly associated with high muscle water content (81-82%), suggesting that the "normal" muscle water content of small juveniles may be greater than 80.5%. However, geographical differences (northeast vs northwest Atlantic) may also be important.

In the northeast Atlantic, muscle water content of cod exhibits an annual cycle; the highest water concentration is observed in March which has been attributed to starvation of juveniles and spawning in adults (Love 1960). Results presented here suggest that the relatively high condition of small juvenile cod over the winter is associated with zooplanktivory and the consumption of lipid-rich prey. At high latitudes, large calanoid copepods build up relatively large lipid reserves in their oil sacs prior to overwintering (Lee 1974; Sargent 1976; Sargent and Falk-Petersen 1988) and for *Calanus* species, total lipids often exceed 50% dry body weight throughout the winter (Gatten et al. 1980; Sargent and Falk-Petersen 1988). Evidence of decreased metabolic expenditure of small juvenile cod in cold water (Brown et al. 1989) and the high HSI values of cod captured at low temperatures during this study in February and March, suggest a long history of lipid-rich prey.

In this study, cod within the cultured population were approximately the same age, but exhibited a high divergence in size over time (5.4 to 11.3 cm), indicating that growth depensation had occurred. Studies show that growth depensation often takes place in domestic populations, even in the presence of excess food resources (see review by Ruzzante 1994). Social hierarchies are common under laboratory conditions and differences in body size can have significant effects upon an individual's ability to compete within a social situation (Abbott et al. 1985; Ruzzante 1994). Cod have been shown to exhibit size-specific social hierarchies in the wild, where larger fish controlled larger territories (Tupper and Boutilier 1995a). In the laboratory, reduced growth and relatively lower lipid reserves of smaller subordinates may result from limited access to food and (or) increased physiological stress induced by the presence of larger dominant fish (Ruzzante 1994). This study supplies little insight into the mechanism leading to growth depensation in captive populations. However, if enlarged fatty livers of the largest individuals results from size-specific social hierarchies, then future studies should focus on the effects of controlling size variation under hatchery conditions.

In Chapter 4, I found no relationship between HSI and body size for wild age 0 cod in Goose Cove during the autumn and early winter of 1993, which may be attributed to the small size range of cod studied. In this study, relationships between liver condition and body size were negatively correlated for wild cod, even during the winter months when lipid-rich prey appeared to dominate. One possible explanation for this negative correlation may be the high utilization of dietary lipids by larger juveniles in order to meet the increased metabolic expenditure associated with feeding on small prey items. Small juvenile cod exhibit a size related dietary shift from small planktonic Crustacea to larger benthic invertebrates at a size range of about 8 to 10 cm (Chapter 2; Lomond et al. 1998; this study). Growth efficiency models for fish that exhibit ontogenetic shifts in prey size (Kerr 1971a; 1971b) are based on differences in metabolic expenditure associated with feeding on small and large prey. I suggest that increased activity associated with the pursuit, capture, and consumption of small planktonic Crustacea, which provide less instantaneous energy than larger prey (Kerr 1971a; 1971b), resulted in increased metabolic expenditure, which in turn led to increased metabolism of dietary lipids by the larger juveniles.

Simple measures of condition can be a useful means of assessing energy deposition in cod because the bulk of the protein and lipid is located within contractile muscle and liver tissue, respectively. The development of enlarged fatty livers in small juvenile cod indicates the need for future studies to focus on the effect of feed formulation (protein/lipid energy: total energy) on the deposition of growth energy of hatchery reared juveniles. Methods of reducing size-specific social hierarchies, such as the effects of size-matched populations, should also be investigated. Development of enlarged fatty livers in captivity suggests that grow out and stocking programs may benefit by feeding lipid-rich food for a short period prior to release since high lipid reserves may provide a buffer, increasing survival of newly released fish until they become established in natural populations. The juvenile cod studied appeared to consume sufficient quantities of lipid-rich prey during the winter months to maintain a relatively high condition. I conclude, from results presented in this study and

Chapter 4 on condition in relation to diet, that shallow nearshore regions of coastal Newfoundland may serve as trophically adequate rearing grounds for juvenile cod during the first several months post-settlement.

Table 5.1. Water temperature (T; °C), number (n), range in length (L), and mean values for hepato-somatic index based on dry (HSI_{DRY}) and wet (HSI_{WET}) weights, liver (L_{H2O}) and muscle (M_{H2O}) water content, body ash content (ASH), and condition factors for wet (K_{WET}), dry (K_{DRY}), and ash free dry ($K_{ASH\ FREE}$) body weight for juvenile cod collected in Goose Cove, Newfoundland, from September 1994 to March 1995 and 1994-95 laboratory cultured cod. Significant correlations between condition indices and body length are also indicated ($p < 0.05$).

Sample	T	n	L	HSI_{DRY}	HSI_{WET}	L_{H2O}	M_{H2O}	ASH	K_{WET}	K_{DRY}	$K_{ASH\ FREE}$
Sep 16	12.8	50	4.8-6.6	9.87*	3.34*	50.53**	80.66*	15.03**	1.06*	1.60*	1.36*
Oct 15	7.4	75	3.7-8.7	6.76*	2.66*	59.33**	81.45*	15.88**	1.01	1.52*	1.28*
Nov 13	3.7	50	6.3-10.2	4.16**	2.01**	67.30*	81.12	15.31	1.01	1.60	1.36
Dec 10	3.2	66	3.9-10.6	4.93**	2.11**	65.45*	81.30**	15.81*	0.97**	1.51**	1.27**
Feb 19	-1.2	30	6.2-12.6	6.18**	2.59**	61.39*	81.41	16.01	0.93	1.47	1.24
Mar 26	0.5	100	5.1-13.1	8.74**	3.56**	58.91*	81.38	14.81	0.96	1.51	1.28
Cultured	1.0	50	5.4-11.3	16.66*	4.37*	36.57**	80.89	13.09	1.22	1.70*	1.48*

*index positively correlated with body length

**index negatively correlated with body length

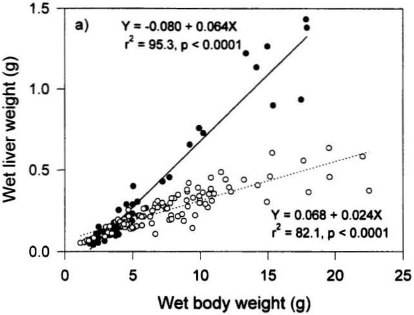
Table 5.2. Regression statistics of ash body weight on length for wild juvenile Atlantic cod captured in Goose Cove, Newfoundland, September 1994 to March 1995 and 1994-95 laboratory cultured cod. The regression equation is $\log_{10}$ weight = a + b $\log_{10}$ length.

Sample	a	b ± 95%CI	r^2
Sep 16	-3.66	3.06 ± 0.20	94.9
Oct 15	-3.70	3.07 ± 0.08	99.1
Nov 13	-3.64	3.03 ± 0.23	93.9
Dec 10	-3.65	3.03 ± 0.08	99.0
Feb 19	-3.72	3.10 ± 0.12	98.9
Mar 26	-3.69	3.04 ± 0.07	98.6
Cultured	-3.74	3.10 ± 0.15	97.4

Table 5.3. Variation in relative importance of various prey types present in the diet of juvenile Atlantic cod from the (S_1) September, (S_2) October, and (S_3) November-December settlement periods in Goose Cove, Newfoundland, September 1994 to March 1995. Apart from February (S_3; n=5), ten cod were analysed for each settlement class.

	Sep 16	Oct 15		Nov 13	Dec 10			Feb 19			Mar 26		
Prey type	S_1	S_2	S_1	S_1	S_3	S_2	S_1	S_3	S_2	S_1	S_3	S_2	S_1
Calanoida													
Temora longicornis	22.67	67.66	53.15	60.79	93.08	64.40	45.67						
Calanus finmarchicus	40.73	16.26	19.08					58.78	45.93	50.49	41.93	59.81	66.35
Pseudocalanus sp.		7.85	12.71		6.92			12.28	17.62	14.22	16.85		
Acartia sp.		3.26	2.11					3.14					
Metridia sp.								25.42	36.45	30.11	34.12	40.19	33.65
Centropages sp.			3.07							5.17	7.09		
Other													
Harpacticoida													
Cladocera	19.68												
Amphipoda	2.12			9.49		14.61	10.97						
Mysidacea				9.82			4.49						
Euphausiacea			1.97			15.92	36.35						
Mollusca	14.80	4.97	7.91	19.90		5.07	2.53						

Figure 5.1 Linear relationships between liver and body weight based on (a) wet and (b) dry weights for wild (○) and cultured (•) juvenile Atlantic cod. Regression equations, coefficient of determination (r^2), and p-values are presented for each relationship.


a)
Y = -0.080 + 0.064X
r² = 95.3, p < 0.0001
Y = 0.068 + 0.024X
r² = 82.1, p < 0.0001
Wet liver weight (g)
1.5
1.0
0.5
0.0
0
5
10
15
20
25
Wet body weight (g)

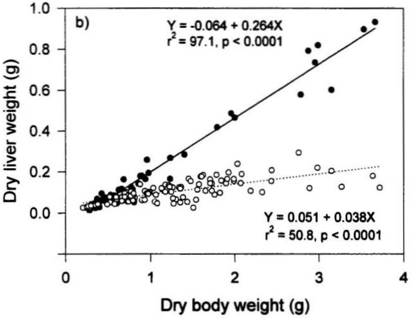
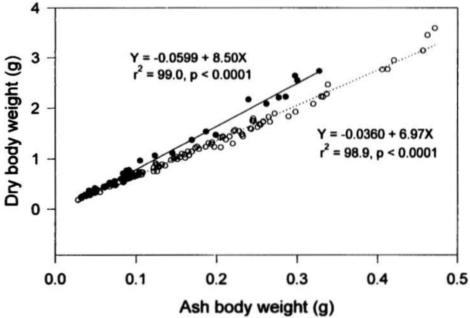

b)
Y = -0.064 + 0.264X
r² = 97.1, p < 0.0001
Y = 0.051 + 0.038X
r² = 50.8, p < 0.0001
Dry liver weight (g)
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
Dry body weight (g)

Figure 5.2. Linear relationships between eviscerated dry body weight and ash body weight for wild (○) and cultured (•) juvenile Atlantic cod. Regression equations, coefficient of determination (r^2), and p-values are presented for each relationship.



Y = -0.0599 + 8.50X
r^2 = 99.0, p < 0.0001
Y = -0.0360 + 6.97X
r^2 = 98.9, p < 0.0001
Dry body weight (g)
4
3
2
1
0
Ash body weight (g)
0.0
0.1
0.2
0.3
0.4
0.5

CHAPTER 6. Summary and conclusions

The most important original contributions of this thesis are outlined below. In Chapter 2, I established that the ontogenetic shift from feeding on zooplankton to benthos by small juvenile cod inhabiting shallow coastal waters of Newfoundland was related to the light period. Specifically, juvenile cod exhibited a size related shift from feeding predominantly on zooplankton by day to benthos at night. My findings on increased abundance of 2-3 year old cod in shallow waters at night and availability of both trophic levels of prey throughout the diel period are not new, however, when combined with my findings on differences in feeding time and location of age 0 and age 1 cod during the diel cycle they provide new evidence to explain why the shift to larger prey does not occur until juvenile cod are at least 8-10 cm in length. Specifically, my results suggest that cod accrue a size benefit at 8-10 cm in shallow coastal waters of Newfoundland and are above the upper limit of prey size for nocturnal predators. In Chapter 3, I established that post-settled age 0 cod exhibit site fidelity during the first several weeks after settling from a pelagic habit in shallow coastal waters of Newfoundland and I also provide evidence that they remain localized in shallow coastal waters over their first winter. Movement levels and behaviour in my study area differed from age 0 cod that exhibited site fidelity in Nova Scotia. Specifically, I established that in coastal Newfoundland, age 0 cod 1) form aggregations within shallow nearshore waters, 2) exhibit frequent lateral movements during the day, 3) do not move further than a few hundred metres in eelgrass habitat, but may move at least 1.2 km in no-eelgrass habitat within the first several weeks post-settlement, and 4) aggregate in relatively lower numbers at night, at which time they may disperse. In Chapter 4, I established 1) that simple indices of condition are suitable for assessing the physical fitness of small juvenile cod, 2) once small juvenile cod fall below the "normal" condition, they exhibit a depletion pattern of lipids first, followed by proteins, similar to that of larger juvenile cod, 3) critical indices of condition at which small juvenile cod die due to exhaustion of their energy reserves, thereby providing a meaningful criterion for interpreting field data on feeding, condition, and survival, 4) that as long as small juvenile cod are above the "normal" condition they may increase their body length during a decrease in condition, and 5) that shallow nearshore waters of Newfoundland may serve as trophically adequate rearing grounds for age 0 cod for the first several weeks post-settlement. In Chapter 5, I established that small juvenile cod develop enlarged fatty livers when fed high-energy lipid-rich food in captivity, similar to larger juvenile and adult cod. In Chapter 5, I tested hypotheses put forward in previous chapters, specifically that decreased prey and meal size (Chapter 2) and decreased condition (Chapter 4) of small age 0 cod prior to overwintering may influence their survival over the winter months. In Chapter 5, I established that small and large age 0 cod may consume sufficient quantities of lipid-rich prey over the winter months to maintain condition well above that of the critical condition identified in Chapter 4, indicating that shallow coastal waters of Newfoundland may serve as trophically adequate rearing grounds for the first several months post-settlement. These findings are briefly summarized below in the overall context of the risks to survival that age 0 cod are confronted with while living in the Newfoundland nearshore environment.

This thesis investigated the importance of nearshore nurseries as rearing grounds for age 0 cod by indirectly examining effects of seasonal variation in food quantity and quality on condition for the first several months post-settlement. Risk of predation was also indirectly determined during the first several months post-settlement. Although analysis of stomach contents of age 0 cod suggests that short-term variations in abundance and availability of prey occur in the nearshore environment, I conclude from related studies on condition, that nearshore regions may provide trophically adequate rearing grounds for age 0 cod in coastal Newfoundland. However, complimentary studies examining the level of movement, spatial distribution, and behaviour of age 0 cod in the natural environment provided a more complete picture of the risks to survival associated with living in the nearshore. Behaviour patterns that I identified for age 0 cod, i.e., restricted movements in shallow nearshore waters, formation of mobile aggregations (i.e., shoaling), and preference for structurally complex habitat, are mechanisms for predator avoidance. Further, my investigations on the diel behaviour patterns of age 0 cod indicated that they do in fact separate the day into an active, food gathering phase and a relatively inactive resting phase which appears to be related to predator avoidance. These results support the general conclusion of Helfman (1986) on factors affecting the diel behaviour of fish. In the present study, the relatively inactive resting phase of age 0 cod coincided with a nocturnal increase in abundance and feeding intensity of older conspecifics. Evidence of increased activity and shoreward migrations of older conspecifics at night throughout many coastal regions of the north Atlantic (Pihl 1982; Clark and Green 1990; Keats 1990; Cote et al. 1998) and evidence of relatively high rates of cannibalism on very young juveniles in coastal regions (Bogstad et al. 1994) suggests that cannibalism can reduce recruitment from nearshore nurseries in years/locations where the abundance of older juveniles is high. Mehl (1989) and Bogstad et al. (1994) have shown that density dependent predation on demersal juveniles can significantly reduce recruitment in some cases.

Size-dependent predation has been documented in piscivorous fish (Nursall 1973; Bogstad et al. 1994). Chapter 2 of this thesis provides the first documented case of a size related shift in feeding time and location of juvenile cod in coastal Newfoundland, implying that there is a high survival advantage associated with increased body length in the nearshore environment. The shift to nocturnal feeding at a size range of 8-10 cm suggests that nearshore stocking and grow out programs may benefit by releasing cod once they have reached this length-class. Results presented in Chapter 4 also imply a survival advantage associated with body size as small (i.e., <8.0 cm) age 0 cod appeared to sacrifice high pre-winter energy reserves for increased body length. A pre-winter shift in growth energy by age 0 cod and a pre-winter build-up of lipid stores in certain genera of calanoid copepodites in the marine environment suggests that maximizing growth in body length represents an evolutionary strategy that is related to high risk of predation in the nearshore environment of Newfoundland. If growth in body length is maximized by age 0 cod and an excessive build-up of energy reserves in the form of lipids diverts growth energy away from body length increases, then physiological and behavioural characters should have evolved to economize the build-up of lipid reserves in the wild. Juvenile cod held under laboratory conditions outlined in Chapter 5 may have built up excessive lipid reserves because they were growing at their maximum rate. Increased physiological stress or reduced access to food induced by the presence of larger dominant fish (Ruzzante 1994) may have reduced the maximal growth potential of the smallest individuals in the cultured population. The development of corpulent livers may reflect an "overweight" condition that influences survival by limiting the ability of small juvenile cod to escape predation in the wild. Future studies should seek to investigate the possibility that juvenile cod regulate their consumption of lipid-rich prey under natural conditions.

This study has provided fundamental information on the ecology of age 0 cod in the nearshore environment of Newfoundland and represents a step towards obtaining a clearer understanding of factors affecting survival and recruitment in these nearshore nurseries. Additional information is needed on the extent of predation mortality in coastal regions of Newfoundland, such as effects of year-to-year variation in strength among the autumnal settlement pulses of age 0 cod and movement rates and extent of cannibalism by older juveniles in shallow water habitats. High settlement strength for any particular settlement pulse may result in an increase in the abundance of larger conspecifics in shallow nearshore waters at night as well as during the daylight period. As such, nearshore regions that exhibit high densities of age 1 to 3 cod during the day may also exhibit high densities of age 0 cod. Studies in coastal regions of the northeast Atlantic show that 1 to 3 year old cod exhibit site fidelity (Smedstad et al. 1994; Hawkins et al. 1985). Evidence of a response by age 0 cod to the shoreward movement of older conspecifics (Chapter 2) and evidence of nocturnal homing to specific nearshore sites by older conspecifics in coastal Newfoundland (Clark and Green 1990), implies that future studies should seek to determine whether 1 to 3 year old cod do in fact make repeated nocturnal forays into nearshore areas that exhibit high densities of age 0 cod. Repeated nocturnal forays and search area may be related to local densities and localized movements of age 0 cod in shallow coastal waters, thus future studies should also examine the ability of older conspecifics to regulate abundances of younger juveniles in various nearshore habitats (i.e., eelgrass versus no-eelgrass). In coastal Newfoundland, age 0 cod exhibit predator avoidance behaviour during both light periods, shoaling during the day and dispersal into very shallow waters or complex bottom habitat at night. Thus, I recommend that future studies seeking to determine the magnitude of juvenile cod predation mortality in shallow nearshore waters of Newfoundland sample potential predators at regular time intervals throughout the diel period.

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