DENSITY OF JUVENILE COD IN COASTAL NEWFOUNDLAND HABITATS: MULTISCALE ANALYSES OF SPATIAL AND TEMPORAL VARIATION

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Density of Juvenile Cod in Coastal Newfoundland Habitats: Multiscale Analyses of Spatial and Temporal Variation

by

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To Jennifer; for patience,
understanding, and encouragement

Abstract

This thesis examines the relative importance of small-scale spatial and temporal variation in density of coastal populations of juvenile cod, *Gadus morhua* and how identification of this variation may contribute to a better understanding of the early life history and to the design of better sampling programs. This thesis also considers sampling variation due to fishing equipment and species identification. Populations of marine fish exhibit strong variation in yearclass strength. Hence annual variation in density was expected to exceed variation at monthly and hourly scales. Contrary to expectation, temporal variation was highest at a monthly scale for two intensively sampled sites, and was attributed to cod settling in coastal habitats in pulses during May-June, August-September, and after mid October. Settlement in May-June and after mid October was due solely to *G. morhua*. Settlement in August-September was by *G. morhua* and *G. ogac*, a sibling species that is presently difficult to identify at <50 mm. Larger cod *G. morhua* (87-135 mm) identified in this study by electrophoresis and discriminant function analyses had larger eyes and were not as deep and heavy-bodied as *G. ogac*. Highest spatial variation occurred at the scale of individual sites and was consistent with the expectation that cod were selecting specific habitats. Cod density, however, varied markedly at the same sites from year to year, indicating factors other than just habitat selection were determining local density. Variation in density of juvenile cod decreased with increasing size indicating older individuals were more evenly dispersed than younger cod. Small-scale spatial and temporal changes in catch were independent of fishing equipment. Density of juvenile cod was higher at night than during the day and higher at 4-7 m than at greater depths. These observations establish that the coastal zone represents the centre, and not the edge, of the distribution of age 0 cod during autumn. Nursery areas in the early 1990s, a time of low stock biomass must be identified as the coastal zone, not offshore.

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Chapter I Background and Approach

This thesis focuses on the early life history of the recently-settled juvenile stage of Atlantic cod (*Gadus morhua*) in coastal Newfoundland. It examines the importance of small-scale variation in population density relative to larger-scale variation. The goals of the thesis are: (i) to identify potentially important processes that contribute to variation in population density of juvenile cod at three different spatial and temporal scales, (ii) to better understand the biology of the early demersal stage, and (iii) to provide results leading to better routine sampling of juvenile cod in coastal habitats and hence contribute to the management of this species.

1.1 Importance of the juvenile stage in fisheries management

The study of variation in fish recruitment originated when Hjort (1914) hypothesised that the level of recruitment was determined during the period between hatching and yolk-sac absorption, a critical period when mortality is high and when larvae must make the successful transition to first feeding. This hypothesis continues to be the basis of research even though it has yet to be shown that yearclass strength is regulated during a particular or critical stage in the early life history of fish (May 1974, Hunter 1981, Saville and Schnack 1981, Sissenwine 1984, Leggett and DeBlois 1994). Peterman et al. (1988) suggested that research must be done on all life stages of the northern anchovy (*Engraulis mordax*), especially on individuals closer to age 1, if variation in recruitment is to be better understood. Similar conclusions were reached by Sinclair (1988) and de Lafontaine (1992) for north-temperate fishes, and by Jones (1991) for tropical reef fishes.

Recent awareness of the importance of the juvenile stage stems in part from the realization that most fishes spend only a tiny portion of their life (days to several weeks) in the egg and larval stages. It is frequently forgotten that a substantial proportion of life

is spent in the post-larval juvenile stage (several years; Sissenwine 1984, Rothschild 1986, Jones 1991) where cumulative mortality can represent a significant proportion of the total mortality encountered prior to recruitment. Sissenwine (1984) reasoned that yearclass strength was determined by the product of mortality M and the duration of time t over which mortality applies. The product of $M \cdot t$ for late larval stages and juveniles was either equal to or greater than that for eggs and early larval stages of haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*) (Sissenwine 1984). Mortality during the juvenile stage was concluded to be a significant source of mortality during the early life history of fishes and hence influence yearclass strength (Sissenwine 1984, de Lafontaine 1992).

The realization that periods of high mortality are not confined to the yolk-sac stage of fishes and that biologically significant mortality can occur after settlement is further evidence justifying the inclusion of the early demersal juvenile stage in management decisions. Two important periods of high mortality for recently-settled juveniles are settlement and overwintering. Overwintering mortality, especially during the first winter, is a well documented source of mortality for freshwater fishes (Hunt 1969, Oliver and Holeton 1979, Cunjak and Power 1987, Henderson et al. 1988, Post and Evans 1989, Miranda and Hubbard 1994). Small juvenile fish entering their first winter have lower energy stores and high metabolic rates than large juveniles and hence likely experience higher mortality in winter or spring (Paloheimo and Dickie 1966). Juveniles also undergo high mortality during settlement from pelagic to demersal habitats (Leis 1991). This is best documented for tropical reef fishes where mortality due to predation just after settlement can exceed 10% per day (Doherty 1991); consequently, many reef fishes settle at night (Victor 1991). High predation during settlement can occur when little shelter is available (Shulman 1985, Behrents 1987, Carr 1991, Tupper and Boutilier 1995a).

High mortality during yolk absorption, settlement, and overwinterning suggests that net

mortality throughout the early life of fishes may be a better indicator of the strength of a cohort than mortality determined solely at the first-feeding stage. High annual variation in recruitment (Anderson 1988, Leggett and DeBlois 1994) may therefore result from several punctuated events at different life-history stages, that may not occur in the same way from year to year. Thus a given level of survival can come about by entirely different processes that act on different stages (sizes or ages) in different years (Jones 1991, Ellertsen et al. 1995).

1.2 Life history of juvenile cod in coastal Newfoundland

Concentration of research on the adult stage, and to a lesser extent on the pelagic egg, and larval stages, has resulted in the juvenile stage of many commercially exploited fish species, (including cod, *Gadus morhua*) being poorly known. The juvenile stage is particularly poorly known and is regarded as the "missing link" in life history and fisheries studies (de Lafontaine 1992). This poor understanding of the life history of juvenile fishes is due to the high diversity of habitats used by juveniles (Walters and Juanes 1993) and the difficulties of sampling these habitats well (Horne and Campana 1989, Godø et al. 1989, de Lafontaine 1992, Hanson 1996). This has led to a dearth of studies on juvenile cod and hinders understanding the processes that influence the spatial and temporal distributions. Prior to the collapse of the Northern Newfoundland and Labrador cod stock (NAFO Divisions 2J, 3K, 3L) in 1992, there were only six refereed publications on juvenile cod (<4-yr-old) from coastal Newfoundland. These studies were done at a variety of spatial and temporal scales in shallow water (usually <30 m) using SCUBA, beach seines, and sonic telemetry. Juvenile cod (age 0 and 1) were found to be abundant in shallow water (<5 m) during autumn (Lear et al. 1980), often in areas containing macroalgae (Keats et al. 1987). Juvenile cod were also collected during winter at temperatures <1°C (Brown et al. 1989). Feeding occurred during the day, not at night when juveniles were abundant in shallow water (Keats 1990, Keats and Steele

1992). Using SCUBA and sonic telemetry, Clark and Green (1990) showed 3-yr-old cod were wide ranging (>3 km/d), nocturnally active, and migrated daily between deep cold water where they were inactive and shallow warm water where they fed during summer. In autumn, cod stayed in shallow water where they were inactive within home ranges (Clark and Green 1990).

With the exception of Lear et al. (1980), all of these studies were done at single sites or within relatively confined geographical areas and often at small temporal scales (Table 1.1). No study compared variation in density of cod among different spatial or temporal scales. For example, the study by Keats (1990), discusses variation in density of juvenile cod at the scale of approximately 12 hours (i.e. day-night). How variation compares at this scale to smaller (e.g. tidal) or larger (e.g. annual) scales is unknown because most studies describe variation at a single scale. An increasing number of studies now recognize that variation depends on the scale of observation (Schneider 1994) and are quantifying variation at multiple scales. Quantifying variation at multiple scales can lead to the identification of the spatial or temporal scale where variation is highest. Sampling effort can then be focused at this scale to help identify the processes that might be causing the variation. Multiscale studies have been used to judge the applicability of small-scale experiments to larger scales, to identify domains of equivalent spatial variation, to identify scales of maximum variation, and to provide clues to the scale of biological or physical processes that generate observed patterns of variation (Horne and Schneider 1997).

1.3 Scale, pattern, and process

In this thesis I quantify variation in the population density of juvenile cod over several spatial and temporal scales. The objective is to determine the relative contribution of small- and large-scale variation and in so doing evaluate the relative contributions of small- and large-scale processes in structuring spatial and temporal distributions of juvenile cod in coastal Newfoundland. This thesis examines the general expectation that small-scale variation can exceed variation at larger scales. This is contrary to expectation because as of yet, there is limited evidence that spatial variance in the distribution of mobile animals is concentrated at small-spatial scales (Horne and Schneider 1997). It is known that population densities of juvenile cod vary greatly at small-spatial and temporal scales (e.g. Keats et al. 1987, Keats and Steele 1992), but there has been no comparison with larger-scale variation. This lack of synthesis across small- and large-scale studies is probably due to a lack of knowledge about the relative importance of variation at different spatial and temporal scales (Downes et al. 1993).

Quantifying variation in population density at different scales can provide valuable insight into potential processes that may be important in structuring of fish communities. If variation in fish density is highest at a particular scale or over a range of scales (i.e. domain) then this hints that processes operating at this scale (or domain) may be responsible for the observed variation. For example, if variation in density is quantified at three temporal scales (among days, between day and night, and between high and low tides) and is found to be highest between day and night than this suggests that diel processes are very important in influencing the density of fish at small temporal scales. The process responsible for the variation can then be potentially identified by making a prediction and conducting appropriate experiments (Hairston 1989) at the scale where variation in highest. This experimental approach of linking process(es) with variation at

the same scale assumes experimentation is possible at the spatial and temporal scales where variation is the highest. Conducting experiments at small-spatial and temporal scales for example, is often possible. For logistical reasons alone, conducting experiments at much larger scales is much more difficult (Diamond 1986). Well designed experiments with appropriate treatments, controls, and replicates conducted at the scale of maximum variation should help isolate the source of the variation. Repeating the experiment some time later or conducting the experiment at more than one site provides additional information about the spatial and temporal scale over which the results apply (e.g. Hewitt et al. 1996).

Explaining observed patterns of variation in terms of particular processes has proven difficult (Horne and Schneider 1995). Matching pattern with process assumes that there is a direct link between variation and the process(es) that produce it (Wiens et al. 1986, Denman 1992, Horne and Schneider 1995). Matching observed patterns of variation with particular processes is difficult because variation is often the result of several processes that operate over a range of scales. For example, variation in density at an intermediate spatial scale may result from smaller or larger scale processes in addition to processes operating directly at the intermediate scale. Consequently, variation at a particular scale may not be due to any one single process operating alone at only one scale. Multiscale analyses quantify variation at several scales in the absence of any single characteristic or right scale (Levin 1991). The multiscale approach provides a more complete understanding of the relative contributions of small and larger scale processes in structuring the spatial and temporal distributions of organisms, including juvenile cod in coastal Newfoundland.

1.4 Research objectives and thesis outline

This thesis investigates four sources of variation likely to be encountered when sampling

coastal populations of juvenile cod in Newfoundland: (i) sampling variation due to species identification, (ii) sampling variation in catches and size of juvenile cod due to sampling equipment, (iii) spatial variation, and (iv) temporal variation.

Chapter II addresses the problem of distinguishing juvenile *Gadus morhua* (Atlantic cod) from *Gadus ogac* (Greenland or rock cod). These sibling species occur together as recently settled juveniles in coastal Newfoundland habitats. Despite hundreds of years of commercial fishing, over half a century of research on Atlantic cod, and several taxonomic and life-history studies (Wise 1961, Bergstad et al. 1987, Scott and Scott 1988) it is still difficult to distinguish between the recently settled juveniles of these species without the use of electrophoresis (Hovgård and Lehmann 1986). Chapter III addresses the problem of sampling juvenile cod in diverse coastal habitats and compares standardized catches from both active and passive sampling equipment. The objective was to determine if standardized catches of juvenile cod were consistent across sampling equipment deployed in the same habitat at the same time. This chapter also addresses whether size modes (age classes) of juvenile cod are consistent among sampling equipment and whether sampling equipment show consistent patterns of standardized catches at small-spatial (depth) and temporal (diel) scales. Chapter IV quantifies variation in population density of juvenile cod over three spatial scales (sites, bays, and coastal sections of 750 km) and examines the expectation that small-scale variation may be related to habitat selection. Spatial variation is compared among years (1960-1964, 1992-1996) and age classes (ages 0, 1, and 2) to determine if variation has a temporal or body size (i.e. age) component. Chapter IV quantifies variation at three temporal scales; years, months, and hours. It identifies the scale with greatest variation and determines if temporal structure is consistent at two distant sites sampled in the same manner. Processes are suggested that may contribute to the observed variation at each scale. The final chapter summarizes the contributions of this thesis.

Table 1.1 Spatial and temporal scales of studies on juvenile cod done prior to 1992 in coastal Newfoundland. ? = not stated.

Study	Spatial extent	Temporal extent	Spatial resolution	Temporal resolution	Sampling equipment	No. of observations
Lear et al. (1980)	ca. 1500 km	6 yr	?	1 yr	25 m seine	41-149 tows/yr
Keats et al. (1987)	ca. 16 km	2 yr	?	?	SCUBA	?
Brown et al. (1989)	ca. 50 m	5 mo	ca. 50 m	ca. 2 wk	9 m seine	14 tows
Clark and Green (1990)	> 8 km	6 mo	ca. 1 m	?	sonic telemetry	18 fish
Keats and Steele (1992)	?	1 mo	a SCUBA dive	?	SCUBA	?
Keats (1990)	100 m	24 hr	100 m	< 1 hr	SCUBA	9 dives

Chapter II

Distinguishing juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*)

2.1 Introduction

Species identification of fish eggs, larvae, and juveniles is usually based on one of two approaches (Berry and Richards 1973, Powles and Markle 1984, Sandknop et al. 1984). The most common approach relies on field collections and works back from known adults using diagnostic characters common to smaller individuals of a size series. A second approach relies extensively on eggs and larvae reared from known parents, and works forward. Both approaches have been used to identify *Gadus ogac* and *Gadus morhua*, two species of cod (Gadidae) that, as demersal juveniles occur together in coastal areas of the northwest Atlantic (Scott and Scott 1988, Cohen et al. 1990).

Yolk-sac larvae of *G. ogac* reared to 5.2 mm notochord length (NL) from known parents were distinguished from *G. morhua* by the absence of dorsal pre-anal pigmentation and by the maximum size of larvae that retain a yolk sac (Andersen et al. 1994). Identification of larger field-caught specimens was based mostly on body shape because counts of vertebrae and finrays overlap (Jensen 1948, Markle 1982, Scott and Scott 1988, Cohen et al. 1990). Adult *G. ogac* are described as having a more plump shape, with a thicker and broader forehead and a thinner caudal peduncle than *G. morhua* (Jensen 1948). Interorbital width as a percentage of head length is a measurement often reported to separate these species; however there is overlap (*G. ogac*: 18.0-32.9%, *G. morhua*: 15.0-23.8%; Vladykov 1945, Jensen 1948, Svetovidov 1948, Cohen et al. 1990). Other differences include colour of the lateral line (Vladykov 1945, Jensen 1948) and of the peritoneum (Svetovidov 1948, Mckenzie 1952, Scott and Scott 1988, Cohen et al. 1990).

These characteristics were based on large juvenile and adult fish. Jensen (p. 158; 1948) stated "it would presumably be difficult to distinguish the young of Ogak [=*ogac*] from those of the common cod" and this is substantiated by Hovgård and Lehmann who in 1986 reported difficulty identifying individuals <200 mm without the use of protein electrophoresis (see Renaud et al. 1986). Consequently the two species remain difficult to identify as larvae, pelagic juveniles, and metamorphosed demersal juveniles <200 mm. Individuals within this size range have not been formally compared and identified. Consequently, estimates of demersal juvenile cod (*G. morhua*) abundance from surveys in coastal nursery areas and from ichthyoplankton surveys for larvae and pelagic juveniles may be biased due to mis-identifications.

The objective of this study is to identify attributes that distinguish specimens of small (87-135 mm SL) demersal *G. ogac* from those of *G. morhua*. The approach taken was to determine species identity using protein electrophoresis and then use discriminant function analyses to identify morphological characters that can be used in the field to distinguish between these species.

2.2 Materials and methods

Juvenile *Gadus* were collected by beach seining in Little Mosquito Cove, Trinity Bay, Newfoundland (47°50.5' N, 53°53.9' W) on 23 November 1993 and 6 May 1994. Cod were placed in plastic bags (10-20 fish/bag), labelled and frozen (-7 to -10°C) within two hours of being collected. All cod were identified to species based on differences in the electrophoretic mobilities of creatine kinase and esterase proteins (described below). A total of 16 *G. ogac* were collected. All *G. ogac* were between 87-135 mm SL. Forty *G. morhua* were collected within this same size range. These 56 specimens were examined for morphometric, meristic, and pigment characters that would separate them. Additional specimens (n=47, within the same size range) from Buckleys Cove in Newmans Sound,

Terra Nova National Park (48°35' N, 53°55' W; 4-5 October 1995) and from Little Mosquito Cove (28 October 1995) were collected to test the validity of diagnostic characters established from the initial 56 specimens. Five representative specimens have been deposited at the Atlantic Reference Centre (Huntsman Marine Science Centre) in St. Andrews, New Brunswick. Reference numbers are ARC 9613048 to ARC 9613050, ARC9813166, and ARC9813167.

2.2.1 Morphometric characters

Measurements on 14 morphometric characters were taken (to 0.1 mm) on freshly thawed specimens using dial calipers (Fig. 2.1). Characters shown in Figure 2.1 are defined by Hubbs and Lagler (1958) except for the following:

- pre-anal length (PAL): tip of snout to origin of first ray of the first anal fin;
- post-orbital length (POL): posterior edge of eye to the posterior edge of opercular membrane;
- body depth at the first dorsal fin (BDD1): body depth measured at the origin of the first ray of the first dorsal fin, and similarly for body depth at the second (BDD2) and third (BDD3) dorsal fins.

2.2.2 Biochemical characters

Approximately 0.1 g of skeletal muscle from the caudal peduncle was removed from each fish after morphometric characters were quantified. Muscle tissue was stored at -70°C for electrophoretic analysis. Species identity of each sample of muscle was then determined from differences in the electrophoretic mobilities of creatine kinase and esterase proteins, as previously demonstrated by Renaud et al. (1986). Protein

electrophoresis was carried out following Ridgway et al. (1970). Gels were stained for creatine kinase and esterase using standard techniques (Harris and Hopkinson 1976). After identification of the creatine kinase band, screening for this protein was carried out using the R-250 general protein stain. When staining for esterase, α-naphthyl butyrate was used as substrate.

Prior to the study, 21 known adult *G. ogac* (ca. 305-552 mm) and 20 known adult *G. morhua* (277-375 mm) were screened with both stains to confirm that the two species could be positively identified using this method. In addition, seven known *Microgadus tomcod* (123-209 mm SL) were collected in New Brunswick, Canada and were screened to ensure that this species was not among those in field collections from the northeast coast of Newfoundland.

2.2.3 Discriminant function analyses (DFA)

DFA requires that individuals be assigned to species groups prior to analyses. Unambiguous differences in the electrophoretic mobilities of muscle proteins allowed each specimen to be classified to species. A second requirement of DFA is that the distribution of characters within groups be approximately multivariate normal (Pimentel 1979, Klecka 1980, SAS 1988). Eight of 15 measurements in the *ogac* group and 4 of 15 measurements in the *morhua* group listed in Table 2.1 showed significant deviations ($\alpha = 0.05$) from normality (Shapiro and Wilk 1965). Bliss (1967) and Pimentel (1979) report that multivariate normality is usually more closely approximated when data are log-transformed. Deviations from normality were reduced to 2 of 15 *ogac* variables and 2 of 15 *morhua* variables after morphometric characters were $\log_{10}$ transformed ($\alpha = 0.05$, Shapiro and Wilk statistic). A third requirement of DFA is homogeneity of variances. A comparison of variances by the F_{max} test (Sokal and Rohlf 1995) indicated none of the variables in the non-transformed and $\log_{10}$-transformed data sets showed

significant heteroscedasticity ($p < 0.05$). I therefore used $\log_{10}$ transformed data in the DFA given that this is a robust technique that can tolerate some deviation from the assumptions (Lachenbruch 1975, Pimentel 1979, Harris 1985).

Data analyses by the STEPDISC and DISCRIM procedures of SAS, version 6.09 (SAS 1988) were used to identify variables that contribute most to distinguishing between species (STEPDISC) and to develop equations (DISCRIM) to classify individuals. Analyses were done on 56 specimens within a size range common to both species (87-135 mm SL). Fourteen measurements listed in Table 2.1 were $\log_{10}$ transformed and examined in a forward stepwise analysis using the STEPDISC procedure. The variable that contributed most to the discriminatory power of the model at each step, as judged by the Wilks's Lambda statistic (λ), was included. This resulted in nine of 14 morphometric characters being selected: LOE ($F_{1,53}=50.0$, $p<0.0001$), WT ($F_{1,52}=50.9$, $p<0.0001$), BDD2 ($F_{1,51}=12.3$, $p=0.0009$), SNL ($F_{1,50}=8.5$, $p=0.0052$), POL ($F_{1,49}=9.2$, $p=0.0038$), HL ($F_{1,48}=5.4$, $p=0.0236$), BDD3 ($F_{1,47}=5.9$, $p=0.187$), BDD1 ($F_{1,46}=2.85$, $p=0.0978$) and UJL ($F_{1,45}=5.0$, $p=0.0291$). The value of Wilks's Lambda after inclusion of just the first two variables (eye diameter, mass) was low ($\lambda = 0.2597$) indicating that the model had reasonably good discriminatory power. These were the best two variables for discriminating between *G. ogac* and *G. morhua* at sizes from 87 to 135 mm SL. Body depth at D2 also contributed to species identification but was less important. The value of Wilks's Lambda was lowered from 0.2597 to 0.2090 with the inclusion of body depth at D2.

DFA was repeated on the residuals of morphometric data once the effect of standard length was removed from each variable by linear regression. This procedure reduced the potential for error caused by differences in the lengths of fish examined within the range 87-135 mm SL (Pepin and Carr 1993). Reanalysis resulted in the same variables, eye diameter and mass, still being the most important when distinguishing between *G. ogac*

and *G. morhua*.

Discriminant functions generated by the DISCRIM procedure (SAS 1988) were derived for each species and can be used directly for classification. Only eye diameter (LOE) and total body mass (WT) were included in the discriminant functions. The inclusion of variables with weaker explanatory power complicates the analyses and may increase the number of mis-classifications (Klecka 1980). Discriminant functions can be based on the within-group covariance matrices or on the pooled covariance matrix. The within-group covariance matrices were not significantly different (χ^2 = 0.2966, df=3, p=0.9607). Discriminant analyses were therefore based on a pooled covariance matrix. The linear discriminant function takes the general form:

$$H_t(x) = a + bLOE + cWT \qquad [1]$$

where $H_t(x)$ is the score for specimen x of species t, and a, b and c are unstandardized discriminant coefficients. The posterior probability of specimen x belonging to species t is given by:

$$pr(t \mid x) = \exp(H_t[x]) / \sum \exp(H[x]) \qquad [2]$$

where specimens were classified to species giving the highest value of H (equation 1) or highest value of p (equation 2).

I tested the effectiveness of the discriminant functions using a cross-validation procedure where a linear discriminant function, as in equation 1, was developed based on n-1 observations in the data set (Lachenbruch and Mickey 1968). The single observation not included was classified by the discriminant function and this procedure was repeated for all observations. I also determined mis-classification by applying discriminant functions

to a test data set of cod (n=47; 87-135 mm SL).

2.2.4 Meristic characters

Counts of finrays and vertebrae were taken on 14-15 *G. ogac* and 35-40 *G. morhua* identified previously to species by protein electrophoresis. All specimens were x-rayed (Hewlett Packard Model 43805N) at the Department of Fisheries and Oceans, St. Andrews, New Brunswick, Canada. X-ray radiographs were examined on a light table using a 10X lens. Counts were made on the first, second, and third dorsal fins (D1, D2, and D3), both anal fins (A1, A2), caudal fin (C), and total vertebrae (including urostyle). Counts of total gillrakers from the first gill arch were taken from 8 additional *G. ogac* for comparison with Scott and Scott (1988). Three *G. ogac* were from New Brunswick, (124-155 mm SL) and five were from northeast Newfoundland (305-489 mm).

2.2.5 Other characters

These characters included the shape of the lateral line, and overall body colour (green, red, or brown). Characters were quantified on a nominal scale and their determination was sometimes subjective. Consequently, characters were not recorded for every specimen. The lateral line character is best described by comparing illustrations of *G. ogac* and *G. morhua* in Scott and Scott (1988) on pages 266 and 270. The shape of the lateral line in *G. ogac* has a sharper angle as it descends from above the gut to the midline.

2.3 Results

2.3.1 Biochemical characters

The electrophoretic mobilities of esterase and creatine kinase unambiguously distinguished *G. ogac* from *G. morhua*; however, banding patterns were slightly different from those described by Renaud et al. (1986). When stained for creatine kinase, a single band was observed in all three species analyzed. *Gadus ogac* and *M. tomcod* expressed proteins which migrated at the same rate and were anodal (i.e. faster) to that of *G. morhua* (Fig. 2.2). All three species were fixed for their respective phenotypes. In addition to creatine kinase, the general protein stain detected two unidentified bands of equal mobilities in *G. ogac* and *G. morhua*. In *M. tomcod*, only one unidentified protein band was observed between the other two bands.

When stating for esterase, a more complex phenotype was observed for which interpretation may vary due to electrophoretic conditions or the influence of ontogeny and environment on expression of the enzymes (Mork et al. 1982). In my study, three zones of activity gave consistent results that could be scored reliably. The least anodal zone was represented by a single band that migrated at the same rate in all three species. An adjacent zone was characterized by a single band with fixed differences in electrophoretic mobility for all three species with the *G. morhua* band migrating the least anodally, the *M. tomcod* band migrating the most anodally, and the *G. ogac* band intermediate to the other two species. The most anodal zone of activity had a single banded phenotype of equal migratory distance in both *G. morhua* and *M. tomcod* and a double banded, less anodally migrating phenotype, in *G. ogac*. All three species were fixed for their respective phenotypes in this zone. None of the cod from the northeast coast of Newfoundland were *M. tomcod*.

2.3.2 Discriminant function analyses

Discriminant function analyses indicated that LOE and WT were the two variables that contributed most to distinguishing *G. ogac* from *G. morhua* between 87-135 mm SL.

BDD2 was the next best discriminating variable. LOE and WT showed little overlap between *G. ogac* and *G. morhua* (Fig. 2.3). More overlap was evident for body depth at D2 (Fig. 2.3). In general, *G. ogac* has a smaller eye (mean=26.1%, range=23.7-29.1% head length), is heavier (mean condition factor (mass·100000/SL^3) = 1.269, range=1.110-1.460) and deeper bodied (mean=18.2%, range=16.2-19.8% SL at D2) than similar length *G. morhua* (eye: mean=30.6%, range=25.3-34.7% head length; mean condition factor=1.078, range=0.862-1.419; body depth (D2): mean=17.5%, range=14.9-20.1% SL) within the range 87-135 mm SL (Fig. 2.4). Units for condition factor calculated above are g/mm^3.

The coefficients for the linear DFs with variables $\log_{10}$ transformed were:

G. ogac: $H_t(x) = -228.90 + 701.41\text{Log}_{10}(\text{LOE}) - 132.45\text{Log}_{10}(\text{WT})$ [3]

G. morhua: $H_t(x) = -308.92 + 829.14\text{Log}_{10}(\text{LOE}) - 165.28\text{Log}_{10}(\text{WT})$ [4]

I tested the robustness of the discriminant function using a cross-validation procedure on the original 56 specimens where n-1 observations were used to develop a DF leaving one observation to be classified. This cross-validation procedure was applied to every observation and resulted in 3/56 = 5.3% mis-classification error. When DFs were applied to a test data set (n=46 *G. ogac*; n=1 *G. morhua*) collected after the DFs above were developed, 5/47 = 10.6% fish were misclassified. Five *G. ogac* were misclassified as *G. morhua*.

I examined the effect of prior probabilities on the mis-classification error associated with the DFs. Prior probabilities can be thought of as a weighting procedure for the analyses that takes into account that the ratio of *G. ogac* to *G. morhua* may not always be 0.5 : 0.5. For example, if there is a high probability that most fish are *G. morhua*, then I

would want to classify an individual as *G. ogac* only if the evidence was very strong (Klecka 1980). I examined the effect of prior probabilities using the DISCRIM procedure with prior probabilities covering the range: 0.1:0.9 to 0.9:0.1 (*ogac:morhua*). Modifying prior probabilities affected mis-classification rates only slightly (3.5 to 7.1%) with mis-classification rates being equal between species at low prior probabilities of *G. ogac* (Table 2.2). There was a slight bias towards mis-classification of *G. morhua* at high prior probabilities of *G. ogac* (Table 2.2).

2.3.3 Meristic characters

Finray and vertebral counts from *G. ogac* overlapped those of *G. morhua* (Fig. 2.5). Consequently, counts were of limited use for distinguishing between species. Counts from A2 and C showed the least amount of overlap. Total gillraker counts from the first gill arch were 16-19 in three New Brunswick *G. ogac* and 21-23 in five Newfoundland specimens.

2.3.4 Other characters

Thirty-seven of 47 *Gadus* in the test data set when examined by eye shortly after capture were green in colour. Protein gel electrophoresis identified these 37 specimens as *G. ogac* based on electrophoretic mobilities of esterase and creatine kinase proteins. Nine of 47 cod in the test data set were red in colour. These nine were also identified as *G. ogac* based on protein gel electrophoresis. Colour could not be reliably determined on one specimen. This specimen was identified as *G. morhua* by electrophoresis. In general, the lateral line was more arched in *G. ogac* than in *G. morhua*.

2.4 Discussion

Gadus ogac can be distinguished from *G. morhua* by its smaller eye, deeper and heavier body, arched lateral line and green or red colour at sizes from 87-135 mm SL. The deeper and heavier body makes juvenile *G. ogac* look more robust and heavier set than *G. morhua* at comparable sizes and generally agrees with observations by Jensen (1948) for adults. The mis-identification rate of 5.6-10.3% should be reduced when lateral line and body colour characters are included in the identification process. These were not included in the discriminant function analyses because they were difficult to score on some specimens. Consequently this increased the number of specimens where data were missing. Missing observations destroy morphometric analyses (Pimentel 1979) and would result in a much smaller number of specimens being available for analyses.

Discriminant function analyses determined which of the original 14 morphometric characters were the most important in the identification process. These were eye diameter, total body mass, and body depth at the origin of the second dorsal fin. With respect to the two characters that were difficult to score, body colour (*G. ogac*: red and green; *G. morhua*: brown) and lateral line (*G. ogac*: arched; *G. morhua*: moderately arched) I found that body colour could usually be scored on most specimens and was more definitive than the subjective determination of the lateral line character. Body colour was usually retained in frozen specimens that have not dried but was usually lost when specimens were stored in formalin and ethanol. There are at least three problems with using body colour alone to distinguish between *G. ogac* and *G. morhua*: (i) external body colour has been reported to be related to diet or habitat (McKenzie 1934, Dannevig 1953, Love 1974), (ii) it was sometimes difficult to score colour on each specimen, i.e. determining when the reddish colour of some *G. ogac* looks brown, the colour usually associated with juvenile *G. morhua*, and (iii) small specimens (ca. 25-45 mm) often have

pelagic colour and not the green, red, or brown colour associated with larger more demersal specimens.

Identifications based on protein electrophoresis circumvent the necessity of using size series to identify unknown species of fish. Differences in the electrophoretic mobility of esterase and creatine kinase allowed the use of protein electrophoresis to identify individuals between 85-135 mm SL, even though these individuals were well below (ca. 200 mm Hovgård and Lehmann 1986) and well above (ca. 5 mm, Andersen et al. 1994) the sizes where identifications were previously possible. Future studies on distinguishing these species should focus on specimens between 5 to 80 mm SL, a size range where considerable variation in shape is expected to occur as larvae metamorphose to pelagic juveniles that subsequently settle from pelagic to demersal habitats.

Various characters have been reported to differ between adult *G. ogac* and *G. morhua*, but these were not evident in juveniles examined in this study. White pigment along both sides of the lateral line of *G. morhua* and the absence of light pigmentation associated with the lateral line of *G. ogac* identifies large (ca. >140 mm; Fig. 2.3 this study) specimens (see Figures 2 and 3 of Vladykov 1945, Jensen 1948) but was not evident on the smallest (ca. <100 mm) juveniles examined in this study. The larger interorbital width of *G. ogac* compared with *G. morhua* (*G. ogac*: 28.2-29.4% HL, *G. morhua*: 23.3-23.8% HL, Vladykov 1945; *G. ogac*: 23.0-32.9% HL, *G. morhua*: 19.2-22.2% HL, Jensen 1948; *G. ogac*: 22.6-23.1% HL, *G. morhua*: 15.8-20.7%, Svetevidov 1948; *G. ogac*: 18-25% HL, *G. morhua*: 15-22% HL, Cohen et al. 1990) helps distinguish adults but was not among the top nine of 14 morphometric characters ranked by DFA for juveniles in this study. Interorbital widths for juvenile *G. ogac* (mean=24.1% head length, range=21.4-26.4%) and *G. morhua* (mean=22.5% HL, range=18.8-28.4%) substantially overlapped. A third character, that of gill raker counts for eight juvenile *G. ogac* examined in this study were 16-23. These overlap with *G. morhua* (range=21-26,

Svetevidov 1948; range=21-28, Scott and Scott 1988) but low counts from 16-19 for *G. ogac* may be helpful with species identification. Gill raker counts from more than eight *G. ogac* examined in this study are required to establish this.

Finally differences in gonadal development can help distinguish maturing *G. ogac* from *G. morhua*. These include: (i) demersal adhesive eggs for *G. ogac* (Hansen 1949, Cohen et al. 1990) compared with pelagic eggs for *G. morhua* (Fahay 1983), (ii) black pigment on the ovary (Jensen 1948) or peritoneum (Svetevidov 1948, Mckenzie 1952, Cohen et al. 1990) of *G. ogac*, and (iii) spawning at a younger age or size in *G. ogac* (Scott and Scott 1988, Mikhail and Welch 1989, Morin et al. 1991). Five of the eight *G. ogac* examined for gill raker counts were also examined for black pigmentation on the gonads. Four of the five specimens were spawning and spent males and had no black pigmentation on their gonads. However the single female examined (in spent condition) had black pigmentation completely covering the gonads suggesting that black pigmentation is most commonly observed on the gonads of female *G. ogac*. It was not uncommon to observe (personal observation) *G. ogac* as small as 150-200 mm SL with developing testes in late autumn and early winter (October-December). Testes in similar sized *G. morhua*, though easily observed, remain thin and string-like with no evidence of whitish lobes containing milt. In 200 mm *G. morhua*, ovaries remain small and take up a tiny portion of the body cavity. Gonads from maturing *G. ogac* (ca. 200 mm SL) can fill a considerable portion of the posterior end of the body cavity in late autumn and winter just prior to spawning.

Confusion over the identification of these species stems in part from historically reported differences in eye diameter. Dresel (1884) originally reported that eye diameter of *G. ogac* was larger than that of *G. morhua*. Many of the diagnostic characters, including eye diameter, reported by Dresel (1884) were judged to be in error (Smitt 1892). Presently, the only quantified differences in eye diameter between these species are those of

Svetevidov (1948) who reports eye diameter ranges of 21.4-23.1% HL for *G. ogac* and 15.5-21.7% HL for *G. morhua*. These ranges contrast with the eye diameter ranges reported for juveniles in this study which were lower for *G. ogac* (23.7-29.1 % of HL) than *G. morhua* (25.3-34.7 % of HL). The differences between the findings reported here and those of Svetevidov (1948) may be due to the size of specimens examined. Cod examined in this study were 87-135 mm SL whereas Svetovidov's specimens were larger. Eye diameter expressed as a ratio of HL or SL is variable throughout the life of cod. For example, eye diameter as percent HL, may be 40-50% in larval cod (calculated from illustrations in Fahay 1983). As cod get larger, eye diameter as percent of HL becomes smaller indicating changes in measurements of these body parts are not constant. Allometric growth of body parts may explain differences in eye diameter between this study and larger specimens examined by Svetovidov (1948).

Andersen et al. (1994) warned about possible mis-identifications when analysing plankton samples from eastern Canadian coastal waters, e.g. in the Gulf of St. Lawrence and along the Newfoundland and Labrador coasts and in the Hudson Strait where *G. ogac* and *G. morhua* occur and spawn. This observation also applies to inshore surveys that target the juvenile stage of *G. morhua* in coastal Newfoundland (e.g. Lear et al. 1980, Ings et al. 1997). Consequently many of the small cod that are commonly observed around wharves and harbours of northeast Newfoundland that are locally referred to as tomcods (but not *Microgadus tomcod*) and are thought to be *G. morhua* are likely a mixture of age 0 and age 1 Greenland cod (*G. ogac*) and Atlantic cod (*G. morhua*).

Table 2.1. Statistics of measurements from *Gadus* spp. (87-135 mm SL) used in discriminant analyses. SL was not included in the analyses. Measurements are shown in Fig. 2.1. Variable abbreviations are given in the text. * indicates variable not normally distributed prior to $\log_{10}$ transformation.

	Gadus ogac (n=16)				*Gadus morhua* (n=40)			
Variable	Mean	Variance	Min.	Max.	Mean	Variance	Min.	Max.
SL	*104.4	145.3	87.9	135.8	110.2	113.3	88.2	134.6
SNL	*8.6	1.9	6.9	12.3	9.5	1.8	6.8	12.3
LOE	7.4	0.8	6.0	9.3	*9.4	0.9	7.2	11.5
PDL	34.8	24.1	27.2	47.4	36.9	20.4	28.5	46.3
UJL	12.2	4.9	9.2	16.3	11.9	2.0	9.4	16.5
HL	*28.6	14.6	23.3	39.2	30.9	11.8	24.4	40.5
BDCP	*5.3	0.7	4.3	7.6	5.0	0.5	3.9	6.8
HW	*9.7	4.0	7.0	15.3	*10.9	4.0	5.0	14.2
PAL	52.8	45.3	42.9	68.0	53.4	32.0	43.4	69.4
POL	12.6	3.7	10.0	18.0	12.5	2.5	9.9	16.7
BDD1	21.0	8.8	15.1	26.8	*21.4	9.1	16.9	28.8
BDD2	19.0	7.8	14.6	26.0	19.4	8.5	14.5	26.3
BDD3	*11.1	3.5	9.0	15.9	10.8	2.5	8.1	14.1
IOW	*6.9	0.9	5.6	9.7	7.2	2.5	4.8	12.6
WT	*15.2	44.4	8.0	34.6	*15.0	29.9	6.8	30.0

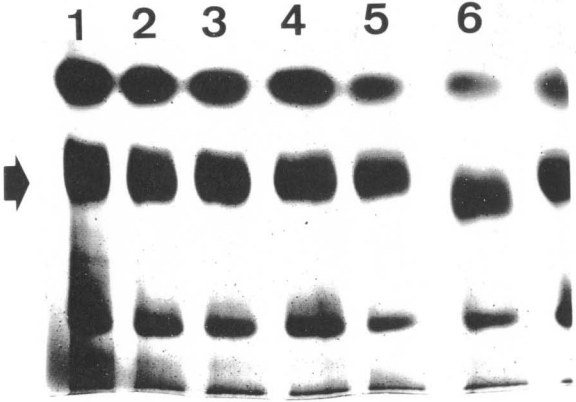
Table 2.2 Effect of altered prior probabilities on mis-classification rates of juvenile *G. ogac* and *G. morhua* in stepwise forward discriminant function analysis. n = 56.

Prior probability		Misclassification (%)		(%) Error
G. ogac	*G. morhua*	*G. ogac*	*G. morhua*	
0.1	0.9	1.8	1.8	3.6
0.2	0.8	1.8	1.8	3.6
0.3	0.7	1.8	1.8	3.6
0.4	0.6	1.8	1.8	3.6
0.5	0.5	1.8	1.8	3.6
0.6	0.4	1.8	3.6	5.4
0.7	0.3	0	5.4	5.4
0.8	0.2	0	5.4	5.4
0.9	0.1	0	5.4	5.4

Figure 2.1 Measurements taken on *Gadus* spp. Abbreviations: Standard Length (SL), snout length (SNL), length of eye (LOE), predorsal length (PDL), length of upper jaw (UJL), head length (HL), body depth at caudal peduncle (BDCP), pre-anal length (PAL), post-orbital length (POL), head width (HW), interorbital width (IOW), body depth at the first dorsal fin (BDD1) and similarly for (BDD2) and (BDD3).

HW
IOW
BDCP
BDD3
BDD2
BDD1
SL
HL
UJL
SNL
LOE
POL
PDL
PAL

Figure 2.2 General protein zymogram of muscle extract from *G. ogac* and *G. morhua*. The anode is located at the top. Creatine kinase moves from the cathode towards the anode. Arrow indicates the position of creatine kinase. 1-5, *G. ogac*; 6, *G. morhua*.


1
2
3
4
5
6

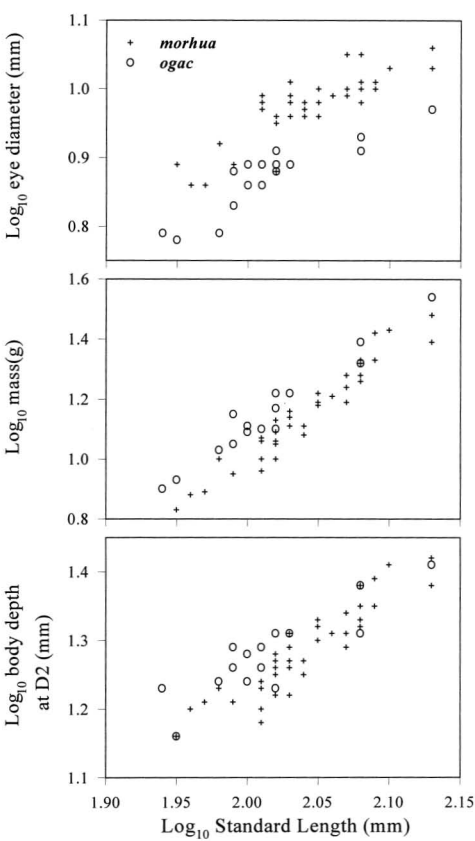


Figure 2.3 Log_{10} eye diameter (mm), total body mass (g), and body depth (mm) at the origin of the second dorsal fin plotted against log_{10} standard ength for *Gadus ogac* and *G. morhua* between 87-135 mm SL.

Figure 2.4 Demersal juvenile cod (top to bottom): *Gadus ogac*, 75 mm; *G. morhua*, 75 mm; *G. ogac*, 144 mm; *G. morhua*, 151 mm; *Microgadus tomcod*, 146 mm. These specimens have been deposited at the Atlantic Reference Centre in St. Andrews, New Brunswick. Reference numbers are: ARC9613048 to ARC9613050, ARC9813166, and ARC9813167. Black scale represents 20 mm.

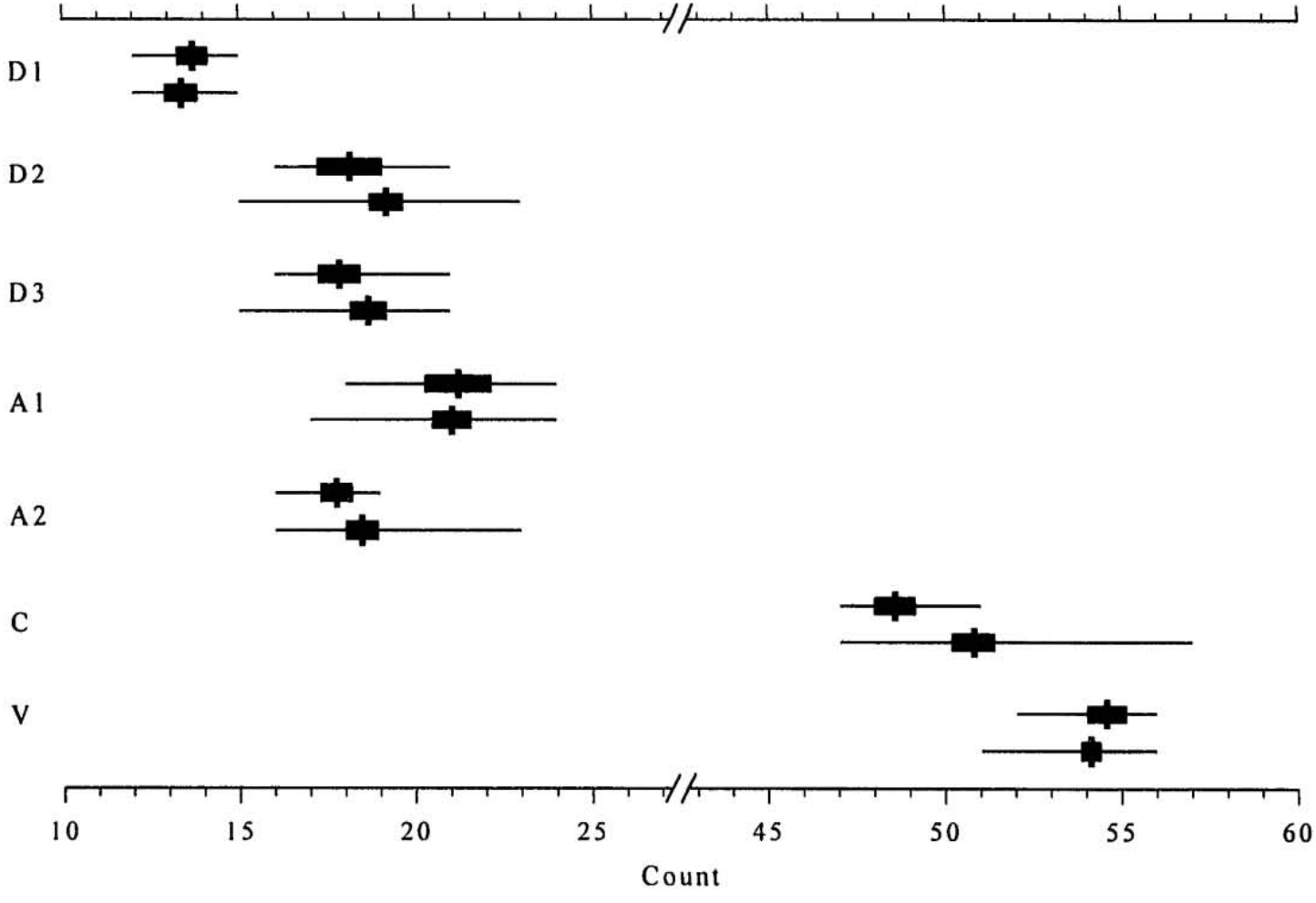


Figure 2.5 Counts of dorsal (D1-D3), caudal (C), and vertebrae (V) of *Gadus ogac* (n=14-15) and *G. morhua* (n=35-40). All specimens were between 87-135 mm SL . The range is indicated by the horizontal line, the mean by the vertical line and two standard errors on either side of the mean are indicated by the darkened box. The upper line for each pair of counts is *G. ogac.*

Chapter III

Independent patterns of variation in catches due to sampling equipment

3.1 Introduction

Variation in and prediction of recruitment are important and long-standing problems in fisheries research. Research has focused on early life stages because it is often theorized that the size of a cohort is established during a brief critical period early in the life of fishes. Hjort (1914, 1926) hypothesised that variation in size of a cohort is related to a critical period in larval life when mortality is high due to depletion of yolk and onset of starvation. The critical period concept, and estimation of recruitment from egg and larval surveys are not universally accepted (May 1974, Cushing 1981, Peterman et al. 1988). An alternative view is that variation in recruitment and cohort size are modified throughout the pelagic stage and during the first few years of life (Sette 1943, Sissenwine 1984). This view places greater emphasis on tracking cohort strength throughout the juvenile stage.

Early juvenile stages of many marine fishes inhabit both pelagic and demersal environments where they are often segregated from adults (Harden Jones 1968). Consequently a variety of sampling equipment, some specifically designed, is required to estimate juvenile abundance. In pelagic habitats, sampling early life stages of cod (*Gadus morhua*) requires relatively few gears, some of which have been quantitatively compared (Schnack 1973, Solemdal and Ellertsen 1984, Suthers and Frank 1989, Potter et al. 1990). Such comparisons have not been made for demersal stages, especially from coastal habitats where juvenile cod are often concentrated. Difficulties arise when comparing catches among demersal samplers. These include: differences between active and passive samplers (Hayes 1989, Hubert 1989), limitations due to habitat type (Godø

et al. 1989), and difficulties relating sampling effort of passive and active samplers to a standard unit of abundance (Ricker 1975, p. 19).

The main objective of this study was to determine if catches of juvenile cod from different coastal habitats could be calibrated among demersal sampling equipment (i.e. the catch of one sampler estimated from the catch of a second sampler deployed at the same time). I compared standardized catches of different sampling equipment deployed simultaneously in the same habitat. If catches can be calibrated it will be possible to estimate mortality
in different cohorts as cod grow, become more mobile, and change habitat. The data so collected allowed the testing of whether spatial gradients and temporal changes in catches were comparable across gears on a relative scale. If gradients are comparable, then pattern can be interpreted as characteristic of fish populations, not just of sampling equipment. I also tested whether size modes were common across all sampling equipment.

3.2 Methods

Most sampling was done at several shallow (usually <30 m) coastal sites using a 6 m open boat powered by a 45 hp outboard motor. Instrumentation included a depth sounder (z = m), speedometer (v = km/hr), and clock (sec). Cod caught by all sampling equipment were counted and measured for standard length (SL = mm). Sampling equipment and its deployment are described in Appendix 3.1.

3.2.1 Comparison of standardized catches

Sampling was done at several coastal sites in southern Trinity Bay, Newfoundland from

July to December 1991 (Table 3.1). Catches were compared only for equipment deployed simultaneously (within 2 hr) at the same site. Sampling equipment included: two beach seines (9 and 30.5 m) deployed from shore; a 14-m beach seine deployed from a boat; 4.9-m bottom trawl; 22.9-m gillnets; and visual observations by SCUBA divers along three fixed transects (Table 3.1). Sampling was conducted primarily during darkness when catches were highest (Methven and Bajdik 1994). Only the 14-m beach seine and gillnets were used in day time.

Catches from sampling equipment were standardized for duration of time (hr), effective fishing area of each sampler (m^2); and number of tows or nets deployed. Units of standardized catch (number hr^{-1} m^{-2}) were therefore the same for both passive (gillnet) and active (trawl, seines) samplers. The standardized catch (SC) for each sampler was calculated as:

$$SC = N\ A^{-1}\ t^{-1}\ n^{-1}$$

where N was the number of cod caught, A was the unit of effective fishing area (m^2) through which fish pass to be caught, t was the duration (hr) each sampler was deployed, and n was the number of units deployed at any one time (e.g. number of gillnets). Alternatively, n can represent the number of times a gear was deployed for a particular comparison (e.g. two trawl tows). For example, SC for a catch of 20 cod from two tows of a bottom trawl (A=5.5 m^2, Table 3.2) deployed for 10 minutes (0.17 hr), would be 20 / 5.5 m^2 x 0.17 hr x 2 = 10.67 cod m^{-2} hr^{-1}. In all cases A was the effective fishing area of the sampler, not the horizontal area swept by the sampling equipment. Table 3.2 summarizes the characteristics of each sampler.

Pearson product-moment correlation coefficients were calculated to determine if a linear relation existed between each pair of samplers for catches of cod. Correlations and

subsequent analyses of catch data were carried out within length groups (LG) that approximated age classes. Length groups (estimated from Methven and Bajdik (1994) and from length frequencies in this study) were: LG0 $\leq$96 mm SL; LG1=97-192 mm SL; LG2=193-290 mm SL.

Differences in catches among samplers were tested by ANOVA using the General Linear Model procedure of SAS (SAS 1988) for each length group. ANOVA was performed on non-transformed and on $\log_{10}(SC+1)$ transformed data. If residuals were not normal, randomization tests (Manly 1991) were used to determine if significant differences in catches occurred among samplers. Standardized catches were randomized 400 times for each length group with sampler type held constant for each test. A p value was calculated by determining the proportion of randomizations with F ratios $\geq$ the observed F ratio for each length group.

3.2.2 Comparison of size selectivity

Data for the comparison of size selectivity among sampling equipment were collected primarily at seven sites in southern Trinity Bay from July to December each year (Table 3.3). Sampling equipment included a 25-m beach seine, a fishing jigger, and the 4.9-m bottom trawl (modified with rock hopper gear), in addition to sampling equipment listed previously. Comparisons of size selectivity were based on samples taken at various times of the day or night. I recorded the method of capture for all gill-netted cod as either entangled around the mouth or around the gills and body as reported by Hovgård (1987) to determine if method of capture was influenced by fish length.

Size selectivity was examined from cumulative length-frequency plots for each sampler by the Kolmogorov-Smirnov (K-S) test statistic d_{max}. In this study, d_{max} was the maximum

absolute difference in the relative cumulative length-frequency distributions of juvenile cod between two samplers. Length data were partitioned into 4 mm length classes. Length classes of 4 mm were chosen as a compromise that minimized the number of empty cells containing zero cod and maximized the total number of cells upon which comparisons were based. Multiple comparisons by the K-S tests were done at the adjusted α of 0.01 criteria of significance as calculated by the Dunn-Šidák Method (Sokal and Rohlf 1995) for five (i-v) sets of planned comparisons: (i) 1 vs. 5 and 7; (ii) 2 vs. 2*, 3, 5, 6, 6*; (iii) [gillnets only] 38.1 mm mesh vs. 25.4 and 50.8 mm meshes; (iv) $mouth_{38.1}$ vs. $gill_{38.1}$; (v) $mouth_{50.8}$ vs. $gill_{50.8}$. Sampling equipment codes in (i) and (ii) are listed in Table 3.1. Significance criteria were adjusted to $\alpha=0.01$ because multiple comparisons lack independence. If the outcome of a single comparison was significant, the outcomes of subsequent comparisons might more likely be significant as well (Sokal and Rohlf 1995). Probability values were calculated by solving equation 11 on page 118 of Miller (1956) for the adjusted α for a known sample size and critical value of d_{max}. This equation was solved for α using only the first two terms which, depending on sample size, produced p values accurate to two or three decimal places. This method of comparing length frequencies independent of site and year assumed cod were randomly distributed with all length groups being equally available to all sampling equipment. The small number of shallow (<30 m) coastal sites sampled (<9 sites for all samplers except the rock-hopper trawl, Table 3.3) and the relatively high number of tows done (mean >50 tows per sampler, Table 3.3) suggested that observed differences in catches among samplers were not due to a few unrepresentative catches and that this method of comparing length frequencies was appropriate.

3.2.3 Spatial gradients and temporal changes in density of cod

I examined small-scale gradients in depth to determine if catches were independent of sampling equipment. Spatial-depth gradients were calculated for the bottom trawl,

SCUBA surveys, 25-m beach seine, and gillnets, all of which were deployed over a relatively wide range of depths (2.5 to 30 m). Spatial gradients were defined as the difference in catch at two locations relative to the separation (Schneider 1994). The spatial gradient ΔC (cod m^{-1}) was calculated as:

$$\Delta C = \frac{C_{zi+1} - C_{zi}}{z_{i+1} - z_i}$$

where C_{zi} was the mean catch at depth interval zi and C_{zi+1} is the mean catch at the next depth interval. For example, a mean catch (C_{zi}) of 10.5 fish at depth interval 10.1-12.5 m and a mean catch (C_{zi+1}) of 22.5 fish at the next depth interval (12.6-15.0 m) yields a spatial depth gradient of $\Delta C = (22.5\text{-}10.5)/2.5 = 5$ cod m^{-1}. Spatial gradients were calculated at a resolution of 2.5 m. The vertical resolution (of 2.5 m) was chosen as a compromise between the number of depth classes and interpretability of the depth gradient pattern.

A further test of the relation between depth and catch was done using gillnets at two coastal sites that differed in offshore depth profiles. At site 4 near Bellevue (Table 3.1), bottom depth decreased rapidly with distance offshore such that depth at 400 m offshore averaged 37.3 m. This contrasts with Hant's Harbour (48°01'N, 53°16'W) in northeast Trinity Bay where the mean depth at 400 m offshore averaged 20.7 m. Seven nets formed a right angle pattern that ran parallel to the shoreline (nets 1-3) and then away from the coast (nets 4-7). Three nets (1-3), with 100 m between each net were set along the shore. Four additional nets (4-7), with 100 m between each net, were set in an offshore direction. Net four, located at the junction of the longshore and cross-shore nets was therefore common to both series of nets. Gillnets were set late in the afternoon then retrieved shortly after dawn the following day. Sampling was repeated four times (i.e. four days) at each site with a total of 7 nets/day x 4 days/site x 2 sites = 56 nets set.

I also examined small-scale temporal changes in catches to determine if day and night differences in catches were independent of sampling equipment. Site 4 was sampled eight times on 23-24 August 1993 with gillnets. Three gillnets were deployed at the same site for three hours then were retrieved and replaced with three new nets. Site 3 was sampled on 13-15 October 1992. Two 5 minute tows by the bottom trawl were done at three hour intervals at this site.

3.3 Results

3.3.1 Comparison of standardized catches among sampling equipment

The Shapiro-Wilks statistic and plots of residuals indicated that residuals were not normally distributed when standardized catches (transformed and non-transformed) were examined for significant differences among sampling equipment by ANOVA. I therefore used randomization tests (Manly 1991) to test for differences in catches among the sampling equipment listed in Table 3.2. Standardized catches differed significantly among samplers for each length group (LG0: $p=0.005$; LG1: $p<0.0001$; LG2: $p=0.015$). Gillnet catches were orders of magnitude lower than all other samplers (Table 3.2).

I tested whether catches could be calibrated across gears by plotting catches of one sampler against a second sampler within each length group. Results for LG1 cod for all paired comparisons (Fig. 3.1) are typical for other length groups. There was only one significant correlation (out of a total of 22 comparisons): LG1 cod in gillnets were significantly correlated with LG1 cod in the 9-m beach seine ($r=0.771$, $p=0.0446$, $n=7$). The lack of correlation in most comparisons indicated that standardized catches could not be calibrated across sampling equipment on an absolute scale.

3.3.2 Comparison of size selectivity among sampling equipment

Gillnets and jiggers primarily collected individuals >150 mm SL whereas trawls and beach seines with 9 mm stretch mesh generally collected juvenile cod <200 mm SL (Fig. 3.2). Length-frequency distributions from most seines and trawls contained one or two size modes at ca. 60-75 and 120-140 mm SL (Fig. 3.2). Consequently, many of the multiple comparisons of cumulative length-frequency distributions among trawls and beach seines (Fig. 3.3) were not significantly different at the adjusted α of 0.01. For example, length-frequency distributions of juvenile cod taken by the trawl and by the same trawl modified with rock hopper gear did not differ significantly ($d_{max}=0.2445$, $n=42$, $p=0.0111$). Length-frequency distributions among the trawl, 9-m and 14-m beach seines, also did not differ significantly ($d_{max}<0.2038$, $n>37$, $p>0.2000$, in all cases). In general, the trawl and beach seines caught a very similar size range of juvenile cod (35-200 mm SL) with either one or two length modes being present. Cumulative length-frequency distributions from gillnets and the fishing jigger always differed significantly from all other gears and from each other ($p<0.0001$) because these gears generally sampled much larger cod (Figs. 3.2, 3.3).

Three size modes (148-189, 190-269, 270-370 mm SL) of juvenile cod were observed in gillnet catches (Fig. 3.4). The three size modes did not directly correspond with the selectivity of the three different mesh sizes (i.e. the 148-189 mm mode from the 25.4 mm mesh, 190-269 mm mode from the 38.1 mm mesh, and the 270-370 mm from the 50.8 mm mesh) because the 25.4 mm mesh was ineffective at catching cod (Fig. 3.4) and accounted for only 1.1% of the total gillnet catch. Size selectivity of gillnets may be related to method of capture (gill or mouth) in addition to mesh size. The two size modes present in each of the 38.1 mm (148-189 and 205-280 mm SL) and 50.8 mm (190-249 and 250-370 mm SL) meshes corresponded to method of capture with cod being meshed

around the body or gills, or alternatively, entangled near the mouth (Fig. 3.4). Mouth-caught cod were generally larger than gill-caught cod within each of these mesh sizes (Fig. 3.4). There were no significant differences between cumulative length-frequency distributions of cod taken by the 25.4 and 38.1 mm meshes (d_{max}=0.3584, n=19, p=0.0119) or between the 38.1 and 50.8 mm meshes (d_{max}=0.2112, n=53, p=0.0153) of gillnets at the adjusted α of 0.01 (Figs. 3.3, 3.4). Differences were found between the 25.4 and 50.8 mm meshes (d_{max}=0.5728, n=16, p<0.0001) and between gill-caught and mouth-caught cod taken by the 50.8 mm mesh (d_{max}=0.7635, n=29, p<0.0001). Gill- and mouth-caught cod from the 38.1 mm mesh did not differ significantly (d_{max}=0.4966, n=9, p=0.0168). Very few cod <150 mm were collected by gillnets and jiggers even though cod of this size were routinely collected by trawls and beach seines deployed in the same area at the same time. The three size modes represented in the gillnet catches (148-189, 190-269, and 270-370 mm SL) likely corresponded to the upper size limit of LG1 (148-189 mm SL), LG2 (190-269), and possibly LG3 cod (270-370 mm SL). Many comparisons of length among sampling equipment were not significantly different at α=0.01, however several comparisons (especially among the different meshes of gillnets) had p values between 0.01 and 0.02 suggesting that significant differences may occur with additional sampling.

3.3.3 Spatial gradients and temporal changes in density of cod

Gradients in catches were examined to determine whether spatial patterns were specific to individual samplers or, alternatively, if patterns were independent of sampling equipment. Plots of catch at depth (0.1 m resolution) and of spatial-depth gradients (2.5 m resolution) showed that highest catches occurred at shallow depths of ca. 5 m for LG0, LG1, and LG2 cod taken by bottom trawl, SCUBA, 25-m beach seine and gillnets (Fig. 3.5). All samplers caught fewer cod at depths exceeding 27-30 m.

A test of the relationship of catch to depth was done using gillnets at site 4 and at Hant's Harbour, two sites that differed in offshore depth profiles. Based on the depth-related pattern of catches described above (Fig. 3.5) I predicted that catch would decline with increasing depth offshore. This was the pattern observed at site 4 where depth decreased from 6.7-8.3 m nearshore to 37 m at 400 m offshore (Fig. 3.6). At Hant's Harbour, a site with a more uniform cross-shore depth gradient (range 12.0-20.7 m, Fig. 3.6), cross-shore catches of gillnetted cod were similar to longshore catches and consequently did not show the decline that was evident with depth at site 4 (Fig. 3.6). Catches differed significantly between longshore and cross-shore gillnets at site 4 (ANOVA, $F_{1,95}=15.16$, $p=0.0002$) but not at Hant's Harbour (ANOVA, $F_{1,95}=0.83$, $p=0.3637$), again indicating the importance of depth.

Temporal patterns in catches among sampling equipment were compared for two 24-hr collections by bottom trawl (11-14 m, site 3) and by gillnet (4-17 m, site 4). At the temporal scale of day vs night a strong pattern was evident with 91.6% (trawl) and 73.8% (gillnet) of all juvenile cod caught at night (Figs. 3.7, 3.8).

3.4 Discussion

Repeated deployment of several demersal samplers in different coastal habitats indicated: (i) catches could not be calibrated across samplers deployed simultaneously at the same site; (ii) size modes of juvenile cod were independent of sampling gear, similar among trawls and beach seines but contrasted with the larger cod taken by gillnets and jiggers; (iii) standardized catches differed among samplers, with gillnet catches being much lower than catches for all other samplers; and (iv) spatial-gradients and diel-changes in catches were comparable across samplers.

Substantial effort was devoted in this study to matching samplers by time and location

to reduce error in calibration. Despite this, it proved impossible to calibrate standardized catches across samplers. It was possible to identify a series of length modes that were consistent across most samplers. Modes occurred at approximately 50-77, 120-140, and ca. 200-300 mm SL. The smallest mode, best sampled by beach seines and trawls with 9 mm mesh, were age 0 cod that settled in autumn (Pinsent and Methven 1997). Cod between 200-300 mm SL were best sampled by gillnets and were in the size range (22-27 cm) of 2-yr-olds (Fleming 1960). The size mode between age 0 and age 2 cod ($\approx$ 120-140 mm SL) likely represents age 1 cod that have overwintered but there appears to be no confirmation of this for cod from Newfoundland based on ages determined from otoliths.

Patterns of relative change in abundance with time of day and with depth could be identified independent of sampling equipment. The different types of sampler (passive, active, and visual observations by divers) used to collect juvenile cod over a 24-hr period at the same site in this and other studies (Keats 1990, Methven and Bajdik 1994, and Gibson et al. 1996) all show higher catches at night indicating this pattern is independent of gear and characteristic of coastal populations of LG0 and LG1 cod. This pattern is interpreted to be due to an inshore movement at dusk or night and not due to a substantial change in catchability. This interpretation is consistent with Keats (1990), Methven and Bajdik (1994), Gibson et al. (1996) who reported higher night-time catches for both active and passive samplers in addition to visual observations by SCUBA divers and underwater video. Rapid inshore and offshore movements at dusk and dawn by a variety of fishes (Helfman 1993) indicate collections taken at these times may not be representative of typical day-time densities.

Spatial-depth gradients were also similar among sampling equipment when averaged across sampling sites. Highest catches occurred at shallow (4-7 m) depths close to the coast. This pattern is not unique to LG0 and LG1 cod in Newfoundland waters. Catches

of 0-group cod off the English and Welsh coasts taken by a 2 m beam trawl were highest at ca. 6 m depth (Riley and Parnell 1984). Highest catches of age 1 cod sampled by gillnets off southwestern Greenland were taken at 3-10 m with lowest catches occurring at depths <3 m and >20 m (Hansen and Lehmann 1986, Hovgård and Nygaard 1990). Gibson et al. (1996) reported highest catches of juvenile cod in Scotland at 5 m over the range 0.5 to 5.0 m. Acoustic surveys in Finnmark, Norway showed that most juvenile cod occurred at depths shallower than 35 m, with highest densities occurring closest to the coast where the vessel could not sample (Olsen and Soldal 1989). These studies sampled a variety of habitats and depths with different equipment and showed that the coastal distribution of 0-group cod occurred at shallow depths with larger juveniles occurring at progressively deeper depths and distance from the coast (Hansen 1966, Hislop 1984, Riley and Parnell 1984, Tremblay and Sinclair 1985, Dalley and Anderson 1997). This positive relation between size and depth is characteristic of many species and implies an movement towards deeper water with increasing size (Macpherson and Duarte 1991). This was first described by Heincke (1913) for plaice (*Pleuronectes platessa*) in the North Sea and was referred to as Heincke's Law (Wimpenny 1953). Consequently juveniles of many temperate demersal fish species occur in shallow, well lit water relative to the adult stages in deeper water.

At the scale of hundreds of kilometres LG0 and LG1 cod were presently (mid-1990s) confined to the coast of Newfoundland during autumn (Dalley and Anderson 1997). This study extends this result to a finer scale of tens of metres. Within the coastal zone, LG0 cod reached maximum densities at depths of 4-7 m. This confirms observations of Lear and Green (1984) that nursery areas for LG0 cod are located along the coast. The prevailing southward flow of the Labrador Current will tend to carry eggs and larvae toward the coast due to Coriolis forces, although this tendency is episodically reversed at the surface by strong wind events from the southwest (Templeman 1966, Frank and Leggett 1982, Rose and Leggett 1988, Schneider and Methven 1988). A physical model

of egg and larval drift (Helbig et al. 1992) showed that eggs spawned offshore generally remained offshore, but more recent models (Davidson and deYoung 1995, Pepin and Helbig 1997) showed that coastal transport was possible for particles seeded along the shelf break to the north of Newfoundland, but not to the east. These observations together with the current absence of LG0 cod away from the coast, a spawning failure of the offshore components of the 2J, 3K, and 3L Newfoundland-Labrador cod stock (Dalley and Anderson 1997), and well documented spawning along the northeast coast of Newfoundland (Thompson 1943, Hutchings et al. 1993, Laprise and Pepin 1995, Smedbol and Wroblewski 1997) are consistent with a coastal origin for many of the newly settled cod collected along the coast in shallow (4-7 m) water. In the past, coastal areas may have served as nursery areas for both inshore and offshore spawning fish (Lear and Green 1984). Concentration of newly settled demersal cod in the horizontal dimension can be achieved either by (i) an active migration towards the coast, possibly in response to light, depth, or salinity gradients (Riley and Parnell 1984, Tremblay and Sinclair 1985, Angel 1992) or, (ii) from wind induced coastal upwelling where demersal juveniles can be moved toward the coast in bottom water drawn shoreward during upwelling.

Because pelagic eggs and newly hatched larvae drift, spawning location cannot account for the smaller-scale concentration of LG0 cod at 4-7 m. I propose that shallow waters act as traps for vertically migrating pelagic cod that settle upon encounter with suitable bottom habitat, and that they undergo increasingly extensive vertical migration as they increase in size before settling. Vertical migration begins during the pelagic stage, as juveniles ascend towards the surface during darkness and descend during daylight (Koeller et al. 1986, Perry and Neilson 1988). On Georges Bank these diel vertical migrations kept cod in contact with their major prey (*Neomysis americana*, *Tisbe sp.* and *Pagurus* larvae) at thermally stratified and non-stratified sites (Perry and Neilson 1988). As the length of individual cod increased, the vertical extent of the pelagic migration

increased (Perry and Neilson 1988) until individuals eventually encountered the bottom. The relation between length of cod and the extent of diel vertical migration is reported for another gadid, walleye pollock (*Theragra chalcogramma*, Bailey 1989) and for fish in general (Neilson and Perry 1990). Predictions based on the combined observations from this and previous studies are: (i) size of individual cod at settlement will be less on shallow banks and coastal areas than on deeper banks, (ii) shallow sites will have a higher proportion of smaller cod than deeper sites, and (iii) recently settled cod will be more aggregated than their pelagic counterparts because shallow banks (and especially coastal areas) act as traps that concentrate settled cod.

Ultimate, or evolutionary factors favouring settlement of juvenile cod in coastal habitats include reducing predation and maintaining contact with a familiar and relatively abundant pelagic food supply. Both factors increase survival. Predation is reduced because larger (predatory) fishes tend to occupy deeper water (Helfman 1978, Macpherson and Duarte 1991). Coastal sites also provide abundant fleshy macroalgae, a preferred habitat that in addition to cobble, provides juvenile cod with cover from predation (Keats et al. 1987, Gotceitas et al. 1995). Settlement in shallow water also helps maintain contact with pelagic food in the surface layer until cod reach 60-100 mm, the size at which they make the transition to predominately benthic prey (Lomond et al. in press).

Preferential settlement in shallow water can explain the coastal distribution of recently settled cod in Newfoundland but, by itself, cannot explain the distribution of newly settled cod off Nova Scotia, New England, and in the Gulf of St. Lawrence where LG0 and LG1 cod were either not collected in shallow water or attained maximum densities at depths greater than the 4-7 m observed in this study (Targett and McCleave 1974, McCleave and Fried 1975, Macdonald et al. 1984, Horne and Campana 1989, Lough et al. 1989, Black and Miller 1991, Hanson 1996, but see Tupper and Boutilier 1995a,

1995b). Warmer surface water may be an important variable that restricts 0- and 1-group cod to deeper water south of Newfoundland. A second possibility relates to spawning locations south of Newfoundland. If spawning occurs primarily offshore and if passive eggs and larvae are not advected towards the coast then extensive settlement may not occur at the coast. For example, similarity in the patterns of egg and larval distributions offshore on the Scotian Shelf at any one time, as well as the persistence of the larval distributions over certain offshore banks led O'Boyle et al. (1984) to suggest that eggs and larvae were retained by gyral circulation associated with offshore banks and that the spawning and nursery grounds are often located within the same geographical area offshore (Gagné and O'Boyle 1984).

At present (early to mid-1990s), the coastal zone nursery area for LG0 cod is the only confirmed source of recruits in Newfoundland. My study, in conjunction with Dalley and Anderson (1997) establishes that shallow coastal depths represent the centre, and not the edge, of the distribution of LG0 cod. These results indicate that a coastal survey (e.g. Schneider et al. 1997, Ings et al. 1997), together with an inshore-offshore survey (Dalley and Anderson 1997) in deeper water are sufficient to track annual changes in distribution and abundance of juvenile cod off eastern Newfoundland during the three years prior to recruitment to the fishery. Each survey has disadvantages. Coastal surveys with large seines do not sample large (>200 mm) juvenile cod well, likely because of gear avoidance. Coastal surveys (e.g. Tveite 1984, Ings et al. 1997) are also restricted to relatively smooth bottom habitats near the coast. Consequently they may not be a good indicator of cod abundance in deeper water. Offshore demersal surveys often use large ships (e.g. Dalley and Anderson 1997) that cannot sample the immediate nearshore zone at 4-7 m where density was highest. In addition, offshore surveys generally do not catch as many LG0 cod compared with LG1 cod, due possibly, to not sampling depths <60 m. Neither survey, by itself can provide an accurate representation of the abundance and distribution of juvenile cod. Both a coastal survey and an offshore survey are required

to track relative cohort strength of demersal cod during the first three years of life.

Table 3.1 Description of sampling sites and location of sampling gear deployment. Gears are: 1 - gillnets; 2 - trawl; 3 - 9-m seine; 4 - SCUBA; 5 - 30.5-m seine; 6 - 14-m seine. (# refers to site number used throughout the text).

(#) Site	Coordinates	Exposure[1]	Equipment	Depth (m)	Substratum[2]
(1) Bellevue	47°38'N, 53°43'W	sheltered	1,2,3,4,5	1.5-4.0	pebble, cobble sand in deeper water
(3) Beach	47°38'N, 53°46'W	intermediate	1,2,4	7-12	pebble, broken shells
(4) Trap	47°39'N, 53°43'W	exposed	1,2,4	5-30	boulder, bed rock, sand at deeper depths
(5) Master's Head	47°43'N, 53°50'W	intermediate	1,6	6-10	coarse sand to cobble
(6) Bald Pt. Beach	47°50'N, 53°52'W	intermediate	1,6	6-25	pebble, cobble, boulders in deeper water
(7) Little Mosquito Cv.	47°50'N, 53°53'W	sheltered	1,6	3-8	pebbles, mud
(8) Deep	47°39'N, 53°46'W	exposed	1,2	18-35	sand

[1] Follows criteria in Steele (1983)
[2] Follows Wentworth Scale (Lincoln et al. 1982)

Table 3.2 Parameters for sampling equipment. A was the effective fishing area of a gear (m^2). t was the total time (hr) sampling equipment was deployed. t was constant for beach seines and variable for other gears. n was the number of nets (i.e. gillnets) deployed, or alternatively the number of tows (i.e. trawls or beach seines) for each comparison. Mean standardized catches (SC = fish m^{-2} hr^{-1}) are given for length groups of juvenile cod (LG0, LG1, LG2) as defined in the text.

				Standardized catches		
Sampler	A	t	n	LG0	LG1	LG2
30.5-m seine	73.2	0.08	1	0.78	3.90	0.32
9.0-m seine	8.2	0.05	2	4.15	4.15	0.17
14-m seine	21.0	0.06	3	6.34	3.43	0.10
gillnets	54.9	≈15.00	3	0.00001	0.00082	0.001
SCUBA	9.0	≈0.36	1	3.31	2.82	0.06
4.9-m trawl	5.5	≈0.17	2	4.93	4.40	0.14

Table 3.3 Sampling effort in study of size selectivity among sampling equipment. Sites 34 and 58 were located in Trinity (48°23N, 53°22'W) and Notre Dame (49°31'N, 54°48 W) Bays respectively. rhg - rock-hopper gear. misc - 24 sites in Trinity and Conception Bays.

Sampling equipment	Month	Sites	Number of times sampling equipment deployed	No. fish measured
30.5-m seine	Sep-Nov 1991	1	5	153
9.0-m seine	Jul-Dec 1991 1982, 1989, 1992, 1993	1	59	945
14-m seine	Oct-Nov 1991	5,6,7	7	387
gillnets	Aug-Dec 1991 Jul-Dec 1993	1,3,4,5,6,7,8 3	165	3143
4.9-m trawl	Aug-Dec 1991	1,3,4,8	64	1593
4.9-m trawl (rhg)	Aug-Dec 1992 Aug-Dec 1993	3, misc.	43	353
jigger	Oct 1991	8	1	135
25-m seine	Jul-Dec 1992 Jul-Dec 1993	6,7,34,58	110	12656

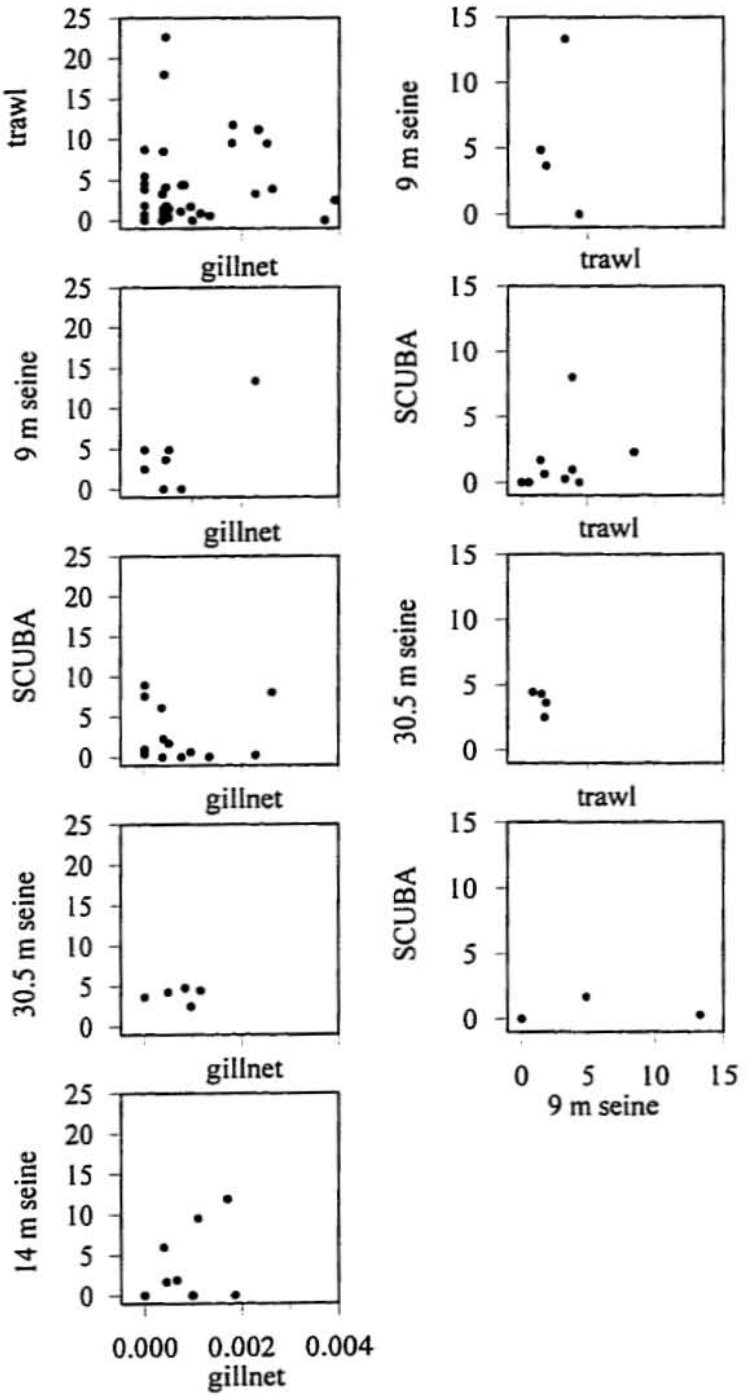


Figure 3.1 Standardized catches (SC = number m^{-2} hr^{-1}; on the y and x axis) of LG1 cod from different sampling equipment that was deployed within two hours at the same site for each paired comparison.

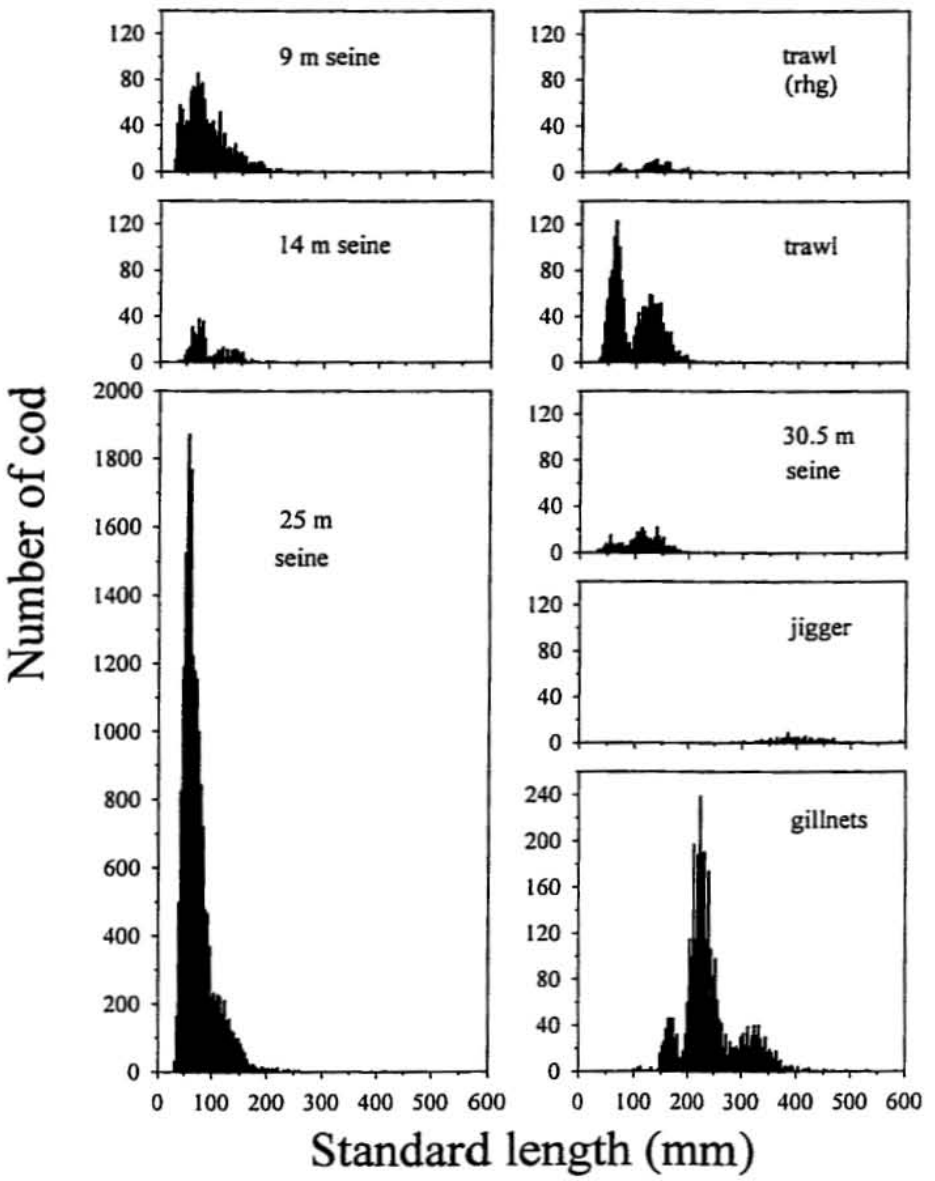


Figure 3.2 Length-frequency distributions of juvenile cod (4 mm length intervals) collected at several sites along the northeast coast of Newfoundland. Sampling equipment is described in the text. (rhg) = rock-hopper gear.

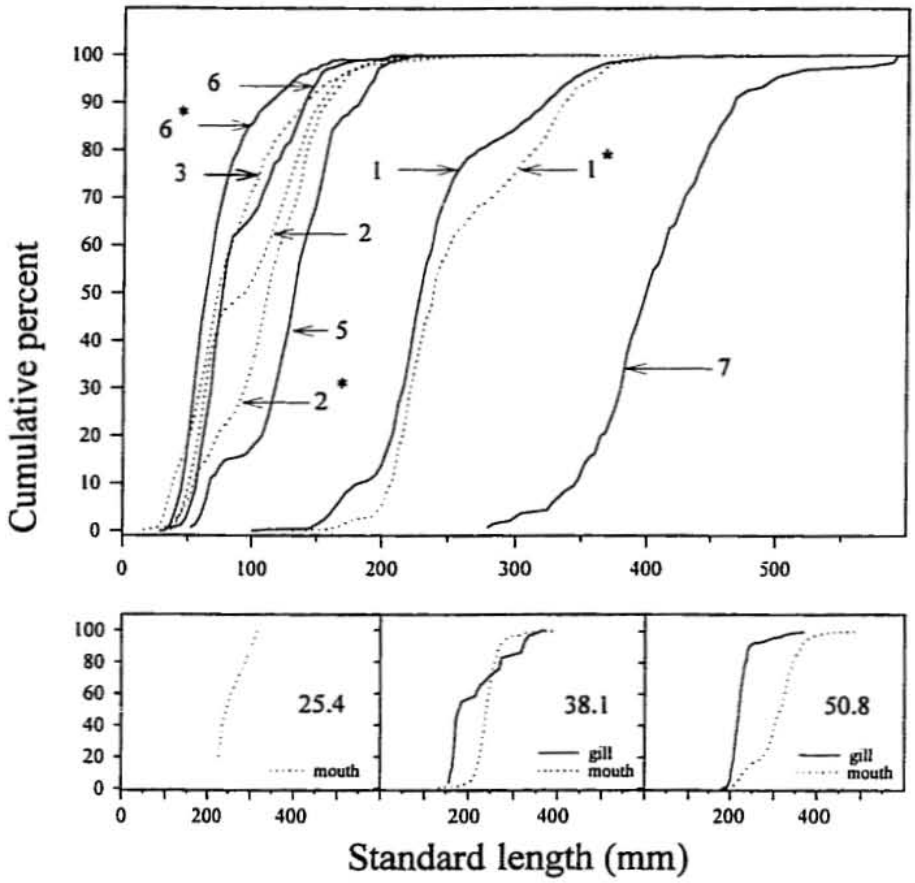


Figure 3.3 Length-frequency data on cod (4 mm length groupings) illustrated as as cumulative frequency (in per cent). Lower panels show cumulative number of cod caught by 25.4, 38.1, and 50.8 mm meshes in gillnets in 1993 for each method of capture (gill, mouth). Gears are: 1 - all gillnet collections, 1* - all gillnet collections from 1993, 2 - bottom trawl, 2* - trawl with rock-hopper gear, 3 - 9 m beach seine, 5 - 30.5 m beach seine, 6 - 14 m beach seine, 6*- 25 m beach seine, 7 - jigger.

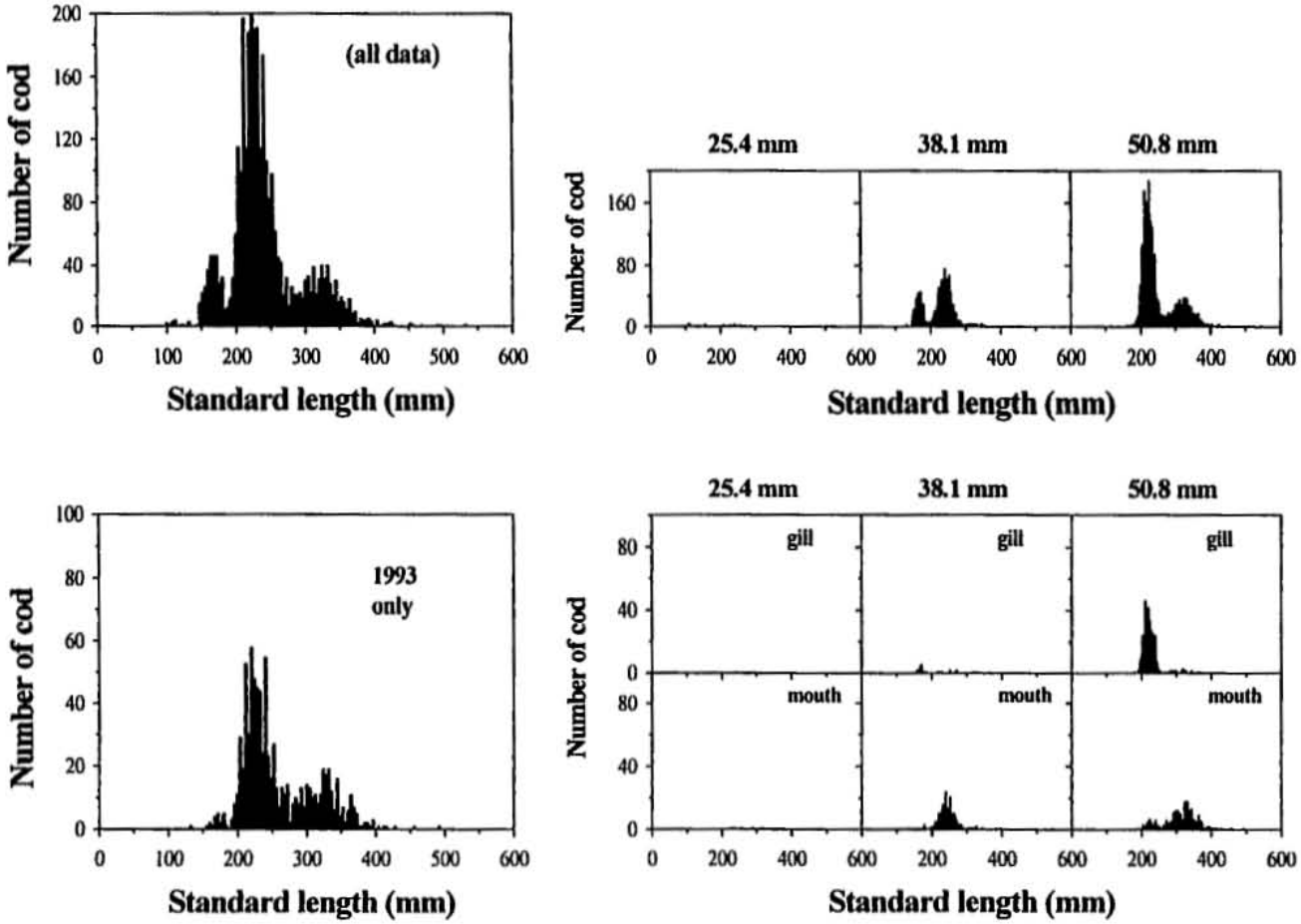


Figure 3.4 Length-frequency distributions of juvenile cod (4 mm intervals) collected by gillnets (upper panels) in 1991-1993, with corresponding breakdown by stretch mesh size (25.4, 38.1, 50.8 mm). Lower panels show length-frequency distribution of all cod taken in 1993 with corresponding breakdown by mesh size and method of capture (gill, mouth).

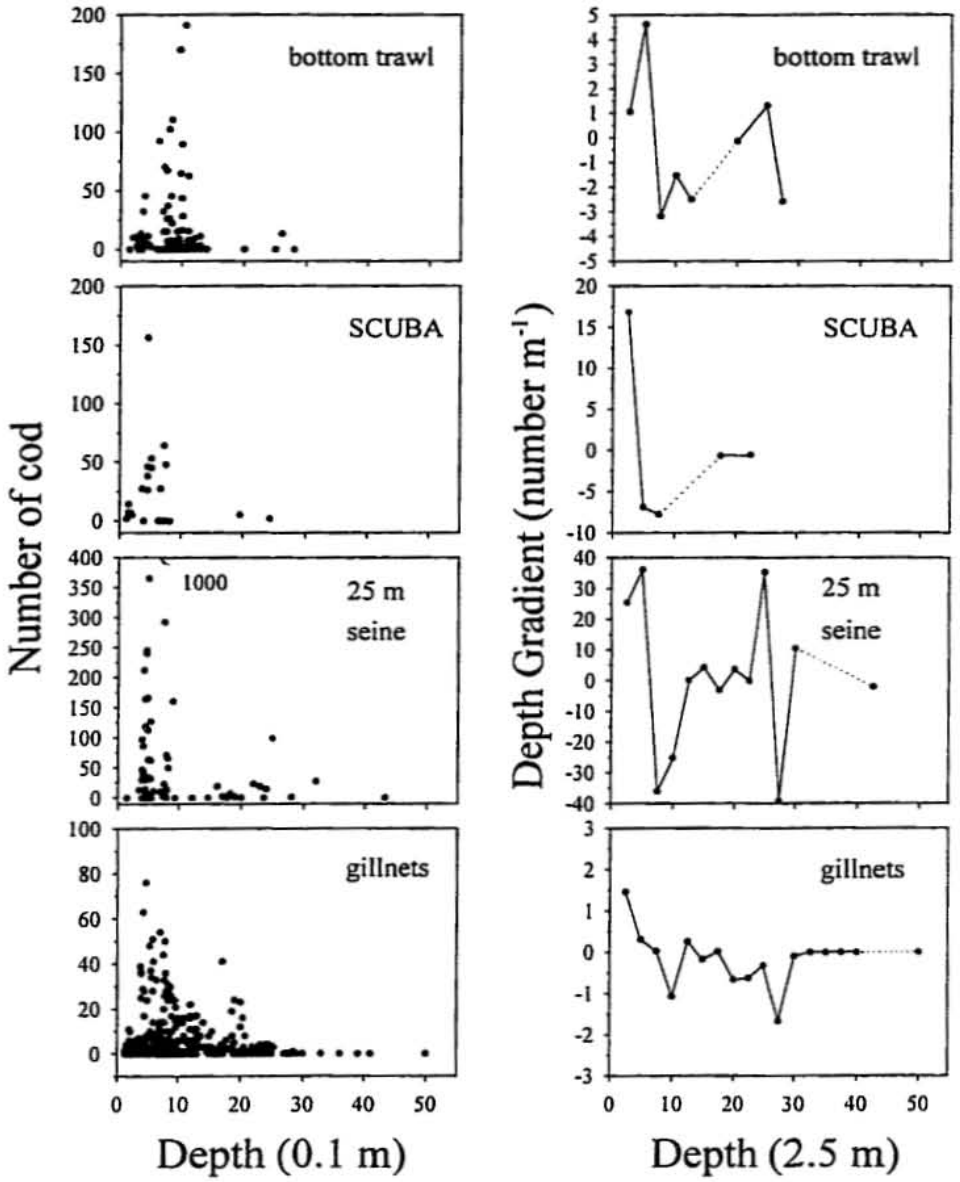


Figure 3.5 Number of cod in relation to depth (0.1 m resolution) and depth gradients (2.5 m resolution). Depth gradients are defined in the text.

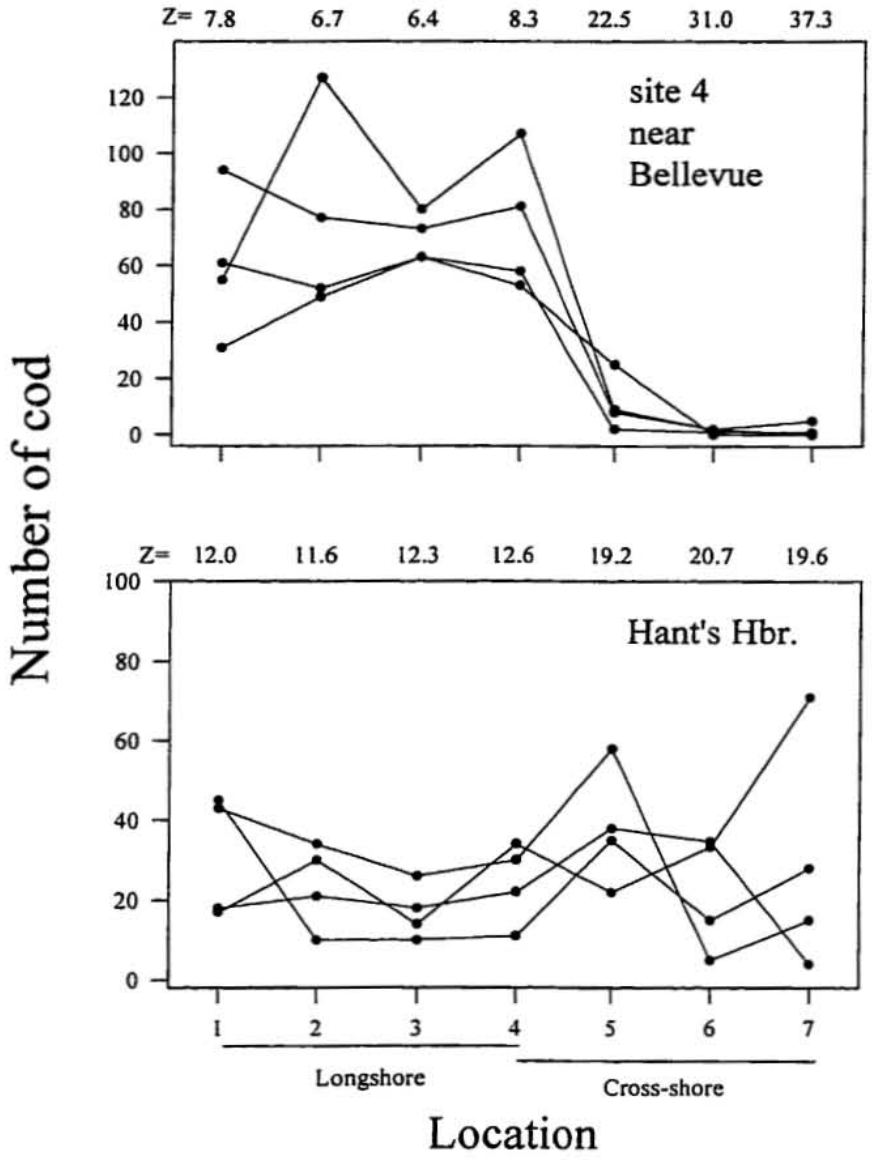


Figure 3.6 Number of cod collected by individual gillnets set ca. 100 m apart in a line along the shore (locations 1-4) and in a line in an offshore direction (locations 4-7) at two sites (upper and lower panels) with different offshore depth profiles. Mean depth (Z in metres) of four gillnets is indicated immediately above each panel over the longshore and cross-shore location to which it refers. Seven gillnets, one at each location were set overnight on each of four occasions (i.e. four lines of data) for each site in August 1992. The seven gillnets set at any one time for each site formed an "L" shaped pattern with the gillnet at location 4 being common to both the longshore series and to the cross-shore series of nets.

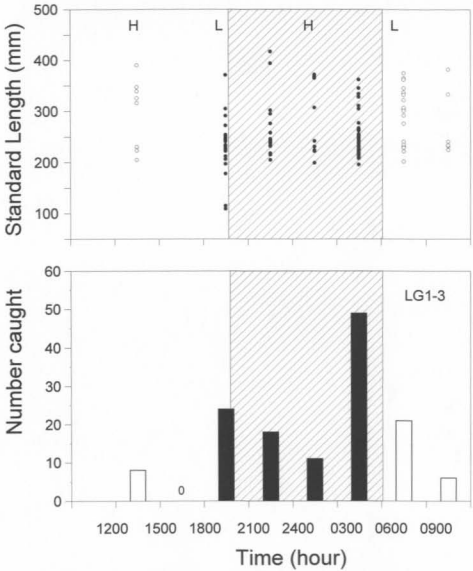


Figure 3.7 Diel variation in mean catches of juvenile cod (primarily LG2-3) taken by gillnets at site 4 on 23-24 August. H = high tide, L = low tide. Diagonal lines indicate hours of darkness.

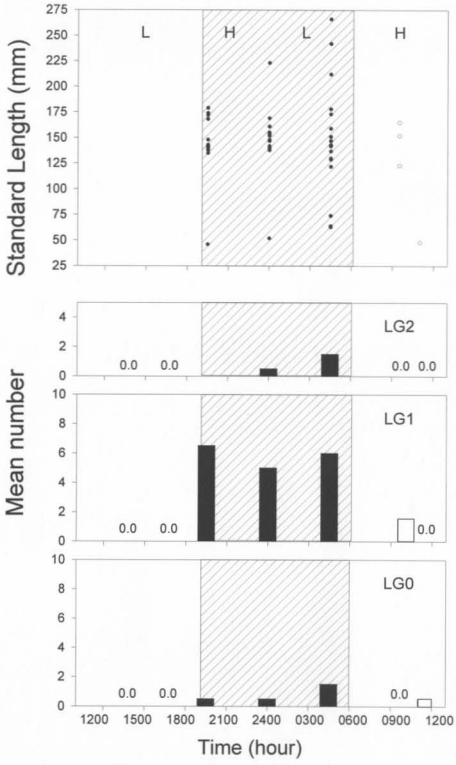


Figure 3.8 Diel variation in mean catches of juvenile cod taken by a 4.8 m bottom trawl at site 3 on the 13 October (1300-2400 h) and 15 October (0100-1200 h) of October. H = high tide, L = low tide. Diagonal lines indicate hours of darkness.

Appendix 3.1 Description of sampling equipment

9-m seine: The 9 by 1.5 m deep beach seine with 9 mm stretch mesh and central collection bag was equipped with small floats (55 cm spacing) located on the headrope and small lead weights attached to the footrope (25 cm spacing). Two wooden poles, each about 2 m long, were tied to the headrope and footrope at each end of the seine. The seine was pulled through the water parallel to the shore (maximum depth 1.2 m) by two people wearing chest waders. That portion of the seine attached to the wooden poles by the footrope was always in contact with the bottom to minimize escapement. The seine fished throughout the water column from the surface to the bottom.

14-m seine: The 14-m beach seine was constructed of 15 mm stretch mesh with a codend liner of 9 mm stretch mesh. This seine sinks to the bottom, and sampled from the bottom to ca. 1.5-2.0 m above the bottom. It did not sample from the surface to the bottom as the 9 and 30.5-m seines did. The 14-m seine was deployed by boat to a distance of 55 m offshore and was hauled towards shore by towing lines. Retrieval of the 14- and 25-m beach seines is described by Lear et al. (1980).

25-m seine: The 25-m bottom seine was hauled by two people towards the shore after being deployed from a small boat. This seine had a headrope length of 24.4 m and a footrope of 26.2 m. The wings, belly, and codend were constructed of knotless nylon netting, 19 mm stretch mesh in the wings and belly and 12.7 mm stretch mesh in the codend. The codend was lined with a knotless nylon netting of 9 mm stretch mesh. The Dan Leno Sticks at the end of each wing of the seine where the two hauling ropes are attached were 75 cm long and 25 mm in diameter and made of aluminum. Dan Leno Sticks kept the wings of the net open when the seine was being hauled towards the shore as described by Lear et al. (1980). Six small (7.6 by 12.7 cm) football shaped floats were equally spaced on the headrope. The footrope was attached to 6.4 mm diameter lead

line that kept the footrope on the bottom. Further description of this seine and method of deployment are given in Lear et al. (1980) and Schneider et al. (1997).

30.5-m seine: The 30.5 by 2.4 m deep beach seine had a 2.4 m^3 collection bag and was constructed entirely of 9 mm stretch mesh. One person remained on shore holding a pole attached to the end of the seine while the other end was taken offshore by a person wearing chest waders. This seine was fished in one arc-like sweep such that the area of ca. 1/4 of a circle was sampled.

Bottom trawl: The trawl was a 4.9-m semi-balloon bottom trawl with a 5.2-m headrope and a 6.4-m footrope. The footrope was fitted with eight 7.6 by 12.7 cm rollers spaced evenly with 69 cm centres between which hung one loop of galvanized chain. The mesh in the wings, top, belly, and codend was 32-38 mm stretch with a 9 mm stretch mesh liner in the codend. Thread size was No. 12 in the body and No. 18 in the codend. Chaffing gear of 63.5 mm stretch mesh was attached to the underside of the net and codend. Trawl doors were made of wood with metal runners and measured 76 cm long by 38 cm deep. Each door weighed ca. 7 kg. The amount of towing warp was 3-4 times the water depth. Tows were usually limited to 5-10 minutes each at a speed of 2.5-3.0 km hr^{-1}. The footgear of the trawl was modified to include rock-hopper gear (Gunderson 1993) in 1992 and 1993. This consisted of groups of four 7.5 cm diameter rubber discs that were evenly spaced every 10.2 cm by metal spacers. The net was attached to a 4 mm diameter wire (that ran through the discs to prevent them from rolling) by 3 links of chain. Each link of chain was 25 mm long, ensuring that the space between the rock-hopper gear and the net was minimized.

SCUBA: SCUBA divers swam after dusk along rope transects that were anchored to the bottom. Transects started in shallow water close to shore and extended offshore for 61 m (site 1), 118 m (site 3) and 113 m (site 4). The start and finish depths were 1.7-4.4

m (site 1), 6.9-10.0 m (site 3) and 4.5-14.5 m (site 4). All cod observed within 3 m of either side of the transect and within ca. 1.5 m of the bottom were counted. Visibility at night depended on the dive site but usually exceeded 4 m with an underwater light. Divers recorded all information on plastic slates. Five underwater transects were done by divers who recorded cod on underwater video (H18 mm Camcorder, Sony Model V101 enclosed in an Amphibico housing with two 50 watt lights). Juvenile cod did not appear to be either attracted to or repulsed by divers (see Keats et al. 1987, Keats 1990) or underwater lights.

Gillnets: Gillnets were 22.9 by 2.4 m deep and contained three 7.6 m panels, each of different size mesh (25.4, 38.1, and 50.8 mm stretch mesh). The floatline was made of foamcore, a flexible styrofoam core running through the centre of a 9.5 mm nylon rope. The footline was 6.4 mm diameter lead line that was attached to building bricks, as weights, at each end of the net. Meshes were made of #69 monofilament line (0.28 mm thick). Gillnets were set perpendicular to the coast in a line from shallow to deep water (sites 3 and 4) or along the shore (sites 1, 6, 7) so as not to interfere with boat traffic. Nets were usually set shortly before dusk and were retrieved by 0800-1000 the next day. Soak time was ca. 15 hr.

Jigger: The fishing jigger is known locally as a Norwegian style jigger and is manufactured by Sølvkroken. It was silver in colour, 21 cm long, weighs 498 g and had a single treble hook with red plastic around the shaft. One jigger was attached to each fishing line that was lowered to within 2-3 m of the bottom. The line was quickly hauled and released such that the jigger would rise 1-2 m and return to 2-3 m off the bottom.

Chapter IV

A multiscale analysis of spatial variation

4.1 Introduction

Random or uniform distributions of animals are rare in nature. Animals occur more commonly in patches or aggregations where resources are adequate and where density-dependent processes of food gathering, predator avoidance, and reproduction are enhanced. Aggregation has usually been quantified at single spatial or temporal scales despite an increased awareness that measurement is dependent on scale (Smith 1978, Wiens 1989). The spatial scale of aggregation is influenced by various biological processes such as shoaling, schooling, the aggregative response by predators to concentrations of prey, and habitat (Schneider et al. 1987, Jones et al. 1990, Piatt 1990, Horne and Schneider 1997). Convergence of predators in areas of high prey density, for example, will increase the spatial variation of the predators distribution at the scale of a prey aggregation (Horne and Schneider 1997). The association of predator with prey therefore depends on the scale of aggregation, suggesting that predator-prey interactions should be examined at multiple scales instead of a single characteristic scale.

Multiscale analyses, or analyses with respect to multiples of a unit of measurement, have become increasingly common, though they are not new to ecology. Early examples include Greig-Smith's (1952) plotting of mean-square against increasing block or quadrat size; spectral analyses of continuous spatial and temporal data covering 2-3 orders of magnitude (Platt and Denman 1975); computing ratios of variance to mean at larger block sizes (Schneider and Piatt 1986, Piatt 1990), and hierarchical ANOVA (Jones et al. 1990, Downes et al. 1993). Analyses typically involve plotting a measure of spatial or temporal variation through a range of resolution scales. The goal is to describe spatial patterns of abundance or variation across multiple scales, identify the scale where

variation is concentrated, and identify processes at the scale of maximum variation to which populations may be responding.

This approach is widely used in physical oceanography and in oceanographic studies of plankton, but it has been applied only recently to larger, more mobile nektonic organisms (Weber et al. 1986, Schneider 1992). Weber et al. (1986) found that water temperature and fluorescence share similar power spectra over the range of 4-20 km, suggesting that variation in the biomass of phytoplankton is largely determined by the same physical processes that structure temperature. Spectral analyses applied to continuous acoustic transects of large-mobile Atlantic cod *Gadus morhua* showed that variation in abundance was highest at large-spatial scales (10s of km), decreased slightly at small-spatial scales, and surprisingly did not peak at the same scale as capelin (*Mallotus villosus*), an important prey species (Horne and Schneider 1994, 1997).

Small juvenile cod are less mobile than larger cod (Danielssen and Gjøæter 1994, Smedstad et al. 1994, Hanson 1996), they perceive habitat at much smaller scales, and appear to be closely associated with small-scale habitat features that include macroalgae (Keats et al. 1987), eelgrass (*Zostera marina*; Gotceitas et al. 1997) suitable substratum (Lough et al. 1989), and structural complexity of habitats (Gotceitas and Brown 1993, Gregory and Anderson 1997). Furthermore, demersal age 0 cod apparently do not school when suitable habitat is available, and can establish home ranges (1-100 m^2) and territories that increase with body size (Tupper and Boutilier 1995b). This leads to the expectation that habitat selection by juvenile cod is fine-grained in coastal habitats, i.e. related to small-scale features of the environment.

I investigated the possibility that variation in population density of juvenile cod was fine-grained, i.e. highest at small-spatial scales, using hierarchical analyses of variance covering three spatial scales. Small-scale variation was predicted to be highest for age

0 cod and lower for older individuals. A second goal was to examine biotic and abiotic factors at the scale of maximum variation to determine if abundance of juvenile cod was related to temperature, salinity, and the presence of larger conspecific fish.

4.2 Methods

Juvenile cod were sampled by beach seine in September-October, 1959-1964 by Alistair Fleming, Tom Collier and others from the Fisheries Research Board of Canada (Lear et al. 1980). Sampling started in St. Mary's Bay on the south coast of Newfoundland and ended in western Notre Dame Bay on the northeast coast (Fig. 4.1). All sites were sampled at approximately the same time each year (September to October), but the number of sampling sites varied (1960, n=17; 1961, n=30; 1962, n=40; 1963, n=41; 1964, n=32) due to weather and sea conditions. Approximately one hour was required to complete the first two tows at each site. The sampling gear, a 25-m beach seine (Lear et al. 1980, Chapter III), was deployed by boat, usually to a standardized distance of 55 m offshore. Sampling was usually done at depths <10 m and was not confined to any particular time of day or tidal level. The initial year of the survey (1959) was not included in this study because only six sites with two consecutive tows per site were sampled. The survey was repeated in 1992-1996 when the same set of sites (n=46, 1992; n=43, 1993; n=40, 1994; n=36, 1995; n=45, 1996) was resampled at the same time of year (September-October), also with a 25-m beach seine. Brief descriptions of the sites are included in Appendix 4.1.

All cod were separated from bycatch and were measured shortly after being caught. In the 1960s it was difficult to distinguish juvenile *Gadus morhua* from *G. ogac* (Greenland cod), a sibling species that is syntopic along much of the Newfoundland coast. Specimens of *G. ogac*, identified in samples from the 1960s were not measured and it is therefore difficult to determine the size range over which mis-identification may have occurred.

This identification problem still exists for surveys in the 1990s though to a lesser extent, and was generally confined to the smallest size classes (ca. <50 mm). Consequently it is likely that some small cod were mis-identified. To estimate the rate of mis-identification I used starch-gel electrophoresis as described in Chapter II and by Renaud et al. (1986) to reidentify 65 cod (30-166 mm SL) collected at site 46 (Indian Bay in Bonavista Bay) when it was sampled in 1996. At this site, six of the 65 cod identified by eye in the field were judged to be Atlantic cod (*G. morhua*). The remaining 59 were identified in the field as Greenland cod (*G. ogac*). Electrophoresis identified only four specimens as *G. morhua*. These four fish were also identified as *G. morhua* by eye before electrophoresis was done. Electrophoresis identified the remaining 61 fish as *G. ogac*. Therefore, two specimens initially identified in the field by eye as *G. morhua* were actually *G. ogac*. This is an error rate of 2/65=3.0%.

Standard length (SL) was used to divide the catch into three length groups (LGs) defined by modes in the catch of 19,365 juvenile cod from several types of fishing equipment deployed previously in shallow water along the coast of Newfoundland (Chapter III). Age groups, estimated from length modes were: LG0, ≤96 mm SL; LG1, 97-192 mm SL; LG2, 193-290 mm SL.

The spatial arrangement of the sampling sites along ca. 1500 km of the Newfoundland coast, the distance between sites, and the beach seine being restricted to a relatively narrow habitat type limited analyses to three discrete spatial scales: (i) coastal section, which roughly divided the survey into halves; sites south of Cape Freels (49°14'N, 53°28'W) and sites to the west of Cape Freels, (ii) bays, St. Mary's and Trepassey Bays (combined as one), Conception Bay, Trinity Bay, Bonavista Bay, New World Island and Gander Bay (combined), Notre Dame Bay, and (iii) individual sites (Fig. 4.1). Spatial variation was quantified using hierarchical analyses of variance (ANOVA). Separate analyses were done for each year of survey and each length group of cod. Variation was

directly partitioned from sums of squares (SS). Sums of squares can be thought of as a measure of contrast among the different sources of variation (in this case, three spatial scales). High sums of squares indicate high contrasts. A second measure of spatial variation, also determined from hierarchical ANOVA is the calculation of variance components (VC; Underwood 1981, Sokal and Rohlf 1995). Variance components, like sequential sums of squares in a purely hierarchical ANOVA are additive and can be expressed as a percentage of the total variation. Despite the calculation of negative variance components, this method remains an important technique for partitioning of spatial variance (cf. Jones et al. 1990, Downes et al. 1993). Negative variance components indicate a relatively low variance (Snedecor and Cochran 1967). The General Linear Model (GLM) procedure of SAS version 6.09 (SAS 1988) was used for all analyses.

An additional objective was to determine factors that influence small-scale spatial variation in catches of juvenile cod. Abiotic (temperature and salinity) and biotic (density of conspecific fish) factors were examined to determine if these might explain the local distribution of juvenile cod. The relation of abiotic factors to catches of LG0, LG1, and LG2 cod was quantified using one way ANOVA with type I sequential sums of squares. The order that the class variables (year of survey, temperature or salinity, site) were entered in the analyses is important if, as is likely, the variables are inter correlated. Sampling site was entered last to determine if site still accounted for a high proportion of the remaining variation once the variation due to year and habitat variables had been removed. Separate analyses were preformed for each habitat variable (temperature, salinity) and length group (LG0, LG1, LG2). Temperature and salinity were measured at the maximum depth sampled by the 25-m seine. Salinity was not measured in 1960-1964. Habitat data were rounded to the nearest full degree of temperature or part per thousand of salinity for the analyses. The catch of cod was plotted against each habitat variable to determine if a pattern in catches was evident. The effects of conspecific fish

on the catch was investigated by plotting the mean catch (n=2 tows/site) of LG0 cod against the mean catch of LG1 cod for each site over all years of survey. This was repeated for LG0 vs. LG2 cod and LG1 vs. LG2 cod.

4.3 Results

Spatial variation, quantified as sums of squares and as variance components from hierarchical ANOVAs, was highest at the smallest scale examined, sites within bays (Figs. 4.2, 4.3). This pattern of high variation in catches at the smallest spatial scale was independent of length (group) of cod and measure of variation (Figs. 4.2, 4.3). Variation in catches of juvenile cod was usually lowest at the largest spatial scale (coastal section). However, for some length groups of cod in some years variation was occasionally lowest at site or bay scales (Fig. 4.3). The overall pattern was one of high variation in population density at small spatial scales with little additional variation occurring at larger scales (Table 4.1). Both measures of spatial variation (SS, VC) indicate that LG0 cod are relatively more aggregated than either LG1 or LG2 cod at the local scale (Table 4.1). Hierarchical ANOVAs for each year and age class are summarized in Appendix 4.2.

There was no consistent pattern in catches of LG0 juvenile cod at the scale of individual sites each year. Neighbouring sites often had very different catches despite their proximity (often within hundreds of metres) (Figs. 4.4 to 4.9) and few sites had consistently high or consistently low catches of juvenile cod each year. Exceptions were limited to just a few sites. Site 34 for example, was the only site with relatively high catches of LG0 cod in most years. Sites with low catches of LG0 cod each year included 29, 35, 72, and 79 (Figs. 4.4, 4.5). These sites represent a relatively small proportion of the total number of sites that were sampled (ca. 40). Similarly, sites 2, 35, and 70 were consistently poor sites for LG1 cod. Sites 2, 10, 20, 34, 45, 46, 52, 53, and 71 were consistently poor sites for LG2 cod. No sites had consistently high catches of LG1

and LG2 cod each year (Figs. 4.6 to 4.9).

Temperature and salinity accounted for a small proportion of the total variation in catches of juvenile cod at the scale of sites. Year and site accounted for most of the explained variation with spatial variation at the scale of sites exceeding temporal variation at the scale of years (Table 4.2). After the effects of year had been removed, temperature accounted for 4.0-4.6% of the total variation in catches of LG0, LG1, and LG2 cod (Table 4.2). Highest catches occurred at 6.0-11.9°C (LG0), 4.0-13.9°C (LG1) and 4.0-5.9°C (LG2) (Table 4.3) but numerous tows at these same temperatures also resulted in no catch (Fig. 4.10). Salinity accounted for 0.8-1.1% of the total variation in catches of LG0 and LG1 cod and 7.9% for LG2 cod (Table 4.2). Highest catches of larger cod were found at progressively greater salinities (LG0, 28.0-31.9 ppt; LG1, 30.0-32.9 ppt; LG2, 32.0-33.9%; Fig. 4.10, Table 4.3). However, as with temperature, there were numerous catches of no cod throughout the range of salinities examined. Most variation in catches of juvenile cod was due to year of sampling (Table 4.2: 3.1-28.5%) and sampling site (Table 4.2: 11.3-41.1%). Site still accounted for a high proportion of the total variation despite it being the last variable entered into the model.

The small-scale local density of LG0 cod was independent of density of larger LG1 cod, as indicated by overlapping 95% confidence limits (Fig. 4.11). Local densities of LG1 and LG2 cod were positively related, but again had high and overlapping confidence limits. LG0 and LG2 cod were negatively related, indicating that few LG0 cod were caught when densities of LG2 cod were greater than 5 cod per haul of the seine.

The high variation and lack of pattern in density at the local scale contrasts with the bay scale where variation in density was much lower (Table 4.1, Figs. 4.2, 4.3) and where a repeatable pattern was observed in nine of ten years. The observed pattern was a consistently high catch of LG0 cod occurring in Trinity or Bonavista Bays (Figs. 4.4,

4.5) with 66.7% of all LG0 cod being collected in these two adjacent bays (Fig. 4.1) on the northeast coast. The overall pattern of LG0 density at the bay scale was one of low catches in the South and Conception Bay, high catches in Trinity or Bonavista Bays and low catches once again in New World Island and Notre Dame Bay (Figs. 4.4, 4.5). The only exception to this general pattern occurred in 1964 when highest catches of LG0 cod occurred in Notre Dame Bay. The high mean catches in Notre Dame Bay were due to one exceptionally large catch of LG0 cod at site 82 in 1964 (Fig. 4.4). The presence of a consistent pattern at the bay scale for LG0 cod contrasted with LG1 and LG2 cod, which showed no consistent pattern from year to year at the bay scale (Figs. 4.6 to 4.9).

4.4 Discussion

Multiscale analyses of cod density indicated that variation in density of juvenile cod was highest at the scale of individual sites (ca. 880 m^2), and that little additional variation was evident at larger scales of bays (10s to 100s of km) and coastal sections exceeding 700 km. This pattern of decreasing variation with increasing spatial scale was independent of age class (length group), measure of spatial variation, and decade (e.g. 1960-1964 compared with 1992-1996). Water temperature, salinity, and the presence of larger conspecific fish did not explain the local distribution of juvenile cod at depths < 10 m, the depth range at which most sampling occurred in this study.

High variation in density of juvenile cod at the local scale indicates a clumped or aggregated distribution. In pelagic habitats the aggregation of fish eggs, larvae, and pelagic juveniles increases with age. Aggregation, or patchiness (quantified using Lloyds index of mean crowding; Lloyd 1967) of several fish species (*Clupea harengus pallasi, Engraulis mordax, Trachurus symmetricus, Scomber japonicus*) in pelagic habitats typically exhibits a "U" or "J" shaped pattern when plotted against increasing length or age (Hewitt 1981, McGurk 1987). Patchiness of recently spawned eggs is initially high

because adults aggregate to spawn. Patchiness of passive eggs and recently hatched larvae decreases due to dispersal processes, but later increases when locomotory skills of individual fish develop with increasing size (Matsuura and Hewitt 1995). Hence juveniles of several fish species are already highly aggregated in pelagic habitats prior to settlement. Acoustic surveys (Olsen and Soldal 1989) and net hauls through the water column (Perry and Neilson 1988, Neilson and Perry 1990) indicate that this observation is also applicable to pelagic juvenile cod that aggregate in mid water and near the bottom prior to settlement. Upon settlement to demersal habitats, this high aggregation is maintained and may even increase for recently settled cod. Settlement has been observed to lead to a reduction in area occupied by settling cod on Georges Bank. Pelagic juveniles were widely spread over the bank in late spring but by late July the now demersal juveniles were only abundant on a pebble-gravel substratum in the northeast portion of Georges Bank (Lough et al. 1989).

Local variation in density of settled cod decreased in this study with increasing size or age as cod vacated the coastal zone and moved into deeper water as age 1 and 2 fish. Older juveniles then occupied a larger area and were less restricted to the coastal shallows, a pattern observed for demersal cod in the southern Gulf of St. Lawrence (Swain 1993, Hanson 1996), North Sea (Heessen 1991) and off northeast Newfoundland (Dalley and Anderson 1997). Consequently the early demersal stage appears to be the life-history stage with the most localized spatial distribution. This large-scale distribution, with the youngest demersal stages being concentrated in a small proportion of the geographic range compared with older juveniles and adults, also applies to other gadids including age 0 haddock, *Melanogrammus aeglefinus*, near Sable Island on the Scotian Shelf (Scott 1982, 1984), age 0 demersal pollock, *Pollachius virens*, in the coastal zone of the Bay of Fundy (Steele 1963, Rangeley and Kramer 1995), juvenile white hake (*Urophycis tenuis*) in the coastal zone of Atlantic Canada and New England (Markle et al. 1982, Fahay and Able 1989), and age 0 red hake (*U. chuss*) that live inside live

scallops *Placopecten magellanicus* (Steiner et al. 1982, Markle et al. 1982). These observations suggest that large-scale variation (hundreds of kilometres) in population density is highest for the youngest age classes and decreases for older fish which occupy a greater proportion of the population range (Swain 1993, Hanson 1996, Sinclair et al. 1996).

Smaller-scale variation (scale of an individual tow, i.e. 880 m^2 for the 25-m beach seine) in population density also appears to decrease with larger and older demersal cod. This was observed for LG0 and LG1 cod in this study (Table 4.1), - the two age classes that were best sampled by the 25-m beach seine. It was also observed for larger juvenile and adult cod when local variation in population density was expressed as the coefficient of variation (CV) for cod bottom trawled in the southern Gulf of St. Lawrence (Sinclair et al. 1996, Table 12, p. 37; Appendix 4.3 this study). In general, for those age classes and habitats well sampled by the bottom trawl during summer in the southern Gulf of St. Lawrence (i.e. where the sample means are >1 cod/tow), the CV decreases with increasing age, indicating less variation in cod abundance among sampling sites with increasing age (and a relatively more even distribution). However, measures of spatial variation (such as the ratio of variance to mean) are known to be positively correlated with the mean (Leps 1993) which makes comparisons among age groups with different means difficult. One solution is to compare variation among populations that have similar means. When this approach was used to examine annual survey data of juvenile and adult cod from the southern Gulf of St. Lawrence (Sinclair et al. 1996; Appendix 4.3 this study), local variation still decreased with increasing age when similar age-specific means were compared within the same year of survey supporting an hypothesis of decreasing age specific aggregation for cod.

Habitat selection is an important process that can influence variation in density of juvenile cod at small spatial scales. For example, demersal LG0 cod select shallow (<10

m) protected sites with suitable substratum and some form of cover (macroalgae, eelgrass, cobble; Godø and Sunnanå 1984, Riley and Parnell 1984, Tveite 1984, Keats et al. 1987, Horne and Campana 1989, Godø et al. 1989, Lough et al. 1989, Gotceitas and Brown 1993, Tupper and Boutilier 1995a, Gregory and Anderson 1997, Gotceitas et al. 1997). Many of these habitat features were present at sites sampled in this study (Appendix 4.1) and have been shown to influence the small-scale spatial distribution of LG0 cod in coastal Newfoundland (Gotceitas et al. 1997) and Nova Scotia (Tupper and Boutilier 1995a). However, if local variation is primarily determined by habitat selection, some consistency in density would have been expected among years at the same sampling sites. No such consistency was observed in this study (e.g. Figs. 4.4 to 4.9) or when these sites were ranked each year based upon local abundance (Schneider et al. 1997). One possible explanation is habitat may not be limiting along the coast of Newfoundland and that individuals may move in a local area greater than the area (880 m^2) sampled by the 25-m beach seine used in this study.

Direct visual observations indicate that LG0 cod will school at sites devoid of cover, such as sandy bottom habitats (Tupper and Boutilier 1995b). Age 0 pollock *Pollachius virens* were also observed to school in the subtidal zone when dense algal mats containing *Fucus* were absent (Rangeley and Kramer 1995). When in the vicinity of *Fucus*, pollock were dispersed and were not observed to school (Rangeley and Kramer 1995). Absence of suitable cover has been reported to influence the behavior and spatial distribution of juvenile cod (Tveite 1984, Keats et al. 1987, Gotceitas and Brown 1993, Gotceitas et al. 1997) and hence small-scale variation in density. These observations and the relatively high proportion (10/45=22.2%; Appendix 4.1) of sites where suitable cover from predation was judged to be absent (i.e. smooth-bottom sandy sites) indicates small-scale movements in the form of shoaling or schooling behaviour (as observed for cod by Tupper and Boutilier [1995b] and for pollock by Rangely and Kramer [1995]) may, in addition to habitat selection be an important source of local, site to site variation in

density of juvenile cod.

Factors that do not appear to influence the local density of juvenile cod at small-spatial (individual sites; 880 m^2) and temporal (ca. 1 hr, the time required to sample a site) scales included water temperature and salinity. Water temperature may better describe the distribution of juvenile cod at larger spatial scales (100s to 1000s of km), where in the southern Gulf of St. Lawrence for example juveniles are absent at depths <10 m because subsurface temperatures are too warm (e.g. age 0 cod, Hanson 1996). The distribution of age 0 cod decreased with increasing salinity at large spatial scales (inshore-offshore direction) in the North Sea (Riley and Parnell 1984, Heessen 1991) but was poorly explained at small spatial scales (880 m^2) in this study.

Juvenile cod did not appear to be affected by the presence of larger conspecific fish at the spatial scale sampled by the 25-m beach seine. This indicates LG0 and LG1, as well as LG1 and LG2 cod occurred in the same 880 m^2. It does not necessarily indicate that these age classes occurred together at smaller spatial scales. Consequently segregation of these age classes due to predation or different habitat preferences is possible at smaller spatial scales (Fraser et al. 1996). Densities of LG0 and LG2 cod were negatively related. These age classes were seldom associated at the scale of 880 m^2, suggesting that different habitats were occupied during the day when sites were sampled or that LG0 cod avoided LG2 cod because of cannibalism (Bogstad et al. 1994).

Mis-identification of *G. morhua* and *G. ogac* may have contributed to the scale-dependent spatial variation observed in this study. How species mis-identification may have affected variation at each scale is difficult to access because errors in identification are not known for each sampling site or year of survey. Mis-identification may have been higher in the 1960s than in the 1990s given that it has only been recently possible to distinguish these species at small sizes (Chapter II). Alternatively, historic rates of mis-identification may

have been lower given that the spawning stock biomass of *G. morhua* was two orders of magnitude higher in the 1960s than in the 1990s (Hutchings and Myers 1994). A mis-identification rate of 2/65 = 3.0% was determined by starch-gel electrophoresis for *Gadus* spp. collected at a single site in this study in 1996. Multiscale analyses of variation in density of juvenile cod was highest at the scale of individual sites (ca. 880 m^2) in 1996 (Appendix 4.2) as it was in most other years (Figs. 4.2, 4.3) suggesting mis-identification may have had little influence on the partitioning of spatial variation.

Results of this study indicate that variation in density of juvenile cod is concentrated at small spatial scales with little additional variation at larger scales. This result is consistent across years and at the temporal scale of decades. The high variation among sites indicates small-scale processes are important in determining local density of cod along the coast of Newfoundland. Decreasing variation with increasing body size observed for small juveniles in this study and for large juvenile and adult cod in the southern Gulf of St. Lawrence is consistent with the observation that increased mobility permits local decoupling with habitat and hence can influence the small-scale distribution of cod. Local decoupling with features of the sea bed was observed for demersal organisms of increased mobility on the Grand Bank (Schneider et al. 1987) and for larger juvenile cod that were less associated with macroalgae than smaller cod (Keats et al. 1987).

Although juvenile cod are abundant nearshore throughout much of the year and hence logistically available to repeated sampling (Methven and Bajdik 1994) they are a difficult species to quantify variation in population density at multiple scales. Optimal methods such as the continuous collection of data by acoustics for krill (Weber et al. 1986) and for larger cod offshore (Horne and Schneider 1997) could not be used in this study because small demersal age 0 cod during the day are strongly associated with the bottom and would be difficult to record. Nevertheless this study has shown that multiscale analyses was possible for an important commercially exploited fish species where very

little is known during the early juvenile stages despite the problems of sampling this stage in coastal habitats.

Table 4.1 Scale-dependent spatial variation in juvenile cod density, quantified by type 1 sums of squares (SS) and variance components (VC) from hierarchical ANOVA and expressed as percentage of total variation.

Length group	Site	Bay	Coast	Error
	mean (range)	mean (range)	mean (range)	mean (range)
LG0 SS	59.4 (37.5-75.1)	12.8 (3.9-34.4)	1.86 (0.0 -6.4)	23.47 (2.6-42.0)
LG1 SS	56.4 (38.3-93.1)	9.3 (2.2-17.7)	2.69 (0.0 -6.4)	31.42 (3.0-48.1)
LG2 SS	55.7 (31.1-86.5)	11.5 (1.0-34.4)	4.10 (0.0-13.2)	28.52 (6.6-49.5)
LG0 VC	42.3 (0.90-64.9)	8.2 (0.0-26.1)	1.7 (0.0-10.9)	47.72 (24.2-79.9)
LG1 VC	33.9 (0.00-90.9)	5.3 (0.0-15.8)	1.8 (0.0 -7.2)	58.85 (5.3-91.3)
LG2 VC	35.0 (0.00-82.3)	8.7 (0.0-44.4)	3.9 (0.0-16.0)	52.39 (11.7-94.0)

Table 4.2 One-way analyses of variance of habitat variables. Class variables included year, a habitat variable (temperature or salinity), and site. Catch (n = 17-46, depending on year) was the response variable. df = degrees of freedom, SS = sums of squares.

Variable	LGO			LG1			LG2		
	df	SS	%SS	df	SS	%SS	df	SS	%SS
year	10	173400	12.5	10	214812	28.5	10	126	7.9
temp	13	55830	4.0	13	30269	4.0	13	74	4.6
site	55	341680	24.6	55	85133	11.3	55	222	13.9
error	250	812836		250	423255		250	1163	
total	328	1383748		328	753470		328	1587	
year	4	4219	3.1	4	6727	6.0	4	15	3.2
sal	8	1120	0.8	8	1259	1.1	8	37	7.9
site	45	54333	41.1	45	32526	29.3	45	95	20.4
error	141	72289		141	70466		141	316	
total	198	131962		198	110980		198	464	

Table 4.3 Mean catch of juvenile cod in relation to temperature (°C) and salinity (ppt). n is the number of sites sampled within each temperature and salinity category.

Temperature (°C)

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
LG0	31.0	--	0.5	0.0	5.8	5.1	19.2	16.1	15.8	21.7	19.2	13.3	4.2	8.2
LG1	0.5	--	0.0	0.0	21.5	16.5	19.4	8.8	4.9	29.0	29.0	35.8	41.1	16.7
LG2	0.0	--	0.0	0.3	2.4	1.4	0.7	0.3	0.5	0.9	0.4	0.6	1.5	0.3
n	1	0	1	2	6	12	20	43	75	52	39	24	23	19

Salinity (ppt)

	24	25	26	27	28	29	30	31	32	33
LG0	0.7	--	4.5	7.5	10.2	18.0	13.4	12.0	2.5	1.0
LG1	0.2	--	8.0	2.8	3.6	2.2	7.9	9.4	7.5	1.0
LG2	0.0	--	0.0	0.3	0.3	0.5	0.5	0.3	3.1	1.5
n	2	0	1	5	15	21	92	57	5	1

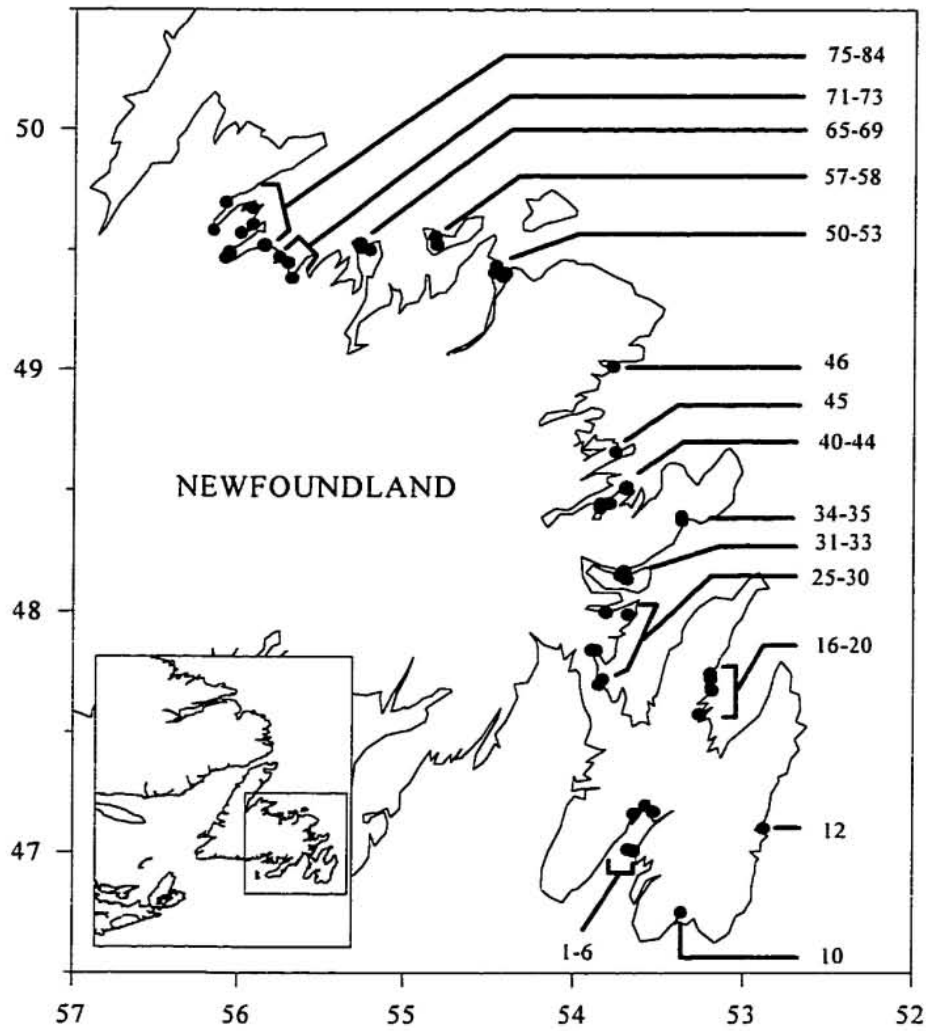


Figure 4.1 Distribution of 56 sampling sites along the east and northeast coasts of Newfoundland. Details are given in Appendix 4.1. Sites 1-12 are located in the South, 16-20, Conception Bay; 25-35, Trinity Bay; 40-46, Bonavista Bay; 50-58, Gander Bay and New World Island; 65-84, Notre Dame Bay.

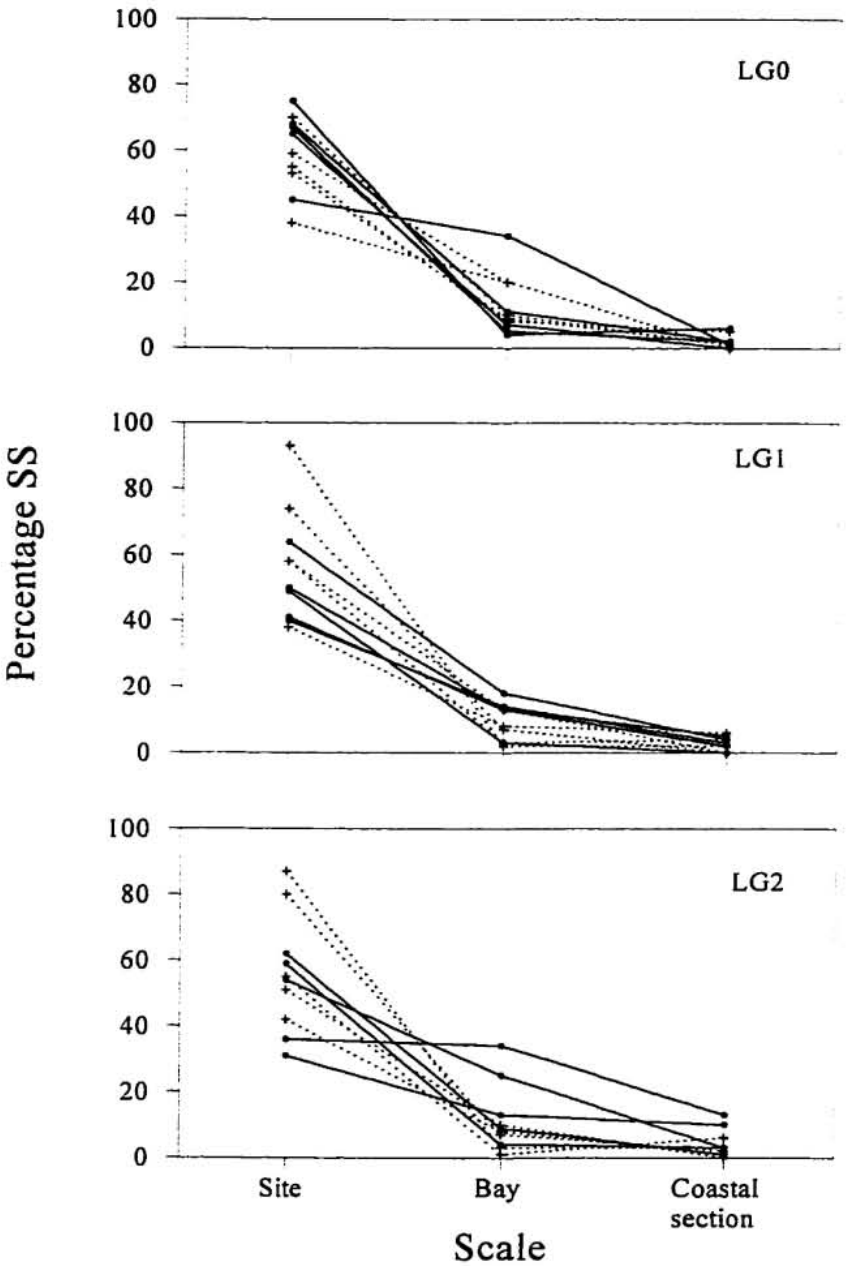


Figure 4.2 Scale-dependent spatial variation quantified as per cent of total sums of squares (SS) for three spatial scales: coastal sections, bays, and individual sites. Lines join data from the same year. • = 1960-1964; + = 1992-1996. 17-45 sites were sampled each year.

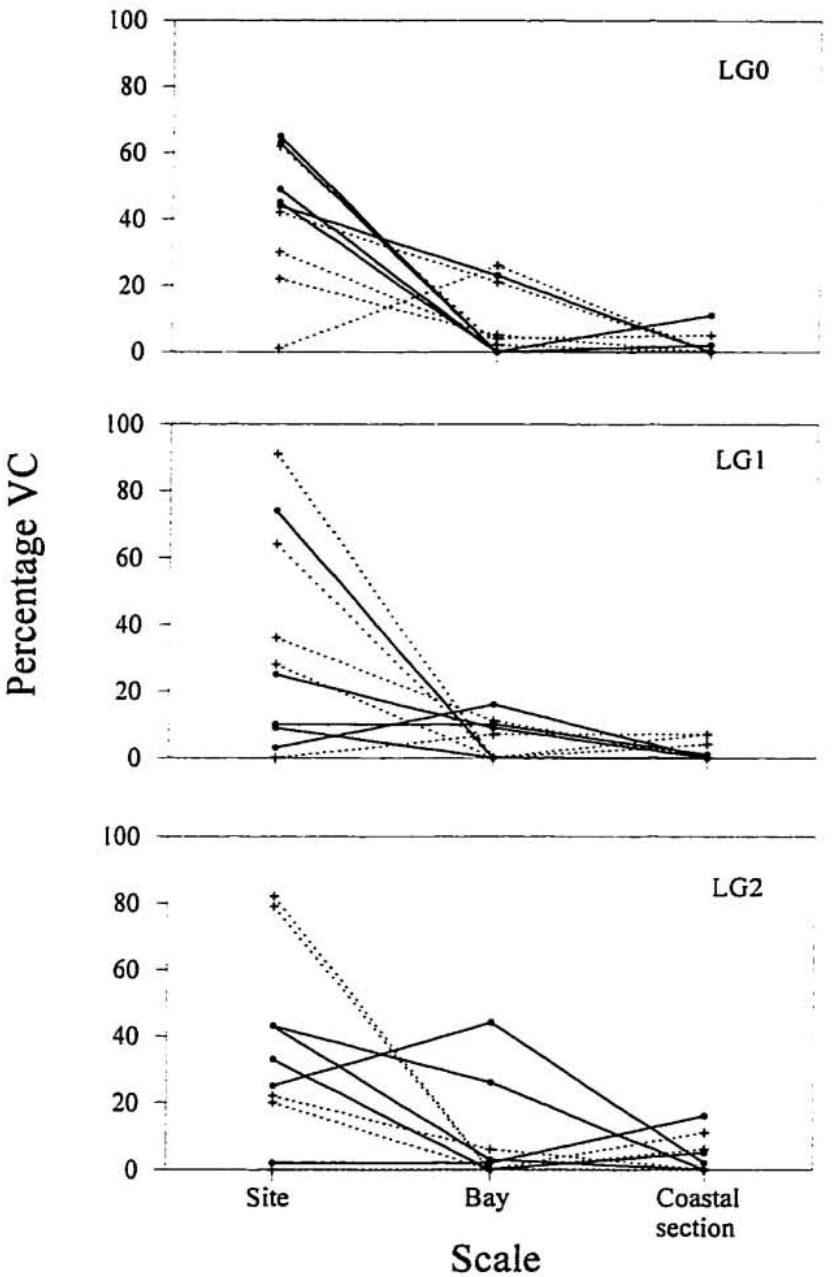


Figure 4.3 Scale-depedent spatial variation quantified as per cent of total variance components (VC) for three spatial scales: coastal sections, bays, and individual sites. Lines join data from the same year. • = 1960-1964; + = 1992-1996. 17-45 sites were sampled each year.

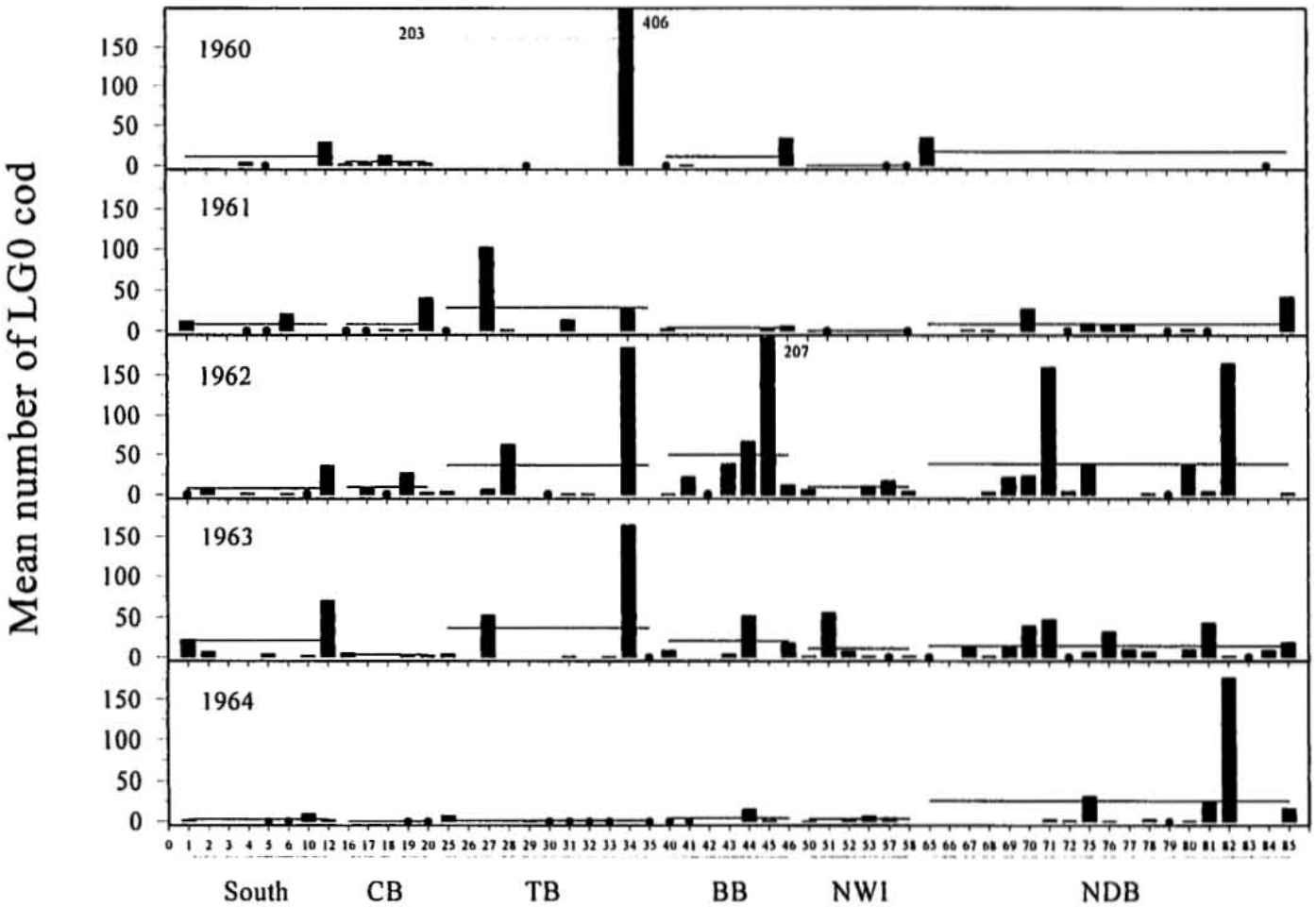


Figure 4.4 Mean catch (n=2 tows) of LG0 cod at each site (1960-1964). Missing data indicates that sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay. Individual numbers in some plots refer to site or bay means that are off scale.

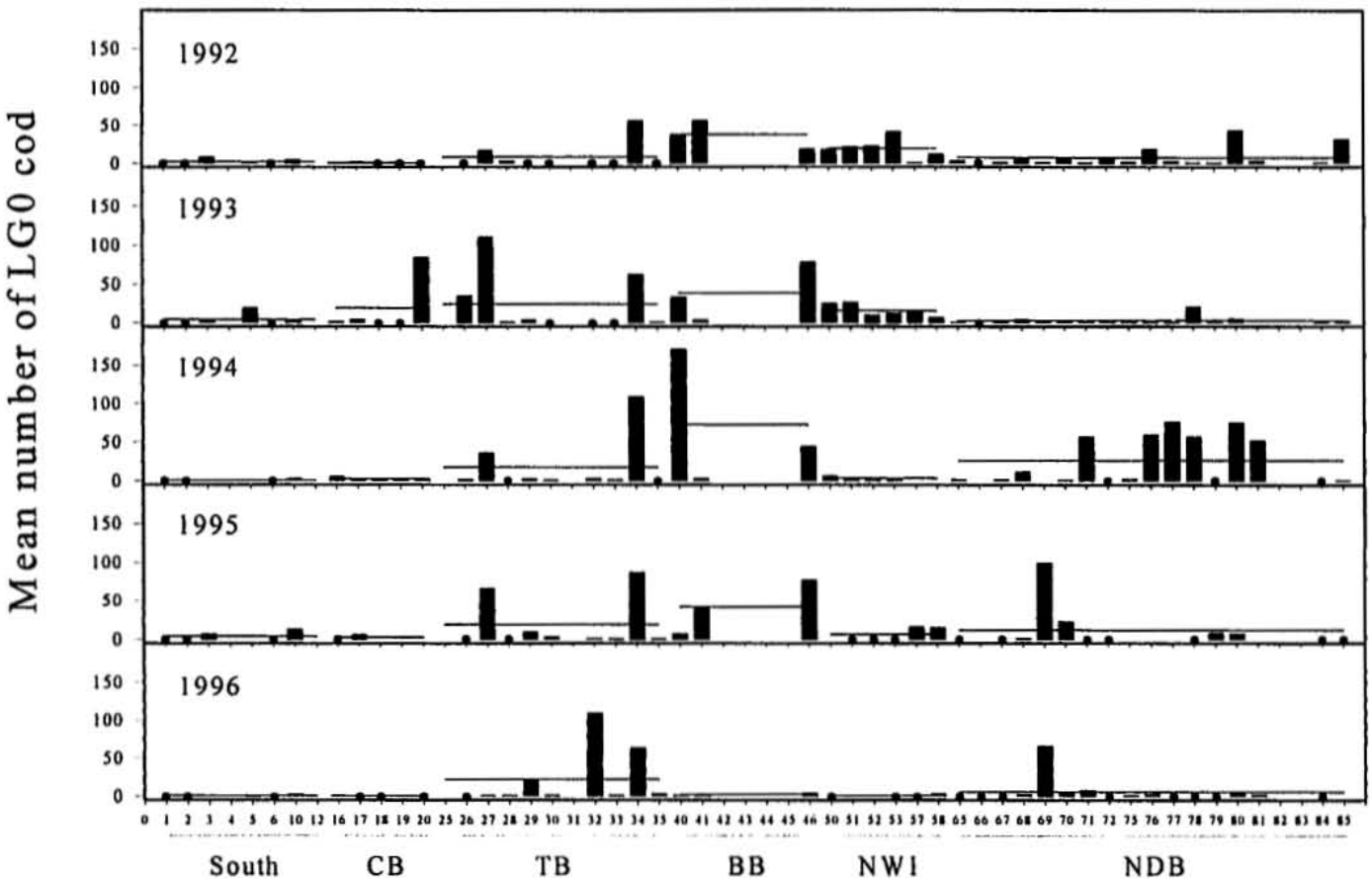


Figure 4.5 Mean catch (n=2 tows) of LG0 cod at each site (1992-1996). Missing data indicates that sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay.

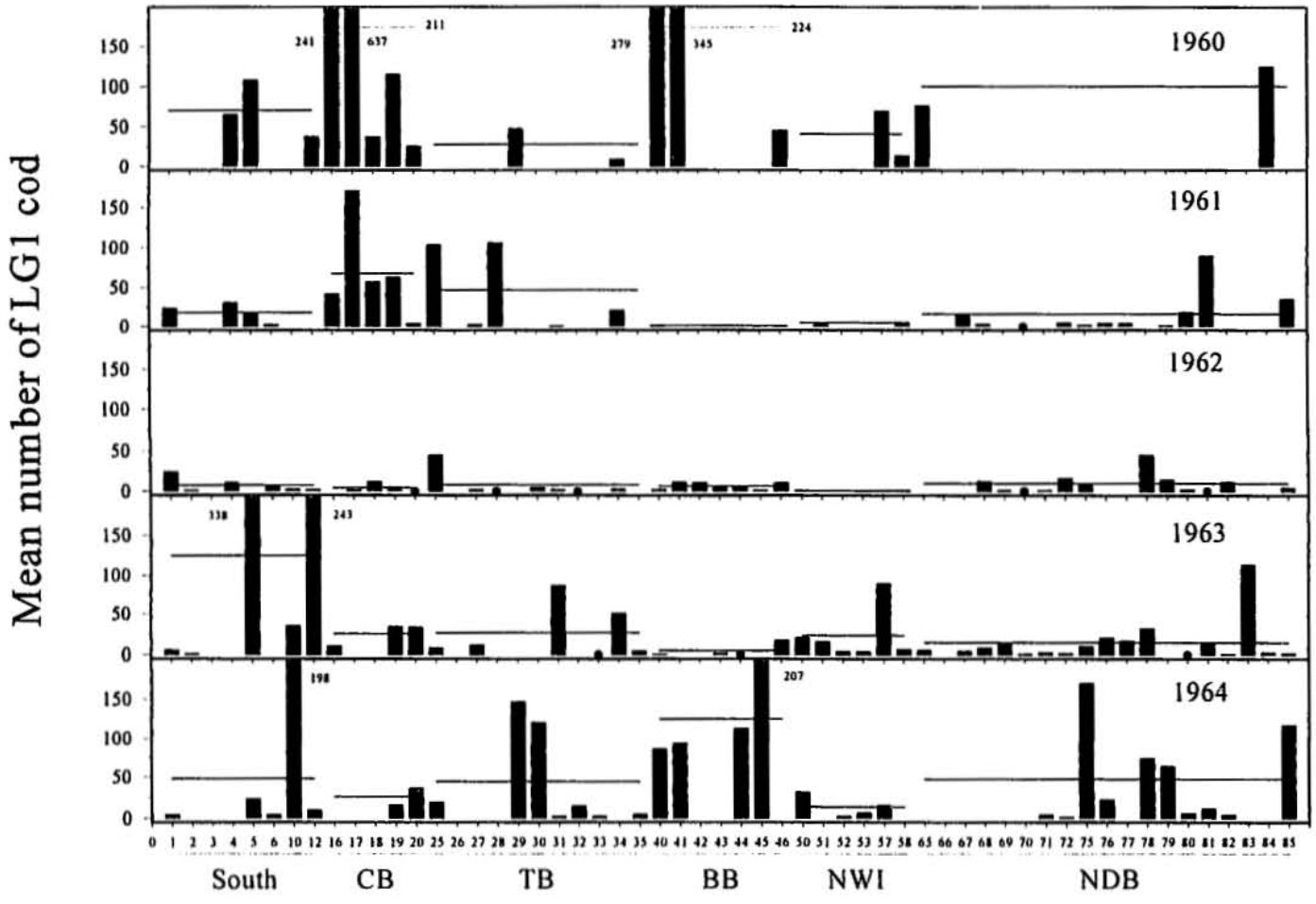


Figure 4.6 Mean catch (n=2 tows) of LG1 cod at each site (1960-1964). Missing data indicates sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay. Individual numbers in some plots refer to site or bay means that are off scale.

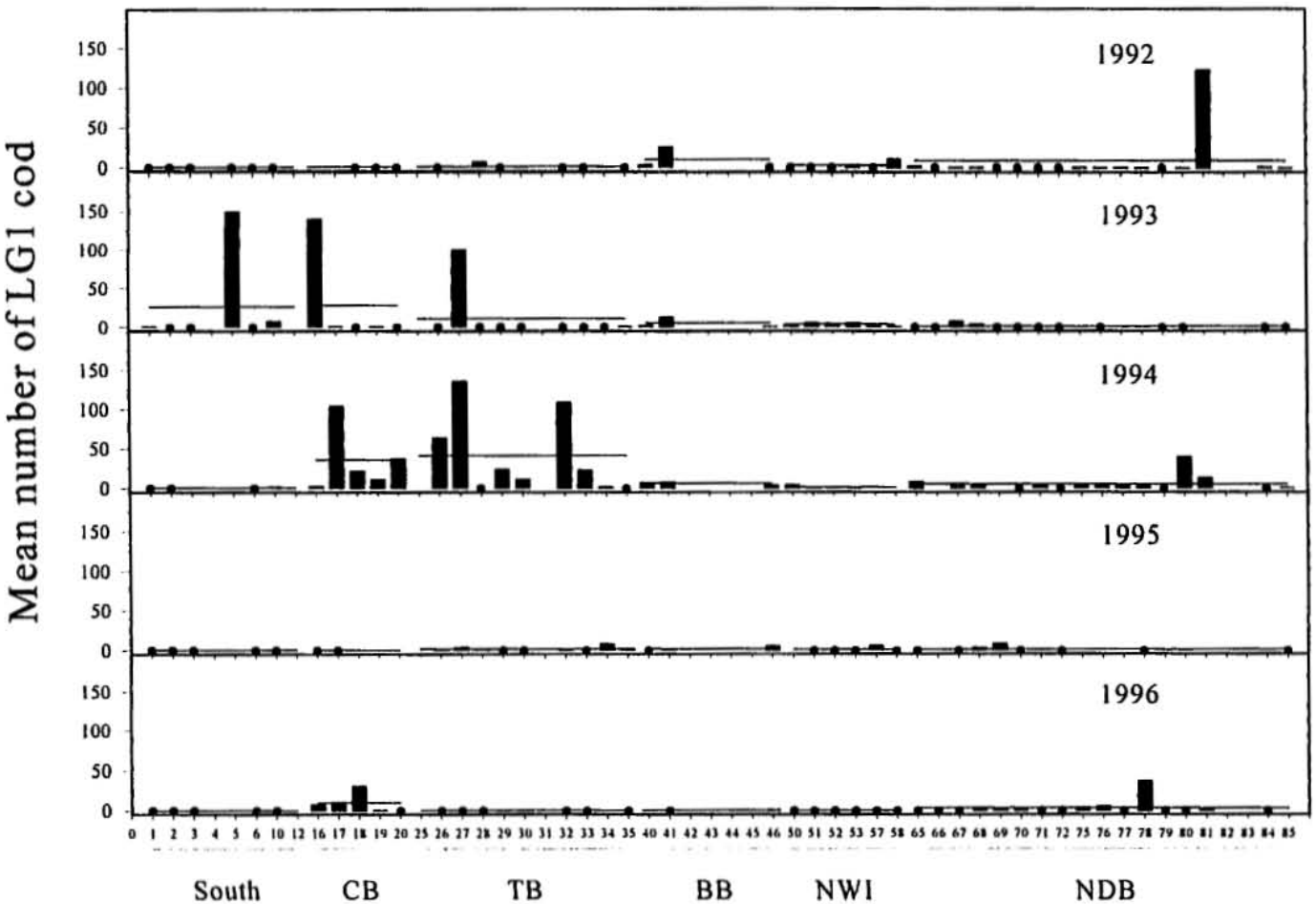


Figure 4.7 Mean catch (n=2 tows) of LG1 cod at each site (1992-1996). Missing data indicates sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay.

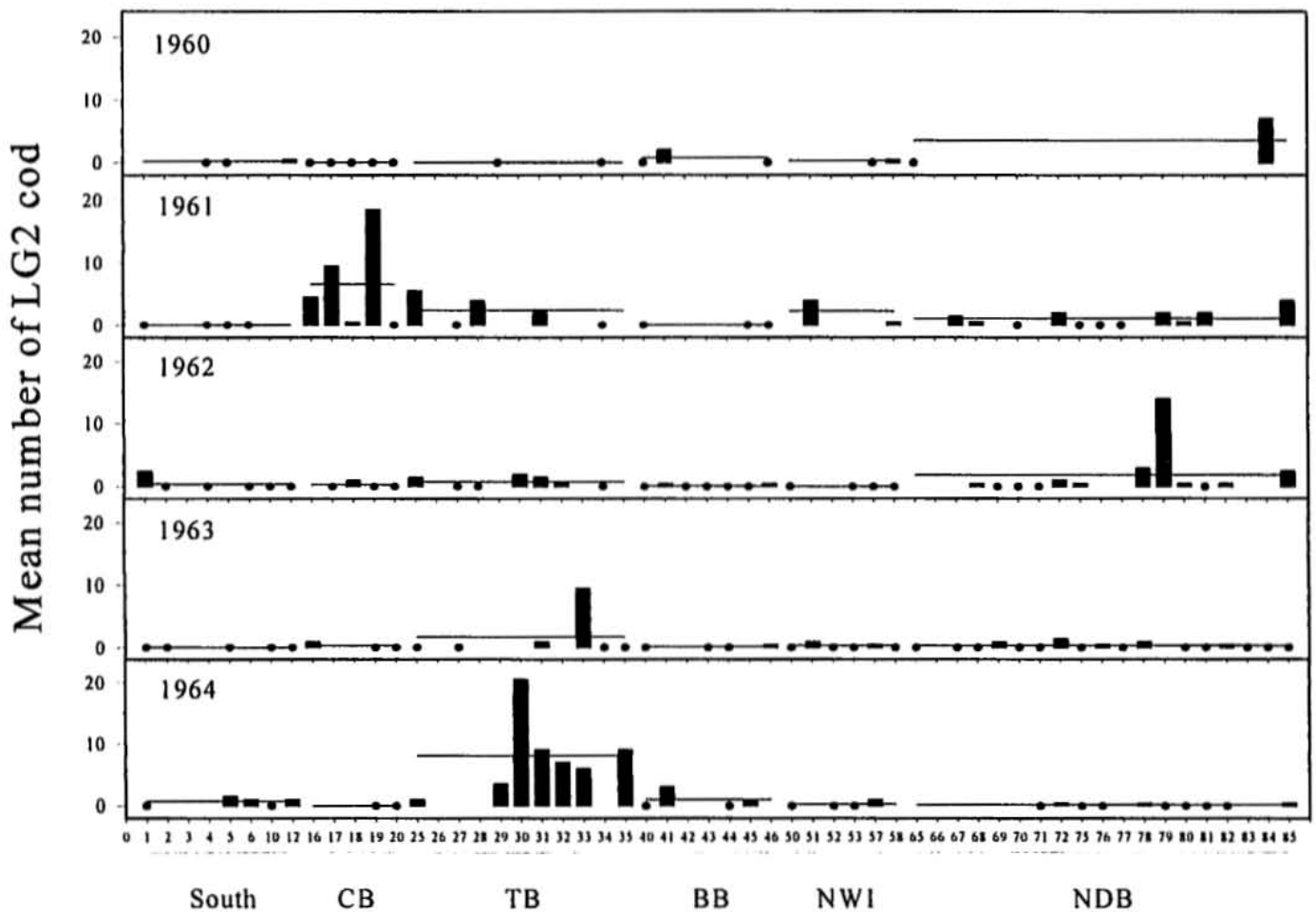


Figure 4.8 Mean catch (n=2 tows) of LG2 cod at each site (1960-1964). Missing data indicates sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay

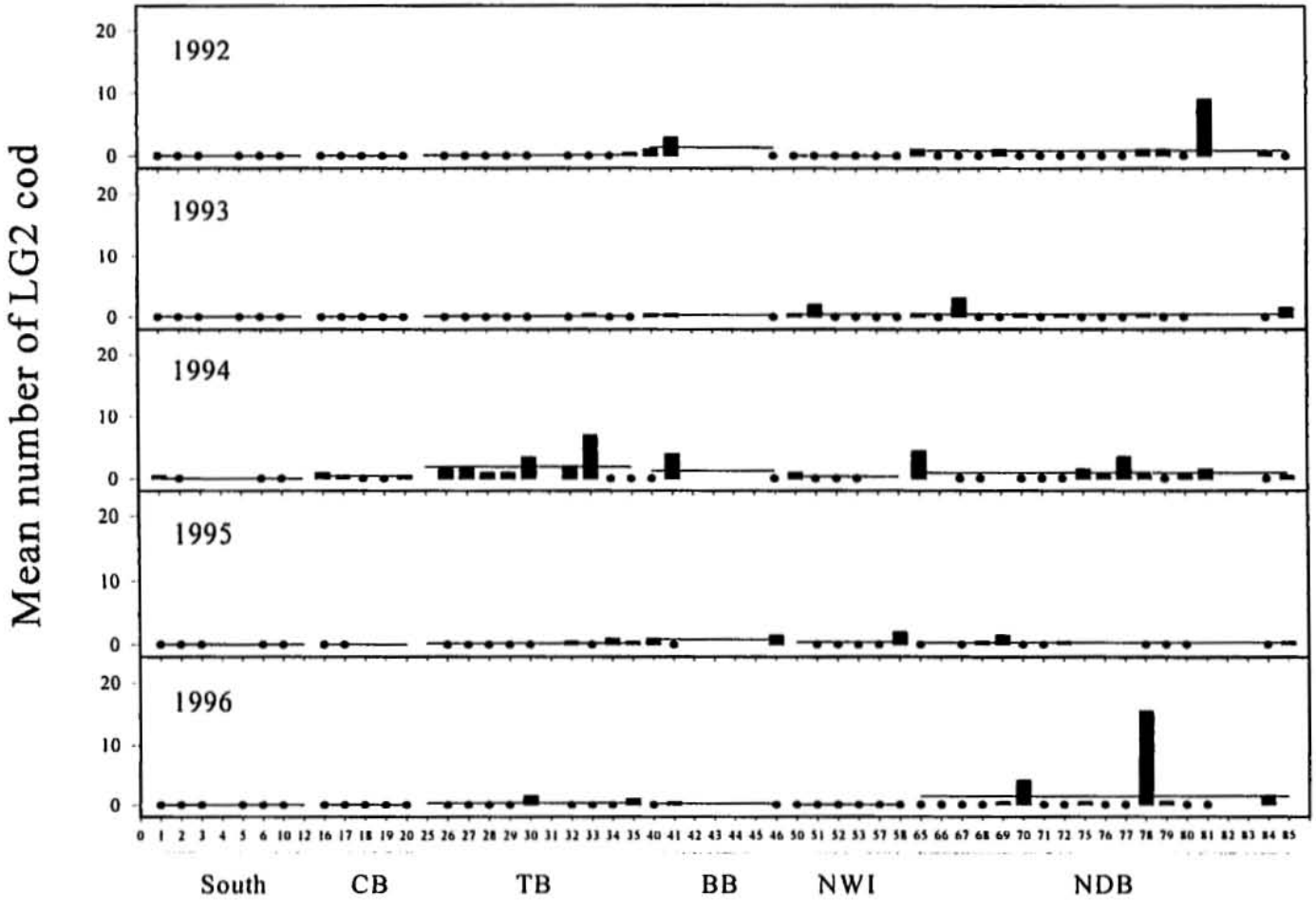


Figure 4.9 Mean catch (n=2 tows) of LG2 cod at each site (1992-1996). Missing data indicates sites were not sampled. • indicates site was sampled but mean catch = 0. Horizontal lines represent bay means. South = Trepassey and St. Mary's Bays (combined), CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NWI = New World Island and Gander Bay (combined), NDB = Notre Dame Bay.

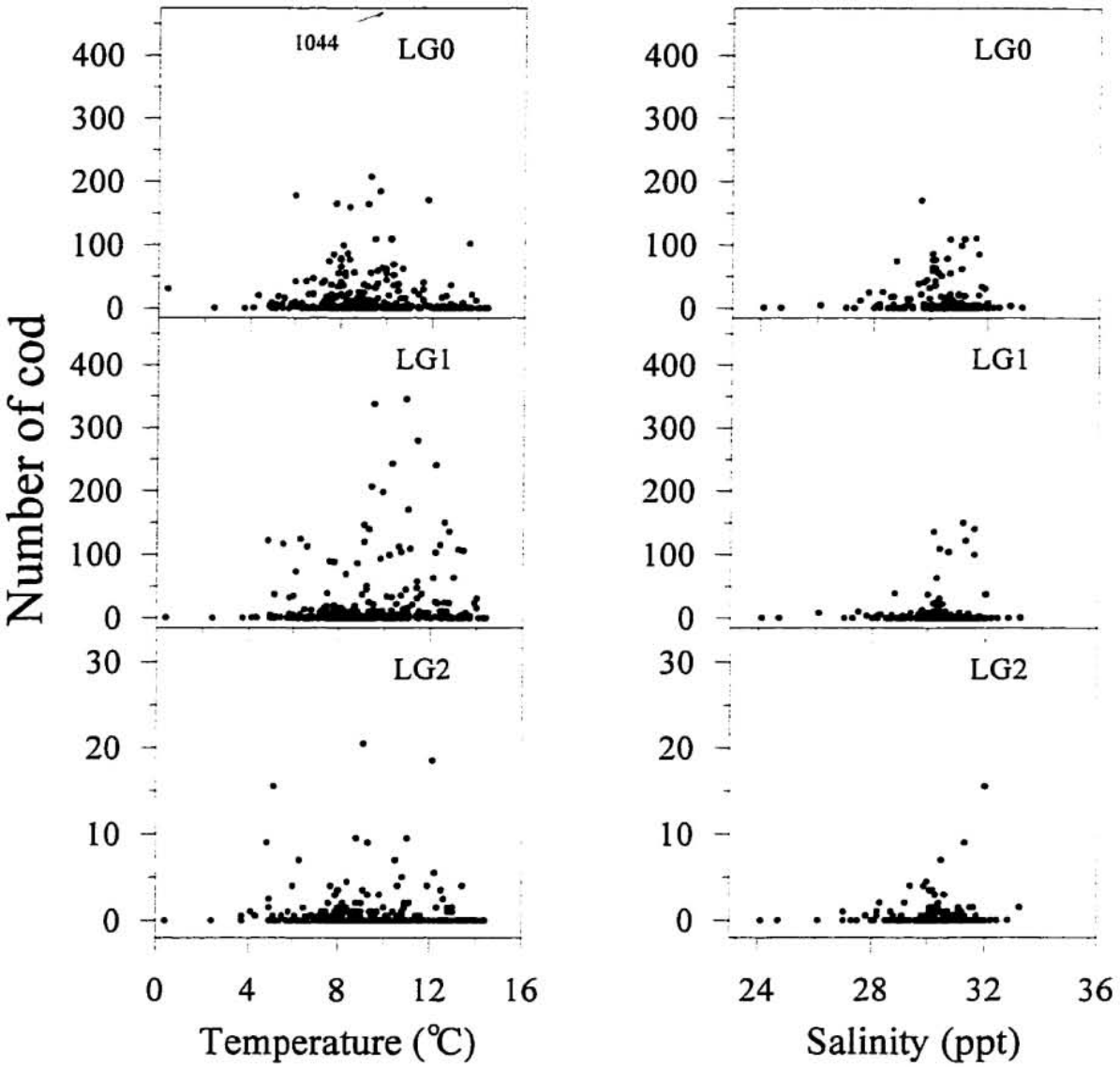


Figure 4.10 Mean number of cod per site (n=2 tows) in relation to temperature and salinity measured at the maximum depth sampled by the 25 m seine. Salinity was not measured in 1960-1964.

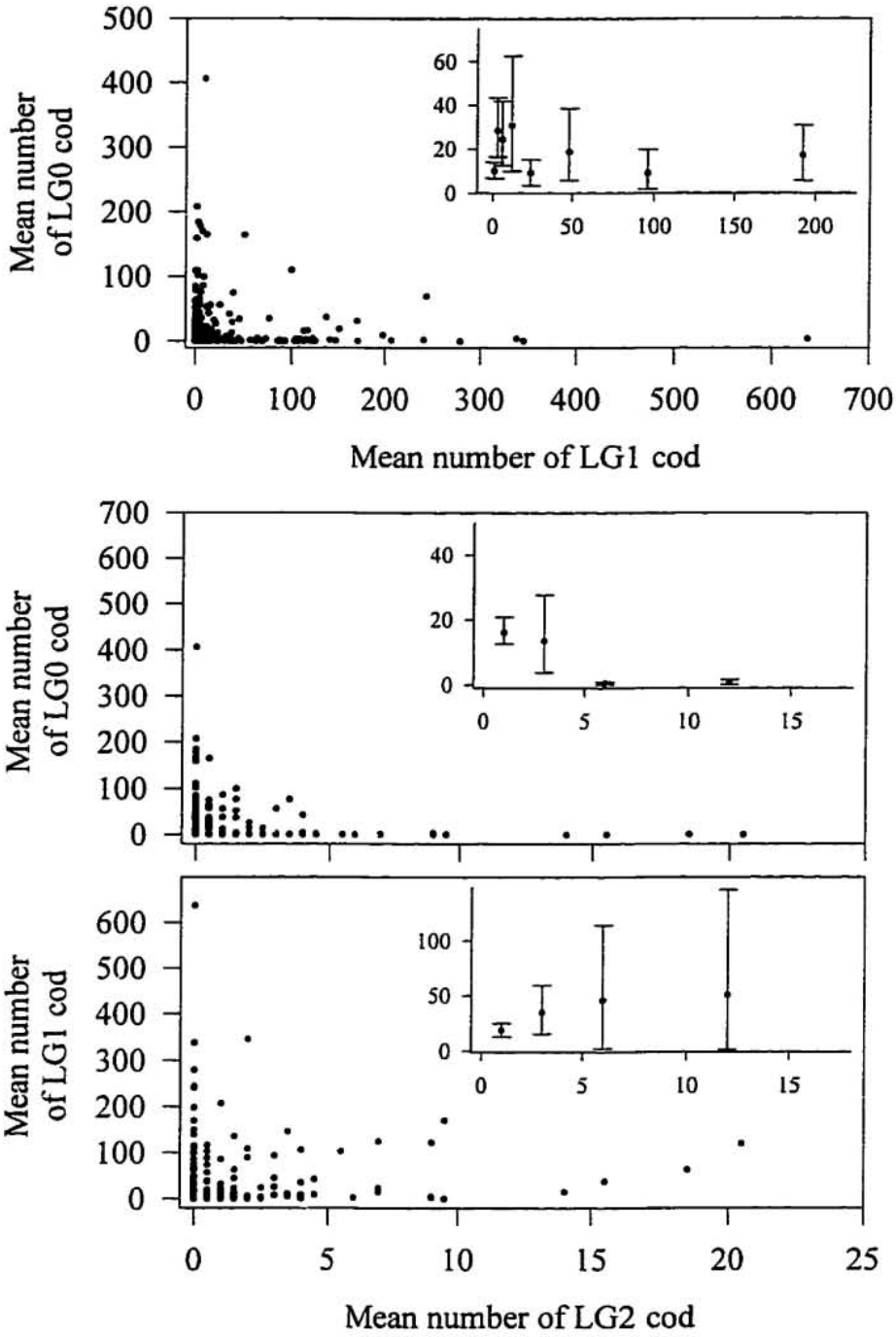


Figure 4.11 Mean number of juvenile cod per site (n=2 tows per site) in relation to the mean number of larger conspecific fish collected in the same net haul. Small panels show mean abundance of cod (y axis) calculated at intervals of 0-2, 2.1-4.0, 4.1-8.0, 8.1-16.0, 16.1-32.0, etc. (x axis). 95% confidence limits were computed using repeated resampling (bootstrap methods). n=375 sites sampled (1960-1964 and 1992-1996, i.e. an average of 37.5 sites sampled per year).

Appendix 4.1. Site locations were determined by differential GPS in 1966. Depth is the average maximum depth sampled (n=2). ✓ indicates observed; • indicates not observed.

Site	Latitude	Longitude	Depth	Sampling Site	Cobble	Macro-algae	Eelgrass
1	47°10.104	53°31.814	5.9	Harricot Beach	✓	✓	•
2	47°11.598	53°34.892	4.4	Half Island	✓	•	✓
3	47°00.643	53°40.748	5.5	Mother Hicks Cv	✓	✓	•
5	46°59.362	53°41.061	—	Mosquito Cv	✓	✓	•
6	47°09.647	53°38.879	3.5	North Harbour	✓	•	✓
10	46°45.076	53°21.870	7.0	Trepassey	✓	✓	•
16	47°34.544	53°15.803	4.8	Davies Head (1)	•	✓	•
17	47°34.552	53°15.884	4.3	Davies Head (2)	•	✓	•
18	47°44.600	53°11.908	3.5	Crockers Cv	✓	✓	•
19	47°40.511	53°11.349	4.5	Bryants Cv	✓	✓	•
20	47°43.160	53°11.812	3.8	Bristols Hope Cv	•	•	•
26	47°43.197	53°50.199	9.6	Masters Head	✓	•	•
27	47°50.506	53°54.081	3.8	Little Mosquito Cv	•	✓	✓
28	47°50.473	53°52.503	16.1	Bald Point Beach	✓	✓	•
29	47°59.758	53°48.864	5.0	Long Beach (E)	•	•	•
30	47°59.851	53°49.155	6.8	Long Beach (W)	•	•	•
32	48°08.886	53°44.000	9.0	Middle Lance Cv	•	•	•
33	48°10.190	53°42.706	7.8	Burgoynes Cv	•	•	•
34	48°23.551	53°22.309	4.6	Lockston's Arm	•	✓	✓
35	48°22.581	53°22.194	9.5	Cap Cv	•	•	•
40	48°26.024	53°51.221	6.2	Cannings Cv	•	✓	✓
41	48°25.739	53°50.972	7.1	Man Point	•	✓	•
46	49°00.925	53°46.944	4.1	Indian Bay	✓	✓	✓
50	49°23.401	54°25.295	3.3	Rubens Cv	✓	✓	•
51	49°24.123	54°24.766	5.1	Grassy Cv	•	✓	•
52	49°26.004	54°28.036	2.0	Seal Island	✓	✓	•
53	49°24.348	54°28.588	2.7	Fox Island	•	•	✓
57	49°33.147	54°50.357	2.0	Bridgeport	✓	•	✓
58	49°31.300	54°48.900	3.1	Luke's Arm	•	•	✓
65	49°31.832	55°16.929	4.3	Fortune Hbr. (1)	•	✓	•
66	49°31.660	55°16.009	7.5	Fortune Hbr. (2)	•	✓	•
67	49°31.481	55°15.996	2.6	Fortune Hbr. (3)	✓	✓	✓
68	49°30.623	55°15.592	1.2	Fortune Hbr. (4)	•	✓	✓
69	49°30.151	55°12.946	7.1	Fortune Hbr. (5)	✓	✓	✓
70	49°22.874	55°41.811	3.0	Wild Bight	•	•	•
71	49°26.722	54°43.136	4.5	Julies Harbour	•	✓	✓
72	49°28.081	55°46.187	6.4	Tommy's Arm	•	•	•
75	49°31.270	53°51.416	5.5	Woodfords Arm (1)	•	•	•
76	49°31.128	55°51.450	3.0	Woodfords Arm (2)	✓	✓	•
77	49°30.975	55°51.389	2.5	Woodfords Arm (3)	✓	✓	•
78	49°29.511	56°04.006	18.4	Lower Wolfe Cv	✓	✓	•
79	49°29.287	56°03.842	8.6	Green Island	•	•	•

Appendix 4.2. Scale-dependent variation determined using hierarchical ANOVA for LG0 cod. df, degrees of freedom; SS, sums of squares; MS, mean squares; VC, variance component.

Year	Source	df	SS	%SS	MS	VC	%VC
1960	coast	1	5344.7	1.4	5344.7	-1973.8	
	bay	4	129066.1	34.4	32266.5	2973.3	23.3
	beach	11	168756.9	45.0	15341.5	5579.7	43.8
	error	17	71096.0	18.9	4182.1	4182.1	32.8
1961	coast	1	527.2	1.8	527.2	-12.5	
	bay	4	3563.3	11.4	890.8	01.1	0.2
	beach	24	21168.3	67.8	882.0	341.8	63.1
	error	30	5947.0	19.0	198.2	198.2	36.6
1962	coast	1	118.0	0.0	118.0	-120.2	
	bay	4	20390.1	6.5	5097.5	-70.9	
	beach	34	201973.0	64.6	5940.3	1847.7	45.1
	error	40	89796.5	28.7	2244.9	2244.9	54.8
1963	coast	1	1782.0	1.8	1782.0	23.3	1.8
	bay	4	4897.4	5.0	1224.3	-57.2	
	beach	35	64991.9	67.1	1856.9	621.1	49.3
	error	41	25197.5	2.6	614.5	614.5	48.8
1964	coast	1	4632.8	6.4	4632.8	146.6	10.8
	bay	4	2819.8	3.9	704.9	-148.8	
	beach	26	54116.2	75.1	2081.4	877.0	64.9
	error	32	10471.0	14.5	327.2	327.2	24.2
1992	coast	1	57.9	0.1	57.9	-59.1	
	bay	4	7320.1	20.2	1830.0	117.8	26.0
	beach	40	13545.5	37.5	338.6	4.3	0.9
	error	46	15176.5	42.0	329.9	329.9	72.9
1993	coast	1	3791.8	4.9	3791.8	43.1	4.7
	bay	4	6409.4	8.3	1602.3	40.8	4.4
	beach	39	42593.2	55.4	1092.1	273.4	29.8
	error	43	24004.0	31.2	558.2	558.2	60.9
1994	coast	1	177.7	0.1	177.7	-245.4	
	bay	4	26043.8	19.5	6510.9	397.2	20.7
	beach	34	79024.3	59.1	2324.2	808.5	42.2
	error	40	28288.0	21.1	707.2	707.2	36.9
1995	coast	1	762.4	1.2	762.4	-24.3	
	bay	4	6117.3	10.3	1529.3	16.6	1.9
	beach	30	40930.6	69.5	1364.3	528.4	61.9
	error	36	11067.5	18.7	07.4	307.4	36.0
1996	coast	1	550.2	0.9	550.2	-22.8	
	bay	4	5176.4	8.5	1294.1	38.1	5.4
	beach	39	31758.9	52.5	814.3	151.6	21.6
	error	45	22993.0	38.0	510.9	510.9	72.9

Appendix 4.2 continued. LG1 cod.

Year	Source	df	SS	%SS	MS	VC	%VC
1960	coast	1	41444.3	4.2	41444.3	-348.4	
	bay	4	174237.6	17.7	43559.4	-2304.6	
	beach	11	623459.8	63.6	56678.1	24191.8	74.4
	error	17	141006.0	14.3	8294.4	8294.4	25.5
1961	coast	1	8255.9	4.9	8255.9	30.9	1.0
	bay	4	21184.0	12.6	5296.0	304.1	10.4
	beach	24	68802.4	41.0	2866.7	277.7	9.5
	error	30	69340.5	41.3	2311.3	2311.3	79.0
1962	coast	1	4.4	0.0	4.4	-2.1	
	bay	4	522.4	3.1	130.6	-8.8	
	beach	34	8005.5	48.6	235.4	18.7	8.6
	error	40	7920.5	48.1	198.0	198.0	91.3
1963	coast	1	21027.7	3.4	21027.7	-197.0	
	bay	4	82511.2	13.6	20627.8	1243.3	15.7
	beach	35	241282.0	39.8	6893.7	261.4	3.3
	error	41	261209.0	43.1	6370.9	6370.9	80.8
1964	coast	1	8519.6	2.3	8519.6	-206.4	
	bay	4	49408.3	13.3	12352.0	575.0	9.4
	beach	26	182919.8	49.5	7035.3	1515.5	24.8
	error	32	128138.5	34.7	4004.3	4004.3	65.7
1992	coast	1	483.9	1.5	483.9	14.3	3.7
	bay	4	684.7	2.2	171.1	-43.2	
	beach	40	28760.5	93.1	719.0	349.2	90.9
	error	46	941.5	3.0	20.4	20.4	5.3
1993	coast	1	6235.5	4.2	6235.5	131.7	7.2
	bay	4	4343.3	2.9	1085.8	-89.7	
	beach	39	85043.5	58.0	2180.6	511.1	28.0
	error	43	50852.5	34.7	1182.6	1182.6	64.7
1994	coast	1	9620.6	6.4	9620.6	134.1	6.6
	bay	4	12390.9	8.3	3097.7	134.5	6.6
	beach	34	57106.1	38.3	1679.5	-34.4	
	error	40	69938.0	46.9	1748.4	1748.4	86.6
1995	coast	1	0.1	0.0	0.1	-0.1	
	bay	4	30.6	6.6	7.6	-0.3	
	beach	30	339.5	73.9	11.3	4.4	64.1
	error	36	89.0	19.3	2.4	2.4	35.8
1996	coast	1	0.5	0.0	0.5	-6.0	
	bay	4	834.9	12.6	208.7	8.7	10.9
	beach	39	3861.1	58.4	99.0	28.2	35.6
	error	45	1909.0	28.8	42.4	42.4	53.4

Appendix 4.2 continued. LG2 cod.

Year	Source	df	SS	%SS	MS	VC	%VC
1960	coast	1	17.3	9.8	17.3	0.90	16.0
	bay	4	22.9	13.0	5.7	0.10	2.2
	beach	11	54.9	31.1	4.9	0.10	1.9
	error	17	81.0	46.0	4.7	4.70	79.8
1961	coast	1	26.4	2.5	26.4	-2.48	
	bay	4	259.1	25.0	64.7	5.17	25.8
	beach	24	563.1	54.4	23.4	8.64	3.2
	error	30	185.0	17.8	6.1	6.16	30.8
1962	coast	1	18.8	2.9	18.8	0.30	4.6
	bay	4	24.2	3.9	6.0	-0.30	
	beach	34	363.6	59.4	10.6	2.70	33.4
	error	40	205.5	33.5	5.1	5.10	61.9
1963	coast	1	3.3	1.3	3.3	-0.06	
	bay	4	21.5	8.5	5.3	0.00	2.6
	beach	35	156.3	61.9	4.4	1.36	42.9
	error	41	71.0	28.1	1.7	1.73	54.4
1964	coast	1	176.6	13.2	176.6	0.40	1.7
	bay	4	460.9	34.4	115.2	10.45	44.4
	beach	26	483.1	36.1	18.5	5.90	25.0
	error	32	217.0	16.2	6.7	06.78	28.8
1992	coast	1	3.5	1.7	3.5	0.00	0.9
	bay	4	14.5	7.3	3.6	-0.02	
	beach	40	158.8	80.2	3.9	1.75	79.3
	error	46	21.0	10.6	0.4	0.45	20.6
1993	coast	1	2.7	5.6	2.7	0.06	10.6
	bay	4	0.5	1.0	0.1	-0.04	
	beach	39	26.2	54.6	0.6	0.12	20.0
	error	43	18.5	38.5	0.4	0.43	69.3
1994	coast	1	2.9	0.7	2.9	-0.17	
	bay	4	30.1	8.1	7.5	0.28	5.9
	beach	34	153.1	41.5	4.5	-0.02	
	error	40	182.5	49.5	4.5	4.56	94.0
1995	coast	1	0.0	0.0	0.0	-0.02	
	bay	4	3.0	10.0	0.7	0.02	5.9
	beach	30	15.3	51.1	0.5	0.09	21.7
	error	36	11.5	38.4	0.3	0.31	72.3
1996	coast	1	17.9	3.3	17.9	0.39	5.8
	bay	4	18.0	3.3	4.5	-0.58	
	beach	39	460.6	86.5	11.8	5.51	82.3
	error	45	35.5	6.6	0.7	0.78	11.7

Appendix 4.3. Mean number/tow and coefficients of variation (CV) for cod from the southern Gulf of St. Lawrence. All data are from Table 12 of Sinclair et al. (1996).

Mean number per tow

Age	1990	1991	1992	1993	1994	1994b	1995
0	0.38	1.50	0.00	0.00	0.00	0.00	0.00
1	0.71	3.28	10.70	0.61	1.13	2.56	1.15
2	7.24	7.45	31.50	3.07	3.80	13.64	4.05
3	45.94	16.22	26.91	7.58	26.65	61.81	2.67
4	31.13	26.00	16.24	8.61	19.79	26.93	6.44
5	15.58	13.53	11.22	13.35	23.37	24.32	8.47
6	10.06	5.42	2.37	8.46	20.95	21.04	6.24
7	6.94	2.39	1.51	3.47	9.34	9.19	11.94
8	2.38	1.52	0.70	1.60	3.31	3.26	6.28
9	1.38	0.25	0.47	0.38	1.30	1.28	1.60
10	1.05	0.15	0.21	0.30	0.59	0.59	0.66
11	0.88	0.13	0.19	0.06	0.45	0.44	0.16
12	0.00	0.18	0.04	0.17	0.14	0.14	0.00
13	0.00	0.02	0.07	0.04	0.15	0.14	0.00
14	0.12	0.09	0.04	0.02	0.04	0.04	0.00

Coefficient of variation

Age	1990	1991	1992	1993	1994	1994b	1995
0	41.20	44.49	0.00	0.00	0.00	0.00	0.00
1	37.37	32.94	84.34	70.78	28.80	57.81	74.22
2	27.62	33.48	44.24	76.99	28.77	72.54	58.83
3	22.81	21.32	33.42	22.82	33.24	58.42	23.42
4	21.62	21.93	28.39	17.04	22.94	30.85	15.18
5	14.74	16.85	24.66	14.91	16.94	15.98	13.44
6	12.68	16.94	22.73	12.27	15.40	14.82	9.95
7	12.19	18.37	20.69	11.74	13.92	13.78	9.04
8	11.75	15.12	20.70	12.32	14.62	14.28	8.50
9	14.48	21.82	49.04	18.66	13.74	13.52	12.31
10	10.44	36.27	21.50	11.26	14.09	13.22	19.41
11	15.31	25.10	53.48	0.00	17.10	16.18	20.09
12	0.00	24.57	0.00	26.94	22.43	23.08	0.00
13	0.00	0.00	48.65	0.00	30.84	32.17	0.00

Chapter V
A multiscale analysis of temporal variation

5.1 Introduction

Most ecological studies describe patterns and quantify variation at a single spatial or temporal scale. An increasing number of studies however now recognize that variation is dependent on the scale of observation and investigate quantities across multiple scales of space or time (Wiens 1989, Schneider 1994). Multiscale analyses typically address how variation of a quantity such as population density depends on spatial or temporal scale. For example, is variation in density concentrated at a single scale or does it vary at multiple scales? The answer has important implications for identifying processes that produce variation and for the design of field surveys (Wiens et al. 1986, Denman 1992). In aquatic systems, multiscale analyses have shown that spatial variation is not concentrated at any characteristic scale in either benthic (Schneider et al. 1987, McArdle and Blackwell 1989, Jones et al. 1990, Downes at al. 1993) or pelagic habitats (Weber et al. 1986, Horne and Schneider 1997). This contrasts with temporal variation which is assumed to be concentrated at periodic scales such as annual, seasonal, or diel (Laevastu and Hayes 1981). Concentration of variation at a particular temporal scale (e.g. annual) indicates that dominant processes operating at that scale may be important sources of variation, e.g. the annual cycle imposed on many ecosystems (Denman 1992).

Differential survival of yearclasses is a well known phenomenon that contributes to variation in abundance at annual and longer scales (Hjort 1914, 1926, Sissenwine 1984, Rothschild 1986, Levin 1991). At small temporal scales, feeding and predator avoidance are daily activities that contribute to variation in population density (Helfman 1978, 1993, Horn 1980, Worgan and FitzGerald 1981, Wright 1989). Population density varies at

other temporal scales as well, e.g. a lunar scale of spawning and settlement occurs in some coral reef fishes (Robertson 1991, Doherty 1991). Variation in population density among temporal scales has seldom been quantified within the same study. Consequently the relative magnitude or importance of variation in population density at different scales is poorly known.

The objective of this study is to quantify temporal variation in density of recently settled juvenile cod from two coastal sites at three temporal scales: years, months, and hours. Hourly variation was expected to be a source of high variation because the local density of juvenile cod should be reduced by repeated sampling at the same site within the time scale of one hour. This in addition to some juvenile cod occupying territories (Tupper and Boutilier 1995b) or home ranges (Hawkins et al. 1985, Clark and Green 1990) where repopulation to a site is expected to be slow after initial sampling is further reason to expect high contrast between consecutive samples at small temporal scales. Annual variation was also expected to exhibit high variation due to the high variability in recruitment and yearclass strength that occurs in may fish species (Hjort 1914, 1926, Peterman et al. 1988, Anderson 1988, Leggett and DeBlois 1994), including Atlantic cod *Gadus morhua* (Hutchings and Myers 1994, Ings et al. 1997). Less variation was expected at the temporal scale of months. Juvenile cod are abundant along the northeast coast of Newfoundland (Methven and Bajdik 1994, Schneider et al. 1997) and are not known to make extensive migrations, except late in the year when movement into deeper water is reported (Pihl 1982, Macdonald et al. 1984). This expectation of low variation in population density at the monthly scale relative to annual variation is consistent with the expectations of Laevastu and Hayes (1981) for marine fishes in general.

The approach taken in this study is to quantify temporal variation at three scales, identify the scale of maximum variation, and determine if the same temporal structure is maintained at two distant sites sampled at the same time with the same sampling

equipment. The maintenance of temporal structure at distant sites suggests that the underlying processes are similar at each site and hence operate over large spatial scales (Hewitt et al. 1996).

5.2 Methods

Sampling was conducted in Trinity Bay (site 34, Fig. 5.1) and Notre Dame Bay (site 58, Fig. 5.1) Newfoundland from May to December 1993 and August to December 1994 (Table 5.1). These sites were initially sampled for juvenile cod in 1959-1964 by A. Fleming (Lear et al. 1980). The site numbers designated by A. Fleming were retained in this study. In 1993-1994, these sites were sampled by local fishermen who were shown how to deploy the 25-m beach seine (9 mm stretch mesh in the codend) with the same fishing effort being applied for each sample. The seine and its method of deployment are described in Chapter III and by Schneider et al. (1997). Sampling consisted of two standardized tows at an interval of 1-2 weeks at each site. The two tows required about one hour to complete. The maximum depth of sampling was <6 m (site 34: mean=4.1 m, range=1.8-5.5 m; site 58: mean=2.8 m, range=1.6-5.5 m). Both sites were sheltered from wave action, as indicated by live terrestrial vegetation growing to within two metres of the high water mark. All cod were frozen within 1-2 hrs of sampling and were measured to the nearest millimetre of standard length (SL) after being thawed in the laboratory. An additional site was sampled by the 25 m seine in southern Trinity Bay (site 27: mean depth=4.4 m, range=2.9-6.2 m; Fig. 5.1). Only one tow was conducted at this site at a 1-2 week interval in 1993 and 1994 (Table 5.1).

Variation in population density was estimated using data collected from August to December each year at sites 34 and 58. Variation in standardized catches was examined at three temporal scales for each site: (i) year - defined as all collections from August to December inclusive in 1993 and 1994; (ii) months - August, September, October,

November, and December within each year; and (iii) hours - there being a maximum of approximately one hour between the two tows at each site. Multiscale analyses were only conducted on cod <96 mm SL. These individuals were estimated to be <1-yr-old based on size modes reported in Chapter III and are defined herein as length group zero (LG0) cod.

The traditional approach to partitioning variation at discrete scales utilizes hierarchical analyses of variance (ANOVA) where sources of variation represent different scales. This approach treats smaller-scale variation as being nested within larger-scale variation. Hierarchical ANOVA has been used to partition population variation at discrete spatial scales nested within each other (Jones et al. 1990, Downes at al. 1993) but has not, to my knowledge, been used to estimate population variation at multiple temporal scales (Gaston and McArdle 1994). Variation was partitioned from sums of squares (SS) calculated at three temporal scales: among years, among months nested within years, and among tows (i.e. hourly variation) nested within months. Sums of squares can be thought of as an unweighted measure of contrast among each of the three levels of variation (in this case, three temporal scales). Sources of variation with high sums of squares indicate relatively high contrasts. Sequential sums of squares in a purely nested model are additive with sums of squares for each source of variation, including the error term, adding up to the models total sum of squares (Sokal and Rohlf 1995). Variation can be partitioned directly as a percentage by dividing sums of squares for each source of variation by the models total sum of squares. This method is direct, does not produce negative variances, and estimates variation at each scale. Variance components (Sokal and Rohlf 1995), a second measure of variation, are also additive and can be expressed as a percentage of the total variation observed. Variance component analyses calculates variation from mean squares in a hierarchal ANOVA. A limitation of this method is the calculation of a zero or negative variance (component) which is taken to be indicative of a low variance (Snedecor and Cochran 1967). Sums of squares and variance components

were partitioned using the General Linear Model (GLM) procedure of SAS version 6.09 (SAS 1988) using type I (sequential) sums of squares.

Differences in catches between tows I and II for each site (34 and 58) were paired by the date of collection to determine if catch in the first tow differed significantly from the second tow at each site. Residuals were tested for normality using the Shapiro-Wilk statistic (Shapiro and Wilk 1965). If residuals were not normal, randomization tests (Manly 1991) were conducted to determine if significant differences in standardized catches occurred between tows. Tow II was randomized 400 times with tow I held constant for each test. A p value was calculated by determining the proportion of randomizations with an F ratio $\geq$ the observed F ratio determined by ANOVA.

Sampling efficiency of the 25-m seine was examined to determine if this might contribute to variation between consecutive tows (I and II) at the same site. For example, a very inefficient sampler would be expected to differ less between two consecutive tows at the same site than a very efficient sampler where the vast majority of fish would be collected in the first tow. Sampling efficiency was determined by SCUBA divers who evaluated whether juvenile cod were actively avoiding the seine. Divers swam slightly behind and above the seine and observed if the footrope remained snug to the bottom. Divers watched for escapement over the headrope and around the wings as the seine was towed over relatively smooth bottoms at sites 34 and 27. Underwater (horizontal) visibility during two dives was estimated to be 9-11 m (site 34) and 15-20 m (site 27). Sampling efficiency was also determined at Hickman's Harbour (48°06.5'N, 53°44.7'W; 4.5 m depth; 15 November 1995) in a small narrow inlet where space for lateral movement of cod was limited. The seine was able to sample the entire inlet in one tow. The catchability of the seine was then determined by rapidly resampling (n=5 tows within 2.5 hr) and determining how quickly the catch decreased using the Leslie Method of population estimation (Hilborn and Walters 1992). An important assumption of the Leslie

Method is no immigration into the sampling area which was assumed to have been met by quickly resampling the entire inlet five times in 2.5 hours.

Catch data from 40-45 sites (Fig. 5.1) that were visited once each year in September or October 1992-1994 (Table 5.1) were examined to determine if patterns of abundance observed at sites 27, 34, and 58 were unique to these sites or if pattern was widespread and characteristic of the northeast coast of Newfoundland. Sites were sampled using a 25-m seine (n=2 consecutive tows) at approximately the same date (to within 1-2 weeks) each year. Sampling started in Saint Mary's Bay in mid September and finished in western Notre Dame Bay in late October each year, a distance of approximately 1500 km (Fig. 5.1). Exact locations and further details of sampling are in Schneider et al. (1997).

To determine whether seasonal recruitment by sibling species (*Gadus morhua* and *Gadus ogac*) contributed to temporal variation it was necessary to identify some specimens using electrophoresis. Presently (mid 1990s), electrophoresis is the only known means of distinguishing between these species at <50 mm (Hovgård and Lehmann 1986, Renaud et al. 1986). They are morphometrically similar at sizes <50 mm SL and occur together as demersal juveniles in shallow coastal waters of northeast Newfoundland. Electrophoretic identifications were made on 264 cod (43-203 mm SL) collected at site 27 on 23 November 1993. This procedure was repeated for juvenile cod collected on 6 May 1994 at site 27 (n=43, 54.2-123.8 mm SL). A third collection from 6 October 1993 at site 34 (n=271, 38-77 mm SL) was also examined using electrophoresis in 1997. Unfortunately, these specimens (6 October 1993) did not exhibit protein banding that was consistent with the banding from known specimens of adult *G. morhua* and *G. ogac*. It was concluded that proteins may have been denatured during four years of storage in a frost-free freezer. These specimens were then identified using differences in pigmentation on the first anal fin, a new character in addition to characters already identified in Chapter II (Appendix 5.1). The validity of this new character was determined in a blind

test of 100 specimens (40-63 mm SL) that were identified previously using electrophoresis (Appendix 5.1).

5.3 Results

All LG0 cod (n=26, 54.2-96.6 mm SL) from the 6 May 1994 collection were identified by electrophoresis as *Gadus morhua* (Fig. 5.2). Larger LG1 individuals from this collection included both species (Fig. 5.2; *G. morhua*: n=5, 104.6-118.5 mm SL; *G. ogac*: n=12, 97.6-123.8 mm SL). LG0 cod collected on 6 October 1993 included both species with 83 of 271 (30.6%) specimens examined being *G. ogac* (Fig. 5.2). *Gadus ogac* (mode=66, range=53-77 mm SL) were generally larger than *G. morhua* (mode=51, range=36-68 mm SL). The final collection (23 November 1993, n=264) consisted mostly of *G. morhua*, with only six specimens of *G. morhua* (Fig. 5.2; *G. morhua*: n=258, 43-203 mm SL; *G. ogac*: n=6, 87-135 mm SL).

Catchability of the 25-m seine used throughout this study was high. SCUBA divers observed no escapement over the headline or around the wings of the seine on both occasions. The footrope remained on the bottom and cod were observed to fall back behind the wings as the seine was towed towards shore. LG0 cod remained strongly associated with the bottom (within ca. 15 cm) and were observed to be corralled before falling back into the seine and codend as the wings were brought closer together before the seine was hauled out of the water. A catchability coefficient q of -0.977 (i.e. the slope of the equation below) was estimated for the 25-m seine using the Leslie Method (Ricker 1975, Hilborn and Walters 1992) for plots of catch (dependent variable) versus cumulative catch. This is comparable to a slope and catchability of -1.0 which, using the Leslie Method indicates each successive catch is approximately halved. The five consecutive collections taken at Hickman's Harbour resulted in catches of 327, 76, 117, 27, and 29 cod being caught (all <176 mm SL) which gave a population estimate of

592.4 cod/880m^2 (0.67 cod/m). The catchability equation estimated from the five catches above was:

catch = -0.97758(cumulative catch) + 579.16 [se of slope = 0.37]

Variation in density of LG0 cod was greater at monthly than at hourly or yearly scales contrary, to expectation (year and hour > month). Monthly variation accounted for 29.6-30.0% of the total variation estimated by sums of squares, and 20.7-24.1% of the variation estimated from variance components (Table 5.2). The rank order of temporal variation in population density at these scales remained the same at both sites, i.e. variation at the intermediate scale of months exceeded variation at hourly and yearly scales (Table 5.2).

Variation in density of juvenile cod at the scale of years accounted for a maximum of 10.2% of the total variation observed (Table 5.2). Standardized catches in 1994 exceeded catches in 1993 at both sites by at least a factor of two (Fig. 5.3), a difference that was significant for site 58 ($p=0.0275$), but not site 34 (Table 5.2). A total of 1715 LG0 cod were collected from August to December in 1993 ($n=44$ tows) with 4182 LG0 cod collected during the same period in 1994 ($n=44$ tows; Fig. 5.3). All but six of the 88 tows collected cod.

At the temporal scale of hours, variation in density of LG0 cod (maximum 13.1%; Table 5.2), was comparable to variation at the scale of years. At this scale, density of LG0 cod did not differ significantly between sites (Table 5.2). Differences in catches between tows I and II were reexamined by pairing them according to sampling site and day of collection to determine if this pairing of consecutive catches would result in a significant difference between tows I and II. This reanalysis, essentially a paired t-test, determined if the mean difference in catches between tow I (mean=78.84 LG0 cod/tow) and tow II

(mean=55.18 cod/tow) was significantly different from zero. Such a difference might be expected if there was little or no lateral recruitment into the area being sampled by the first tow. This reanalysis indicated catches were not significantly different (ANOVA, $F_{1,43}=2.82$, $p=0.1002/2 = 0.0501$ for one tailed test; $H_o=Tow_I \geq Tow_{II}$). However, the Shapiro-Wilk statistic indicated the p value could not be trusted because the residuals were not normally distributed. Randomization tests (Manly 1991) were then used to determine if significant differences in catches occurred between tows. The p value from the randomization test ($p=0.1125/2=0.056$) was essentially unchanged from that of the one tailed test ($p=0.0501$) calculated from an F distribution.

Twenty-six of the 44 tows from sites 34 and 58 had a higher catch in the first tow, 15 of 44 tows had a higher catch in the second tow and three pairs of tows had the first catch equal to the second catch. The relatively high mean catch of tow II coupled with the high efficiency of the seine led to the conclusion that substantial lateral movement in the order of $55.18_{towII}/78.84_{towI}=69.9\%$ occurred between tows I and II in a 1-hr period.

Monthly variation was the largest source of temporal variation (20.7-30.0%; Table 5.2). At this scale, density of LG0 cod was lowest in August, highest in October and decreased again in November-December (Fig. 5.3). This pattern was evident at site 58 in both years but was not observed at site 34 in either year. Mean monthly catches at site 34 were more variable, being highest in September-October, 1993 and in August-September, 1994 (Fig. 5.3).

Juvenile cod at sites 27, 34, and 58 were examined to determine if any patterns in the size structure and phenology were evident at monthly or near monthly scales that might account for high variation in density at this scale. Collections at all three sites were dominated by two length modes (Figs. 5.4, 5.5). The first mode consisted of 35-90 mm SL cod collected in May-June. A second mode of 30-60 mm cod began settling in

August. These length data indicate that small (<50 mm SL) cod were primarily collected beginning at two distinct times of the year: May-June and August-December. Small newly-settled recruits were usually absent in July (Figs. 5.4 and 5.5). A consistent feature of the August-December period of recruitment was settlement of a pulse of small LG0 cod (<50 mm) in mid October. October settlement was observed at all three sites (27, 34, 58) in both years (1993, 1994) though the number of small newly settled cod in October 1994 was low. This influx of small cod in mid October resulted in a bimodal length distribution as shown for site 34 on 16 October 1993 (Fig. 5.6). Bimodality was not evident on any one sampling day at site 58 in 1993 or 1994 due to the much smaller catches of LG0 cod at this site (Figs. 5.6, 5.7). However, there was a clear shift in modal size in mid October, 1993 and 1994, indicating the arrival of small cod (Figs. 5.6, 5.7).

Data from 1992, 1993, and 1994 were then examined to determine if the pattern of settlement observed above (sites 27, 34, 58) was widespread and characteristic of the northeast Newfoundland coast. Survey data (see Schneider et al. 1997, Ings et al. 1997) from St. Mary's Bay to western Notre Dame Bay (Fig. 5.1), were examined for bimodality in size structure of LG0 cod indicative of two periods of settlement, one beginning in August and a second beginning in mid October. These data span the period when recruits from both the August and mid October settlement occur inshore. The hypothesis, based on the phenology of settlement at sites 27, 34, and 58, was that recruitment by individuals settling in August would only be evident at sites sampled prior to ca. late September. Individuals from both the August and mid October settlement pulses would be present at sites sampled after mid October.

Results showed that only one length mode of LG0 cod was evident at sites sampled before late September in 1992, 1993, and 1994 (Fig. 5.8). This mode consisted of individuals <75 mm. Larger individuals represented a mixture of 1-yr-old cod and small

juvenile cod that arrived nearshore in spring (ca. May-June). The length-frequency distributions of juvenile cod from sites sampled from mid to late October showed the presence of two LG0 length modes in 1992 and 1993 (Fig. 5.8) $\leq$96 mm SL indicating these are LG0 young of the year cod. The second of these two modes (65-100 mm) represented settlement prior to late September. The first mode (40-60 mm) represented settlement in mid October (Fig. 5.8). Very few small individuals were collected after mid October 1994.

5.4 Discussion

Analyses of population count data from two coastal Newfoundland sites showed that variation in density of LG0 cod was greater at monthly than at hourly or yearly scales. In general, monthly variation exceeded tow-to-tow variation (hours) which in turn exceeded, or was comparable with annual variation. Variation in population density at monthly or near-monthly scales was likely due to the arrival and subsequent loss of pulses of recently settled juvenile cod in coastal habitats. Arrival at coastal habitats and settlement was synchronous to within 1-2 weeks at three sites separated by hundreds of kilometres. The maintenance of temporal structure due to settlement of small cod at approximately the same time over large spatial scales indicates that these patterns were generated by processes acting over large spatial scales, on the order of hundreds of kilometres.

Multiple pulses of young within a year are best known for tropical species (Longhurst and Pauly 1987, Doherty 1991) but are less commonly reported for temperate species. In the coastal north Pacific, settlement of the Dungeness crab (*Cancer magister*) at two or three times of the year was attributed to physical factors, primarily temperature and oceanic transport during mating, spawning, egg incubation and with larval development

(McConnaughey et al. 1992, Dinnel et al. 1993). Multiple pulses of settlement at temperate latitudes also occurred for two echinoid species and four ophiuroid species (Pedrotti 1993). Studies on the mysid (*Neomysis integer*) suggest that this widely distributed species has a complex life cycle at lower latitudes where it reproduces throughout much of the year (Mees et al. 1994). At higher latitudes (North Sea) pulsed spawning results in 2-3 generations each year (Mees et al. 1994).

Multiple pulses of young within a year are also reported in some temperate fishes: Atlantic and Pacific herring (*Clupea harengus harengus*, *Clupea harengus pallasi*), capelin (*Mallotus villosus*), croaker (*Nibea albiflora*), blue fish (*Pomatomus saltatrix*), windowpane (*Scophthalmus aquosus*), killifish (*Fundulus heteroclitus*) and speckled dace (*Rhinichthys osculus*) (John 1963, Kendall and Walford 1979, Lambert and Ware 1984, Kneib 1986, Ware and Tanasichuk 1989, Takita et al. 1989, Morse and Able 1995). The time between pulses varied from ca. 8-25 days for capelin and herring, where the biological basis for this pattern was a well documented process of older and larger herring spawning in waves before smaller individuals (Lambert and Ware 1984, Lambert 1987, Ware and Tanasichuk 1989). Wave spawning, due to the size structure of the adult population, typically resulted in pulses of larvae being produced at a mean interval of 13.4 days (determined from Table 1 of Lambert 1987) for Pacific and Atlantic herring. Accordingly, the size composition of the herring spawning stock will determine the interval between consecutive spawnings and how eggs are distributed over time (Ware and Tanasichuk 1989).

Size (age) structure of the spawning population has not been advanced as an explanation for multiple pulses when the between-pulse interval (i.e. inter-wave interval) is large, as it is in killifish (1.5 months, Kneib 1986), croaker (2 months, Takita et al. 1989), bluefish (2 months, McBride and Conover 1991), windowpane (ca. 5 months, Morse and Able 1995), and speckled dace (several months; John 1963). Spawning date has been is

independent of body length in killifish (Kneib 1986) and cod (ca. 55-135 cm TL; Kjesbu 1994), indicating that different size classes can spawn at the same time of year and that adult size may not account for multiple pulses of young when the between pulse interval is large. Food intake, a second factor that can potentially influence time of spawning, was observed to delay spawning by <2 weeks for laboratory cod fed on low and moderate food rations (Kjesbu 1994, Karlsen et al. 1995). This in addition to the observation that cod, like many other fishes, stop or reduce feeding prior to or during spawning (Rae 1967, Love 1970, Arntz 1973, Braaten 1984, Kjesbu 1994) suggests that food availability during gonadal development is not responsible for pulsed settlement of juvenile cod.

Pulsed settlement of juvenile cod along a 1500 km stretch of the Newfoundland coast is hypothesized to be due to two sources: (i) coastal settlement by the morphologically similar Atlantic and Greenland, and (ii) protracted inshore (April-July) and offshore (March-June) spawning by *Gadus morhua* (Lear and Green 1984, Myers et. al. 1993, Hutchings et al. 1993).

The protracted spawning period of Newfoundland cod (Myers et al. 1993, Hutchings et al. 1993) is initiated during the spawning migration (Woodhead and Woodhead 1965, McKeown 1984) which, for spring spawners begins as daylength shortens in autumn and early winter with the commencement of vitellogensis and increasing levels of gonadal sex steroids including estradiol-17ß (Norberg and Kjesbu 1991, Kjesbu et al. 1991, Karlsen et al. 1995, Burton et al. 1997). Gonadal development occurs as daylength decreases in autumn, when cod vacate relatively shallow feeding areas and move towards deeper overwintering grounds (Templeman 1966, Lear and Green 1984, Norberg and Kjesbu 1991). Cod form dense spawning aggregations and generally spawn in winter-spring as daylength increases (Harden Jones 1968, Hislop 1984, Lear and Green 1984). Eggs and larvae are pelagic for 1-3 months (Campana and Hurley 1989, Campana 1996) and, in

the Newfoundland region, pelagic juvenile cod arrive and settle in coastal habitats during autumn and spring at <50 mm SL (Methven and Bajdik 1994). Newly settled pelagic juveniles can be distinguished from their demersal counterparts by their smaller size, pelagic colour, and pigmentation, and by the absence of the encysted metacercaria of the digenean parasite *Cryptocotyle lingua*, which is often evident on larger more demersal cod inhabiting the nearshore zone (Methven and Bajdik 1994). Pelagic juveniles arrived nearshore primarily in May-June, August-September, and from mid October onwards.

Small cod that arrived inshore in May-June and after mid October were all *G. morhua*. Young-of-the-year *Gadus morhua* and *G. ogac* both in August-September. *Gadus ogac* were on average larger than *G. morhua* in early October, suggesting that *G. ogac* settled earlier in August-September. Settlement by *G. ogac* occurred in a brief period in August-September which is consistent with a March-April spawning period in coastal waters (Scott and Scott 1988, Mikhail and Welch 1989, Morin et al. 1991) where development and hatching of demersal eggs is followed by a single pulse of juvenile settlement in August and September. The more protracted inshore and offshore spawning by *G. morhua* and the potential for large-scale dispersal of pelagic eggs and young larvae (Helbig et al. 1992, Davidson and de Young 1995, Pepin and Helbig 1997) are consistent with the more protracted settlement observed in this study for *G. morhua* relative to *G. ogac*.

Small cod collected in coastal nursery sites in autumn may originate from inshore (Wroblewski et al. 1994, Goddard et al. 1994, Brattey 1997, Smedbol and Wroblewski 1997) or offshore (Lear and Green 1984, Hutchings et al. 1993) spawning events. Most studies support the conjecture that inshore settlement in autumn originates from spawning inshore. Highest densities of pelagic larvae and juveniles consistently occurred inshore (Anderson and Dalley 1997), where cod are known to spawn during spring and early summer (Thompson 1943, Hutchings et al. 1993, Smedbol and Wroblewski 1997).

Density of demersal LG0 and LG1 cod was also highest inshore and decreased with increasing distance offshore (Dalley and Anderson 1997) where cod stocks in the early 1990s were at historically low levels (Hutchings and Myers 1994, Taggart et al. 1994). Spawning time estimated from counts of daily increments in lapillus otoliths indicated that cod settle at <50 mm SL in mid October, in late June, and early July (Pinsent and Methven 1997) within the range of peak spawning for inshore cod estimated by Smedbol and Wroblewski (1997; mid-June to mid-July) and by Hutchings et al. (1993; May-June). Small juvenile cod (*G. morhua*) that occur nearshore in spring (May-June) may originate from a spawning event late in the previous year or very early in the year they settled. Cold water temperatures during winter mean these cod will grow slowly (Brown et al. 1989) and hence be small in spring.

Hour-to-hour variation accounted for up to 13.1% of the total variation observed in this study. Hourly variation was due to the combined effects of depletion and lateral recruitment of cod into the sampling area. These two processes counteract each other. Depletion, due to the high sampling efficiency of the seine, generates variation at the hourly scale whereas lateral movement reduces variation when cod move into the sampling area. Lateral movement then lowers the contrast between tows I and II and contributes to a non-significant difference between tows. Rapid movement into an area just sampled (disturbed) has been reported for invertebrates and vertebrates, including whiting (*Merlangius merlangus*; Kaiser and Spencer 1994). Such movements are usually attributed to the sampling gear either damaging benthic prey or causing prey to move, both of which may make prey more vulnerable to scavengers that can rapidly move (<1 hr; Caddy 1973) into a disturbed area.

The findings of this study have several implications for designing and conducting coastal surveys for juvenile cod. The high variation in population density at the monthly scale indicates sampling at a fixed time each year is important if survey results are to be

compared among years (e.g. Tveite 1984, Nygaard et al. 1989, Hovgard and Nygaard 1990, Ings et. al. 1997). For example, sampling during October when recruitment of newly settled cod to coastal nursery sites is high will yield a different size structure and density than sampling in November-December when juveniles likely move into deeper water (Pihl 1982, Macdonald et al. 1984, Methven and Bajdik 1994) and possibly out of range of the seine. This study indicates that sampling would have to be conducted within a week or two each year given the rapid change and high variation in population density that occurs at the monthly scale. At smaller temporal scales, the interval between consecutive tows should be consistent at each site. Long intervals between tows at the same site (i.e. 2-3) leads to a lower contrast between tows. The interval between tows is easily standardized but high sea-wind conditions and the seine becoming snagged on the bottom are two situations where the between tow interval may be longer than expected. Consequently a longer between tow interval may be more desirable there by allowing for more difficult sampling conditions.

This approach to partitioning temporal variation at discrete scales led to the unexpected result of low variation in population density at the largest temporal scale examined. How this result was influenced by the presence of small *G. ogac* and by only two years of data is not known but should be considered in the design of future studies. The potential effect of *G. ogac* in the samples can be initially accessed by repeating the hierarchical analyses with August and September densities reduced by 30%, that proportion of the data that may be *G. ogac* (October data in Fig. 5.2). This re-analyses indicated monthly variation (site 34, 24.1%; site 58, 32.5%) exceeded annual (site 34, 1.8%; site 58, 9.8%) and hourly (site 34, 22.9%; site 58, 9.7%) variation at both sites hence maintaining the temporal structure of monthly variation exceeding yearly and hourly variation.

Table 5.1 Summary of sampling effort. All sampling was done during the daytime by a 25-m seine (n=2 tows/visit) from August to December in 1994.

Site (#)	Latitude Longitude	Sampling Frequency	Years	Tide
Little Mosquito Cove (27)	47°50'N 53°52'W	at least twice monthly May to Dec.	1993, 1994	low tide in 1993
Trinity (34)	48°23'N 53°22'W	at least twice monthly May to Dec.	1993, 1994	low tide in 1993
Luke's Arm (58)	49°31'N 54°48'W	at least twice monthly May to Dec.	1993, 1994	low tide in 1993
40-45 sites NE coast of Newfoundland	see Fig. 5.1	yearly, Sep. to Oct.	1992-1994	any stage of tide

Table 5.2 Hierarchical ANOVA of LG0 cod density at years, month, and hours. Variability was partitioned as sums of squares (%SS) and variance components (%VC). y = year, m = month.

Source of variation	df	SS	MS	F	p[1]	%SS	%VC
Site 34							
year	1	25244	25244	2.28	0.1200	4.2	---
month(y)	7	177452	25350	2.29	0.0625	29.6	24.1
hour(y*m)	9	79074	8786	0.79	0.5950	13.1	---
error	26	287383	11053			47.9	75.9
total	43	569154					
Site 58							
year	1	3020	3020	5.03	0.0275	10.2	---
month(y)	8	8867	1108	1.84	0.1000	30.0	20.7
hour(y*m)	10	3244	324	0.54	0.8400	10.9	---
error	24	14421	600			48.7	69.0
total	43	29552					

[1] values calculated by randomization (Manly 1991).

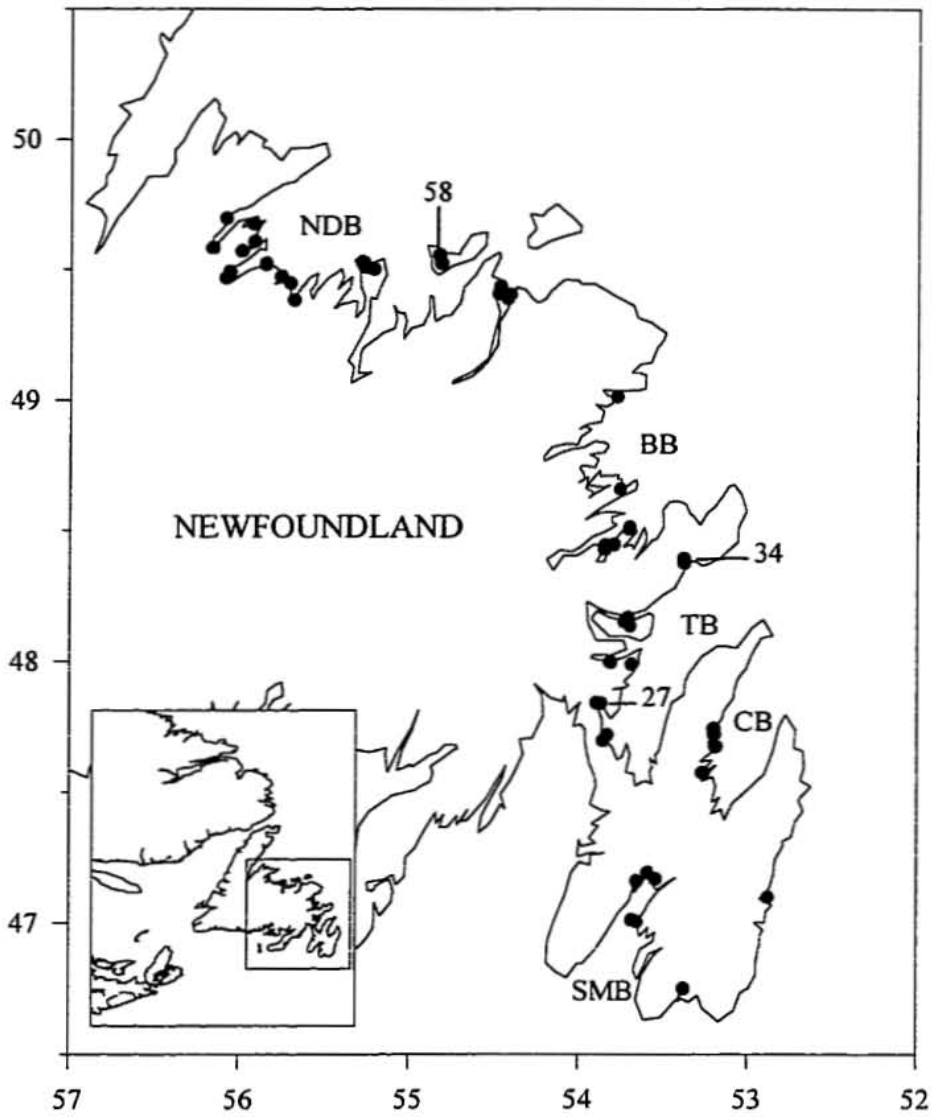


Figure 5.1 Map of Newfoundland showing locations of sites 27, 34, and 58. Labelled sites were visited at least twice monthly (2 tows per visit) from May to December 1993 and August to December 1994. Unlabelled sites were visited yearly in September or October 1992-1994. SMB = St. Mary's Bay, CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, NDB = Notre Dame Bay.

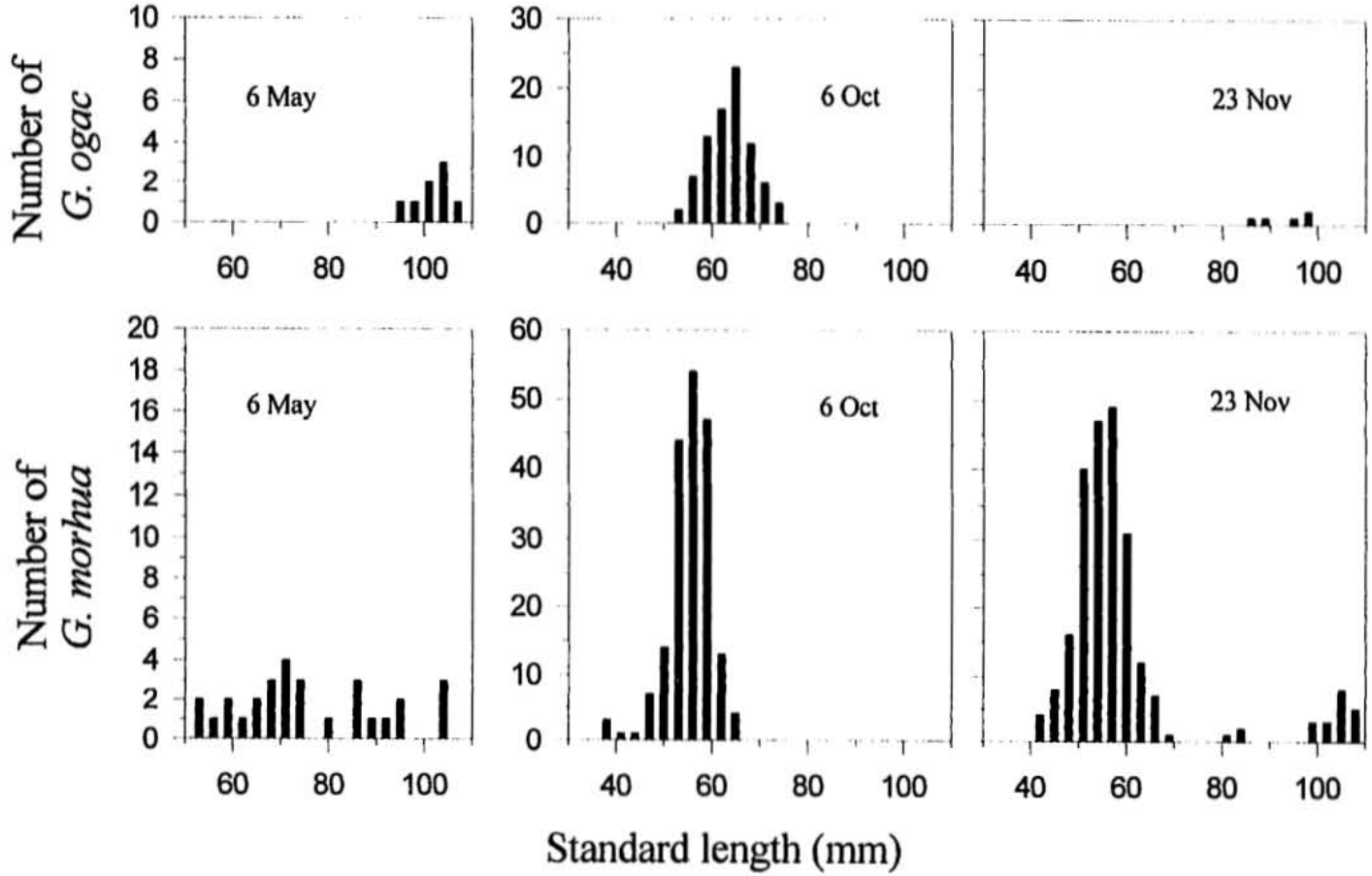


Figure 5.2 Number of *Gadus morhua* and *G. ogac* (3 mm groupings) identified using electrophoresis and diagnostic characters discussed in Methods.

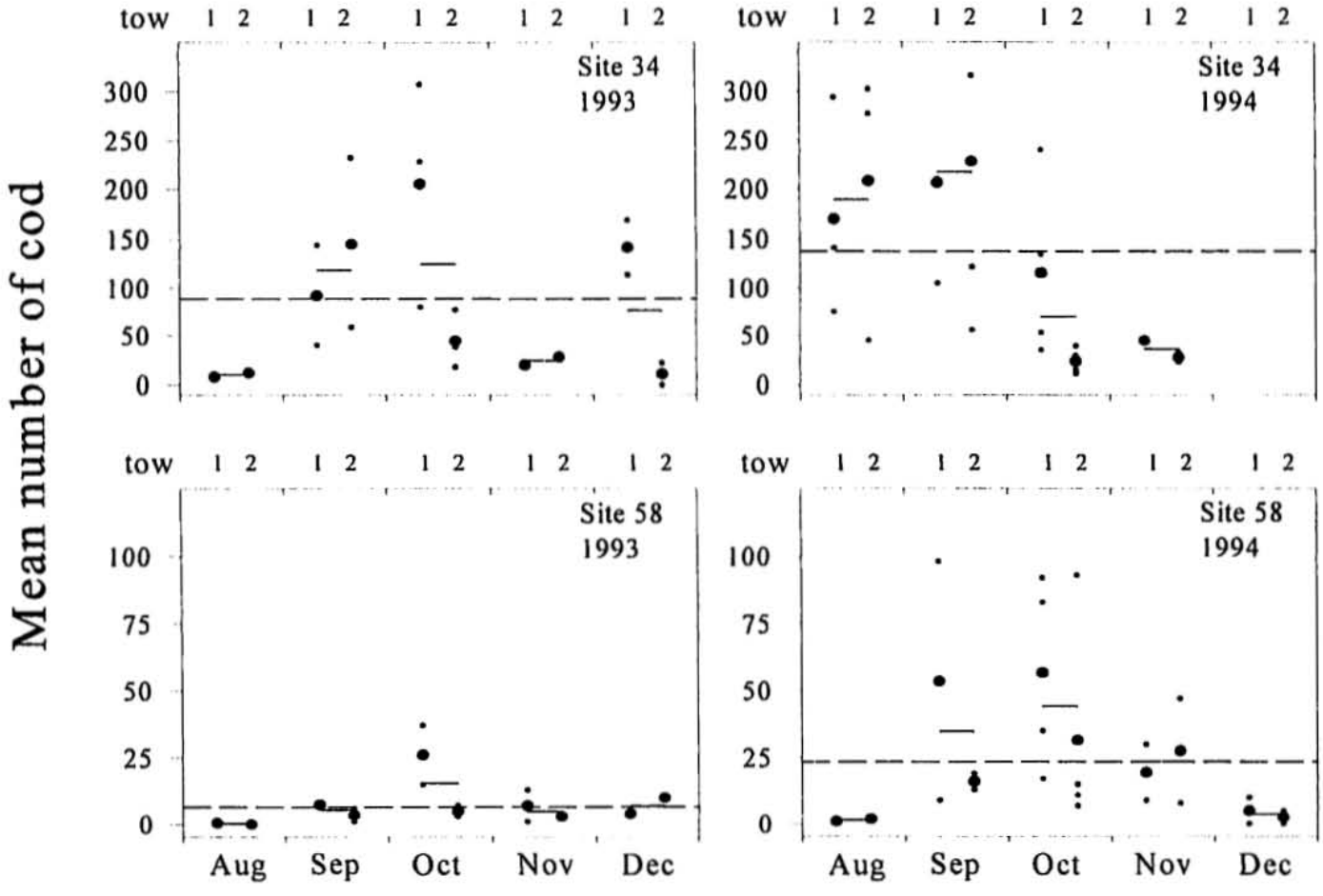


Figure 5.3 Yearly (dashed line), monthly (solid line), and tow (1 and 2; large dots) means of LG0 cod collected at sites 34 and 58 in 1993 and 1994. Individual collections (represented by small dots) were taken at approximately 2 week intervals, i.e. approximately four tows per month.

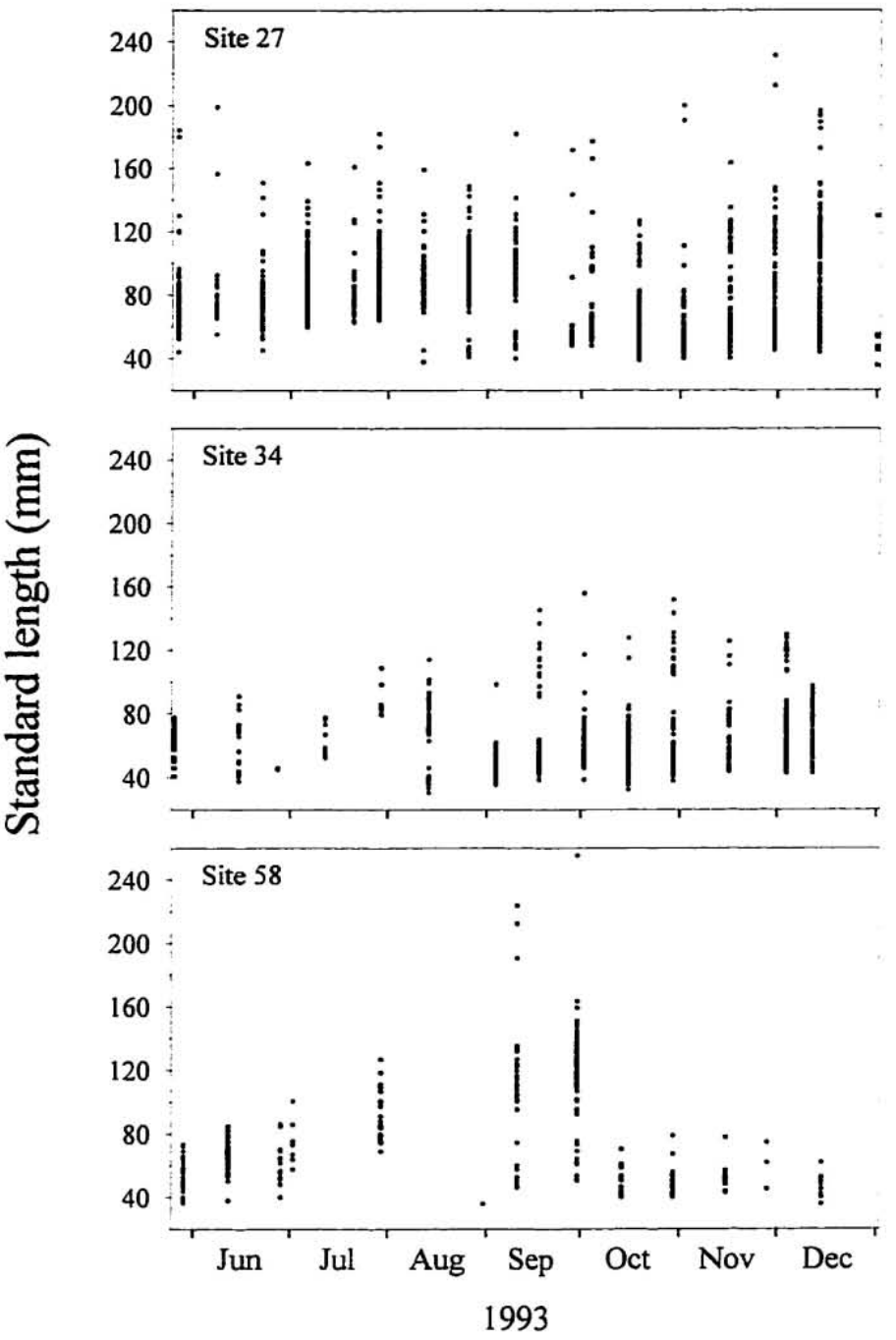


Figure 5.4 Standard lengths of juvenile cod collected at sites 27, 34, and 58 in 1993 at approximately 1-2 week intervals.

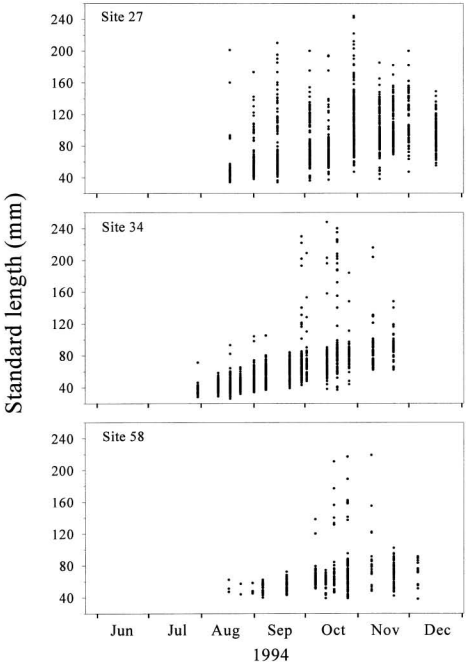


Figure 5.5 Standard lengths of juvenile cod collected at sites 27, 34, and 58 in 1994 at approximately 1-2 week intervals. No sampling was conducted in May, June, and early July.

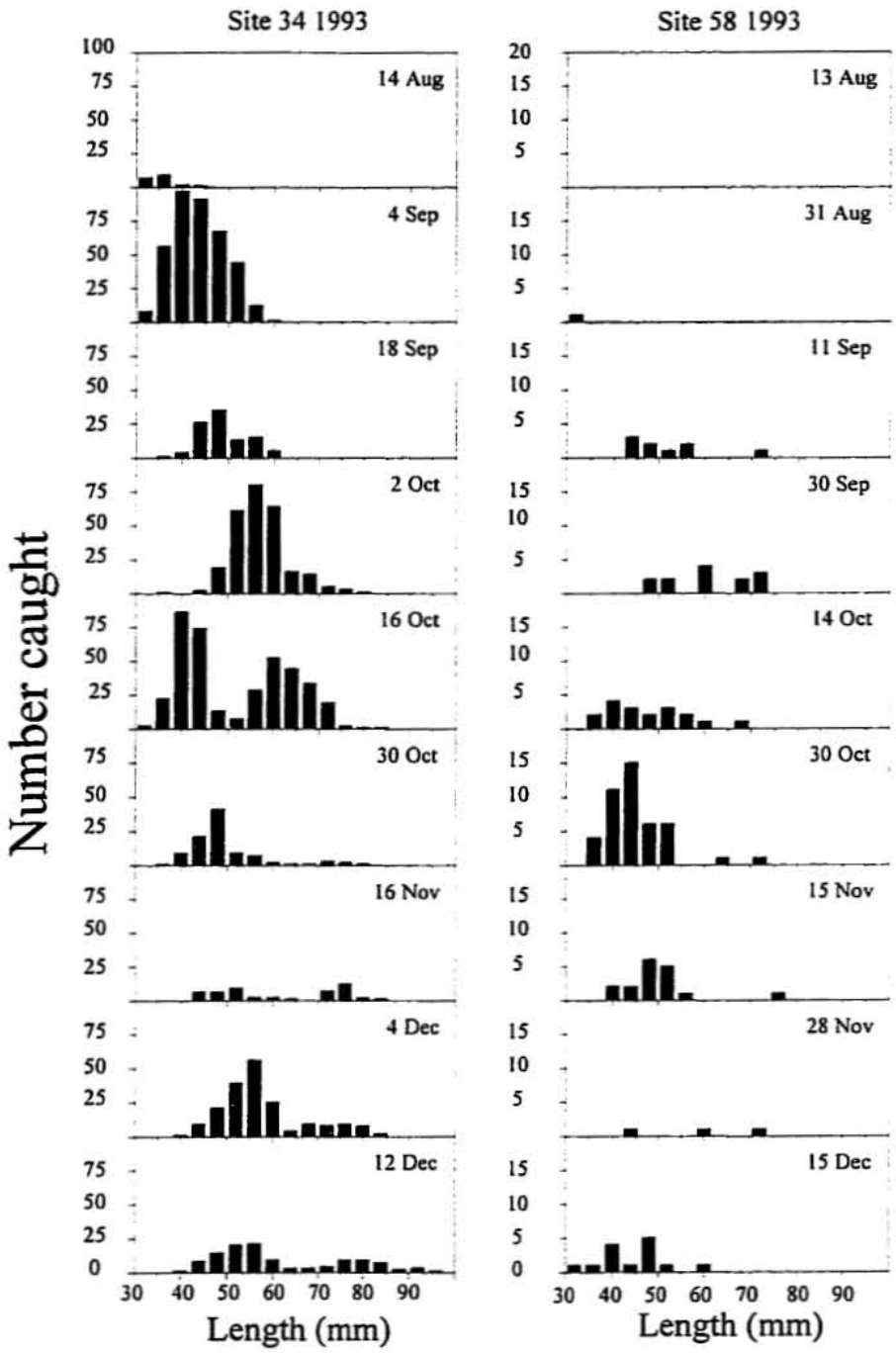


Figure 5.6 Number of newly settled cod (4 mm groupings) at sites 34 and 58 in 1993.

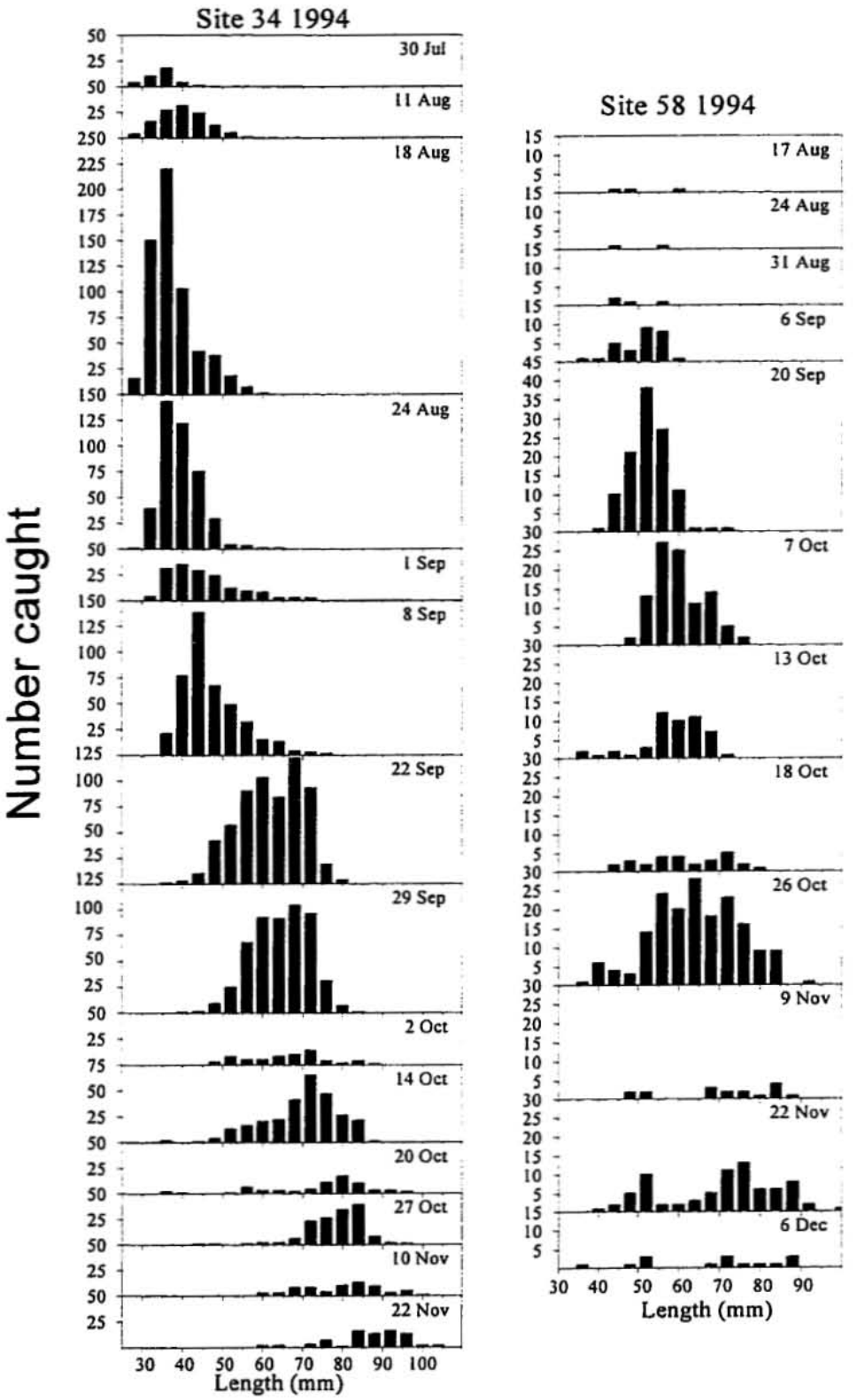


Figure 5.7 Number of newly settled cod (4 mm groupings) at sites 34 and 58 in 1994.

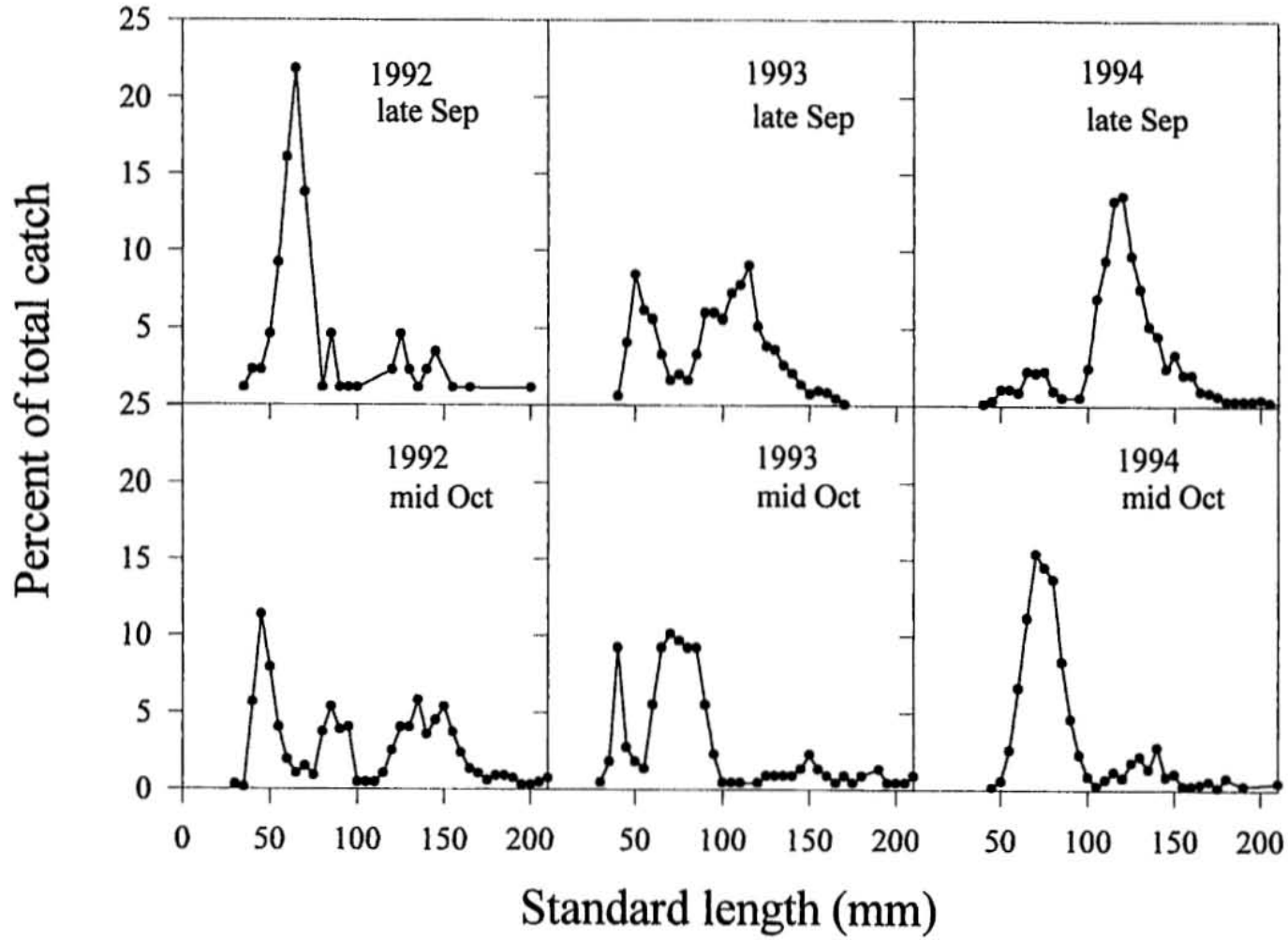


Figure 5.8 Percent frequency of newly settled cod (4 mm groupings) at sampling sites along the northeast coast of Newfoundland sampled before late September (upper panels) and after mid October (lower panels) in 1992-1994.

Appendix 5.1 Blind test of identifying 100 *Gadus sp.* based on differences in pigmentation on the first anal fin in *G. morhua* and *G. ogac* (40-63 mm SL). ID 1 is identification based primarily on anal fin pigment differences. This character, shown to me by Scott Grant (OSC/MUN) compares the extent of pigmentation at the base of the posterior finrays on the first anal fin. The extent of pigmentation is greater in *G. ogac* than in *G. morhua*. ID 2 is known identification established by electrophoresis. **Bold font indicates mis-identification.**

TAG #	ID 1	ID 2	TAG #	ID 1	ID 2	TAG #	ID 1	ID 2	TAG #	ID 1	ID 2
5515	m	m	5516	m	m	7062	o	o	7063	m	m
5517	m	m	5518	m	m	7059	o	o	7061	o	o
5552	o	o	5627	m	m	7054	o	o	7055	m	m
5629	m	m	5630	m	m	7051	m	m	7053	m	m
5631	m	m	5633	m	m	7038	m	m	7039	m	m
5634	m	m	5637	m	m	5947	o	o	7037	m	m
5638	m	m	5639	m	m	5944	o	o	5945	o	o
5641	m	m	5642	m	m	5942	o	o	5943	o	o
5645	m	m	5651	m	m	5940	o	o	5941	o	o
5654	m	m	5656	m	m	5936	o	o	5937	o	o
5658	m	m	5659	m	m	5938	o	o	5939	o	o
5661	m	m	5664	m	m	5933	o	o	5934	o	o
5676	m	m	5678	m	m	5931	o	o	5932	o	o
5680	m	m	5681	m	m	5929	o	o	5930	o	o
5682	m	m	5683	m	m	5927	o	o	5928	o	o
5685	m	m	5686	m	m	5775	o	o	**5798**	**o**	**m**
5687	m	m	5688	m	m	5772	o	o	5773	o	o
5690	m	m	5691	m	m	5770	o	o	5771	o	o
5692	m	m	5693	m	m	5767	o	o	5769	o	o
5694	m	m	5697	m	m	5764	o	o	5766	o	o
5698	m	m	5699	m	m	5761	o	o	5763	o	o
5700	m	m	5717	o	o	5759	o	o	5760	o	o
5718	o	o	5719	o	o	5756	o	o	5758	o	o
5722	o	o	5724	o	o	5753	o	o	5754	o	o
5731	**o**	**m**	5733	m	m	5751	o	o	5752	o	o

Chapter VI Summary and conclusions

The most important original contributions of this thesis include: (i) distinguishing between juvenile *Gadus ogac* and *G. morhua* at lengths as small as 87-135 mm SL (**Chapter II**), (ii) identification of the inshore zone serving as a nursery area in the 1990s for recently settled juvenile cod; that catches are highest at 4-7 m, and that both of these findings are independent of sampling equipment (**Chapter III**), (iii) that juvenile cod are highly aggregated in the coastal zone and that indices of aggregation decrease with increasing fish length and age (**Chapter IV**), and (iv) that seasonal variation in density of juvenile cod exceeded annual variation due to cod arriving and settling in distinct seasonal pulses in the nearshore zone (**Chapter V**). Each of these findings are discussed below in relation to other recent studies on juvenile cod.

This thesis demonstrated that two sibling species of cod, *Gadus morhua* and *G. ogac* occur as recently settled juveniles along the northeast coast of Newfoundland in autumn. Previously, the two species were not distinguished as juveniles and were collectively referred to as "tomcod" (i.e. *G. morhua*). Discriminant function analyses, based on specimens positively identified using starch-gel electrophoresis, indicated that eye diameter and total body mass were the best two characters to distinguish *G. morhua* from *G. ogac* over the size range 87-135 mm SL. In general, *G. ogac* has a smaller eye, and is heavier and deeper bodied than similar sized *G. morhua*. It is expected that rates of mis-identification (5.3%, 10.6%) determined by discriminant function analyses would be improved if overall body colour (*G. ogac*: green and red; *G. morhua*: brown) and shape of the lateral line (*G. ogac*: arched; *G. morhua*: smooth) were included in species identifications.

Small (ca. <50 mm SL) *G. ogac* and *G. morhua* arrive nearshore and occur together on the northeast coast of Newfoundland in August, September, and October. Hence this is the time when mis-identification is most likely greatest. Small Atlantic cod *Gadus*

morhua also arrive nearshore in May-June and from mid-October to January. Positive identification, by electrophoresis, indicated that *G. ogac* do not settle in May-June or after mid-October. Consequently, arrival of small (<50 mm SL) cod to the coastal zone at these times is due solely to *G. morhua*. Identification of specimens from early October (i.e. settlement in August and September) indicated 30.6% (n=83/271) of the August-September pulse of settlement was *G. ogac* and that both species arrived and settled nearshore during this period. This percentage will likely change from year to year and site to site but serves to indicate that a substantial proportion of the small cod collected in early October are *G. ogac*. Consequently, *G. ogac* settles to demersal habitats in August and September, a relatively brief time of year that is consistent with a brief (ca. 2 months; Scott and Scott 1988, Mikhail and Welch 1989, Morin et al. 1991) and localized (i.e. coastal; Jensen 1948) spawning period. This observation in addition to *G. ogac* depositing demersal adhesive eggs in shallow water (Hansen 1949, Cohen et al. 1990) are features that contribute to a single pulse of settlement in late summer. These features contrast with spawning characteristics of *G. morhua* which spawns easily dispersed pelagic eggs (Fahay 1983) in inshore and offshore locations (Hutchings et al. 1993) over several months of the year (Thompson 1943, Myers et al. 1993). These are echaracteristics that lead to more variation in time of settlement, consistent with observations in this study.

The near synchronous (± 1-2 wk) inshore arrival of *G. morhua* in May-June, August-September, and mid-October and the maintenance of temporal structure in population density from year to year at distant sites (hundreds of km) indicates this pattern of settlement was generated by processes operating at large spatial scales. This pattern of settlement was hypothesised to be due to coastal spawning by *G. morhua* and *G. ogac* and also due to a protracted spawning by *G. morhua*. Peak spawning by inshore cod (*G. morhua*) occurs in June (Hutchings et al. 1993, Smedbol and Wroblewski 1997) and corresponds to an autumn settlement given daily growth rates estimated from otoliths of

recently settled cod (Pinsent and Methven 1997). Coastal spawning results in pelagic juveniles settling to the bottom at smaller sizes than pelagic juveniles from offshore spawning events which have to migrate greater vertical distances before making contact with the bottom (e.g. Harden-Jones 1968, p. 148). Consequently, abundance of small cod is expected to be higher in shallower water than in deeper water if, as hypothesised the coastal zone acts as a trap that serves to concentrate cod. This hypothesis is consistent with the inshore-offshore distribution of 0-group cod in Newfoundland (Dalley and Anderson, 1997), Gulf of St. Lawrence (Hanson 1996, Sinclair et al. 1996) and in the North Sea (Riley and Parnell 1984, Heessen 1991) which shows age 0 cod are more abundant in shallower water closer to the coast than in deeper water offshore. Consequently there is a high contrast in density of juvenile cod at large spatial scales (inshore-offshore) which in Newfoundland is attributed to spawning at the coast in the mid 1990s.

Variation in density of juvenile cod was highest at the smallest spatial scale examined, sites, and is consistent with age 0 cod selecting habitats with specific features. These features include shallow (<10 m), protected sites with suitable substratum and some form of cover, either macroalgae, eelgrass, or cobble for protection from predators (Godø and Sunnanå 1984, Riley and Parnell 1984, Tveite 1984, Keats et al. 1987, Horne and Campana 1989, Godø et al. 1989, Lough et al. 1989, Gotceitas and Brown 1993, Tupper and Boutilier 1995a, Gregory and Anderson 1997, Gotceitas et al. 1997). However, if among site variation was primarily determined by habitat selection then some consistency in density of juvenile cod would be expected from year to year when the same sites were re-sampled. No such consistency was observed in this study (Figs. 4.4-4.9). Two explanations seem possible. The first is that cod aggregate either as schools or shoals in the absence of suitable habitat as observed by Tupper and Boutilier (1995b) for age 0 cod on sandy bottom habitats. Aggregation due to shoaling or schooling and movement along the coast can result in increased variation in population

density at small spatial scales. A second explanation proposes age 0 cod are not always associated with habitat at the spatial scale sampled by a beach seine (i.e. 880 m^2). For example, if cod select particular habitat features that are not limiting and occur over several thousands of square metres then cod may be located anywhere within these thousands of square metres at any given time and hence may not be sampled by the beach seine (880 m^2) even though it was deployed in good cod habitat.

High variation in population density was also evident at small temporal scales, day-night. Variation at this scale is typically related to one of two contentious processes, that of a diel inshore migration at dusk, or to gear avoidance during the day. Consistently higher catches during the night by both active and passive gears observed in this study and by Methven and Bajdik (1994) in addition to inshore movements detected by acoustic tagging (Clark and Green 1990), visual observations by SCUBA divers (Keats 1990) and observations from static underwater television (Gibson et al. 1996) indicate gear avoidance is secondary to diel movements in explaining the high contrast between day and night catches of juvenile cod. Diel movements of age 0 cod are not consistent with the establishment and defence of a feeding territory around a shelter site as observed for individually marked age 0 cod in coastal waters of Nova Scotia (Tupper and Boutilier 1995b) unless territoriality only occurred during the day and broke down at night. The high catchability of the 25-m seine and the difference in mean catches between tows I and II indicates juvenile cod appear to rapidly repopulate areas just sampled during the time interval between consecutive tows, i.e. <1 hr. Such rapid movements have been reported for other species and are believed to be due to feeding on prey disturbed by earlier sampling (Caddy 1973, Kaiser and Spencer 1994). Once again these small-scale movements are not consistent with the establishment and defence of feeding territories.

These findings in conjunction with the observation that territoriality often breaks down at high local densities (Wootton 1992), indicates the establishment and defence of feeding

territories likely does not occur at many of the sites examined in this study. Territoriality may occur at locations where coastal density of cod is low, for example in nearshore habitats south of Newfoundland, in the Gulf of St. Lawrence (Hanson 1996), Bay of Fundy (Macdonald et al. 1984), off Nova Scotia (Horne and Campana 1989, Black and Miller 1991, Tupper and Boutilier 1995a, 1995b) and along the New England coast (Targett and McCleave 1974, McCleave and Fried 1975), where recently settled age 0 cod are seldom collected. Consequently territoriality does not appear to be a mechanism of population regulation at sites examined in this study and may only serve to regulate populations at medium to low densities where resources may be limited or where conditions are otherwise suboptimal.

The small-scale movements of cod observed in this study suggest variable predation by larger fish may be a more important mechanism of population regulation than territoriality reported by Tupper and Boutilier (1995b). Small-scale nocturnal inshore movements by juvenile fishes in coastal habitats have been related to predator avoidance and feeding (Helfman 1978, 1993). However, coastal populations of age 0 and 1 cod in Newfoundland feed primarily during the day (Keats and Steele 1992; Grant and Brown, in press) suggesting that the inshore movement of demersal age 0 cod at night is a response to predators, which themselves also move inshore at night to feed. Potential predators of age 0 cod that were observed to move inshore at night included *Myoxocephalus scorpius*, *Myoxocephalus octodecemspinosus*, *Gadus ogac*, *Hemitripterus americanus*, *Scomber scombrus*, *Limanda ferruginea*, *Urophycis tenuis* in addition to larger cod. Nocturnal inshore movements of juvenile cod, age 0 as well as older individuals, can then be viewed as a series of horizontal movements along the bottom into shallower water, the spatial and depth scales of which progressively increase with increasing fish size. Day-night movements of age 0 cod then consist of a movement from deeper water where juvenile cod are concentrated during the day to a shallower site at night time where they disperse (Olsen and Soldal 1989, Lough et al. 1989, Walters and

Juanes 1993). As age 0 cod disperse to shallower water at dusk, larger cod (e.g. ages 1-3) also move inshore at night. These larger cod are often only caught at night (e.g. age 1 cod, Methven and Bajdik 1994; age 2-3 cod Chapter III) and are reported to be cannibalistic on smaller age 0 and 1 cod (Bogstad et al. 1994). Consequently, a vertical movement off the bottom (e.g. Lough et al. 1989, Perry and Neilson 1988) and/or horizontal movement along the bottom towards shallow water during dusk-darkness by age 0 cod will minimize contact with demersal predators that also move inshore at night time.

Predation has been repeatedly suggested to be the main source of mortality in juvenile fishes (Sissenwine 1984, Houde 1987, Anderson 1988, de Lafontaine 1992). Consequently, newly settled and highly vulnerable juveniles have a remarkable variety of spatial refuges and strategies to avoid predation. For juvenile cod these include inshore nursery areas where relatively few larger (predatory) fish occur. At smaller spatial and temporal scales it includes defence of a territory, selection for suitable (complex) habitat (Keats et al. 1987, Gotceitas and Brown 1993, Tupper and Boutilier 1995a, 1995b), diel inshore movements to avoid demersal predators (Keats 1990, Methven and Bajdik 1994, Gibson et al. 1996), schooling (Tupper and Boutilier 1995a) and reliance upon crypsis (Lough et al. 1989, Gregory and Anderson 1997).

Settlement in locations with specific habitat features (i.e. eel grass, Gotceitas et al. 1997), the explicit recognition of a juvenile nursery area where pelagic eggs and larvae drift (Harden-Jones 1968), and the observation that shallow regions may act as traps that concentrate newly settled juveniles all contribute to the early demersal stage having a restricted spatial distribution relative to older cod which occupy a larger geographical area. Concentration of juvenile cod in a limited geographical area (i.e. in shallow water along the coast of Newfoundland in the mid 1990s) means cod are logistically available to repeated sampling at minimal cost by small boats. The relative abundance of demersal

age 0 cod associated with specific habitat features in coastal nursery areas may be a more reliable indicator of future yearclass strength than solely through the abundance of pelagic eggs or larvae which, has met with limited success (Campana et al. 1989). Newly settled juvenile cod have all passed through the highly vulnerable egg and larval stages and the hazardous descent to the bottom and hence should be more closely related to and a more reliable predictor of yearclass strength than the pelagic stages.

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