RECRUITMENT OF ATLANTIC COD TO NEWFOUNDLAND COASTAL WATERS AT DAILY AND SEASONAL SCALES

DANNY WILLIAM INGS

Recruitment of Atlantic cod to Newfoundland coastal waters at daily and seasonal scales

by

Danny William Ings

A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Biology Department/Faculty of Science
Memorial University
April 2005
St. John's, Newfoundland and Labrador

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

0-494-06641-5

Your file Votre référence
ISBN:
Our file Notre reterence
ISBN:

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

ABSTRACT

Recruitment of marine fish is influenced by abiotic and biotic processes operating at many spatial and temporal scales. Recruitment level was thought to be set during the larval stages but recent evidence suggests that year-class strength can be modified during the early juvenile stages. Annual recruitment has received much attention but variation at finer temporal scales may affect biological processes that influence year-class success. I tested the hypothesis that timing of recruitment of fish from the plankton to nearshore benthic areas is determined by water mass movements. I also tested whether seasonal recruitment of fish to near shore bottom habitats was associated with prey availability and growth rates of post-recruited fish. Seining was conducted daily at one location during 2002 and biweekly at 12 sites during 1998-2002 to monitor fish densities and arrival times nearshore. I found that daily recruitment of Atlantic cod (*Gadus morhua*), Greenland cod (*Gadus ogac*) and hake (*Urophycis tenuis*) to sites on the northeast coast of Newfoundland was associated with onshore winds following upwelling. Results were consistent with larval transport onshore during downwelling. Recruitment of Atlantic cod, Greenland cod and hake to the nearshore was not associated with tidal stage. The phenology of Atlantic cod recruitment to near shore benthic habitats appears simple but seasonal growth rates are more complex. During July to November of 2000 to 2002, the monthly pattern of abundance of newly-recruited Atlantic cod near shore was similar to seasonal patterns of zooplankton abundance that I observed near shore. Seasonal zooplankton abundances near shore were similar to those previously reported offshore.

Newly-recruited Atlantic cod were relatively abundant during September and October of 2000-2002. During these months, growth rates of post-recruited fish were also relatively high. However, I found growth rates of post-recruitment fish were comparatively high twice annually with highest growth occurring during June and October. During both of these months water temperatures were near optimum for growth and the ratio of Atlantic cod abundance to zooplankton abundance near shore was similar. Abundance of newly-recruited Atlantic cod near shore was relatively high during May of 2002 when growth rates of fish were low, contrary to prediction. Monthly abundance of newly-recruited Atlantic cod near shore was more closely associated with the amount of zooplankton that fish could utilize at observed water temperatures rather than total abundance of zooplankton. At daily scales, recruitment of Atlantic cod near shore was found to be determined by physical processes but both abiotic and biotic processes were important at seasonal scales.

ACKNOWLEDGEMENTS

I would like to thank David C. Schneider, Robert S. Gregory and David A. Methven for their continuous support, guidance and encouragement. I would also like to thank Barbara Neis and David Taylor for their understanding and patience. I am very grateful to all the students, technicians and volunteers who participated in field work including Erin Alcock, Jessica Anderson, Louise Copeman, Dave Cote, Katie Dalley, Peter Frampton, Doug Gibson, Ann Marie Gorman, Janelle Hancock, Ben Hammond, Brianna Hookey, Chris Howell, Robyn Jamieson, Terra Lynn Lander, Ben Laurel, Janice Linehan, Mike Norris, Miriam O, Adam Ogilvie, Melissa Pink, Dan Porter, Andrea Powell, Heather Reid, Mark Renkawitz, Philip Sargent, Lee Sheppard, Dave Sterling, Steve Sutton, Christine Vickers, Nadine Wells, Richard Wong, and Kimberly Young.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1. Introduction

Recruitment to marine fish populations is often estimated annually and at large geographic scales encompassing entire stocks. However, variation in fish recruitment at smaller spatial and temporal scales influences many biological processes that can moderate year-class strength. In this thesis, recruitment is defined as the period at the end of the larval phase when mortality drops substantially and juveniles are considered to have recruited into the population. Along the northeast coast of Newfoundland, recruitment of Atlantic cod occurs in discrete pulses during summer and autumn (Methven and Bajdik 1994, Pinsent and Methven 1997, Grant and Brown 1998a). This was first demonstrated at a sheltered site in Trinity Bay during 1982-1983 and 1989-1991 by Methven and Bajdik (1994). In their sampling (every two weeks), the smallest juvenile Atlantic cod were collected during two periods, late August-early September and mid to late October, each year. Methven (1993, 1994) showed that recruitment pulses of Atlantic cod occurred at sites from the southern Avalon to western Notre Dame Bay. Three or four pulses of recruitment in Atlantic cod were evident in data collected subsequently from the northeast coast of Newfoundland at time scales of two weeks or less (Pinsent and Methven 1997; Grant and Brown, 1998, Gregory *et al.,* 1999). Although these recruitment pulses were described over a decade ago, the processes generating them have not been determined. This thesis will compile and evaluate theories on the origin of Atlantic cod recruitment pulses in Newfoundland coastal waters using available data augmented by directed investigations.

The basic theory guiding most of the research into recruitment by marine fish during the past century originated with Hjort (1914). He presented two hypotheses: (1) level of recruitment is determined by prey availability to larvae during the period following initiation of exogenous feeding and (2) level of recruitment may be determined by the influence of advective processes on the distributions of larvae. Hypothesis (1) was developed into the match / mismatch hypothesis in a series of reports (Cushing 1969, 1974, 1990). The match / mismatch hypothesis has two components (a) spawning time is fixed among years to correspond to the mean time of production and (b) the degree of overlap between larvae (up to metamorphosis) and their prey determines recruitment success. Cushing (1990) compiled some empirical support for increased recruitment of fish during years with overlap between peak spawning time and periods of high production. Hypothesis (2) from Hjort (1914) influenced development of the "migration triangle" (Harden Jones, 1968); this concept was reviewed by Secor (2002). The central principle of the "migration triangle" is populations are closed (philopatry) with spawning occuring at localized areas but juveniles and adults are widely distributed, requiring seasonal and ontogenetic migrations for fish to return to natal spawning grounds (Harden Jones, 1968; Cushing 1974). The "migration triangle" is difficult to test rigorously because it has complex assumptions (Secor, 2002). Positive correlations between recruitment of fish and transport onshore to suitable nursery areas (e.g. Nelson *et al.* 1977; Bailey, 1981) has been considered to be consistent with a circuit between spawning location and widespread distributions of juvenile fish. Other prominent theories (e.g.

Lasker events (Lasker, 1975; 1978) and member / vagrant (Sinclair, 1988) are similarly related to one of the hypotheses of Hjort (1914).

On the Northeast Newfoundland Shelf, Atlantic cod form a stock component thought to be distinct from the Grand Banks and other areas (Templeman, 1962). The Northeast Newfoundland Shelf extends 150-400 km offshore and includes a series of relatively flat banks divided by deep (< 500 m) channels. Most of the northeast coast of Newfoundland is comprised of large and deep (> 200 m) bays. Areas approximately 25 kilometers off the coast plus the bays have been termed collectively the inshore and the remaining shelf areas are offshore. Oceanography of both the inshore and offshore is dominated by the Labrador Current which begins at the northern tip of Labrador and flows southward. The main branch of the Labrador Current flows along the continental slope with temperatures of 3 to 4 °C. An inshore branch flows along the coast of the island of Newfoundland with temperatures of -1 to 2 °C. A warm water layer develops at the surface during spring (Templeman, 1948). Episodic upwelling occurs along the northeast coast of Newfoundland associated with strong southwest wind events (Sleggs, 1933; Templeman, 1948; Schneider and Methven, 1988). In this area, winds from the west and southwest prevail from June to September. During upwelling events, the seasonal thermocline rises and cold water can be detected at the coast (Leggett *et al.* 1984). Distributions of Atlantic cod were predicted to be influenced by upwelling (Templeman, 1966); this theory is supported by studies on catches using passive fishing gear (Rose and Leggett, 1988; Ings *et al.* 1997). Along the northeast coast of

Newfoundland episodic upwelling influences the density of marine organisms ranging from zooplankton (Frank and Leggett, 1982, 1985) to capelin (Schneider, 1994) and whales (Whitehead and Carscadden, 1985).

The seasonal cycle of production on the Northeast Newfoundland Shelf has been investigated at relatively large spatial scales. Analysis of Continuous Plankton Recorder Data (CPR) for the period 1961-1971 by Robinson *et al.* (1973) showed that phytoplankton were most abundant during spring in the northwest Atlantic. The standing crop of phytoplankton on the Grand Banks was observed to peak in May (spring bloom) during 1980; biomass-normalized production was maximum in August-September (Prasad, 1993). Timing of peak abundance of copepodite stages of *Calanus finmarchicus*, considered to be the primary prey of first-feeding larval Atlantic cod, varied between May and June during 1961 to 1971 (Robinson *et al.* 1973). Analysis of CPR Data collected during 1959-1992 led Myers *et al.* (1994) to conclude that seasonal trends in zooplankton abundance were quite variable. Multi-year studies are not available from the inshore, but Davis (1982) found zooplankton abundance in Conception Bay during 1977-78 to be highest from May to July, low during August and variable between September and December.

Historical data suggests that Atlantic cod spawn over broad areas of the continental shelf, but mostly over the slopes, particularly off Hamilton Bank (Templeman, 1981) or in deep areas near shore (Hutchings *et al.,* 1993). Spawning time differs among offshore areas. Myers *et al.* (1993) found mean spawning time on Hamilton Bank was 7

April while spawning in NAFO Division 3L (Fig. 1) was 9 June. Spawning on the Grand Banks falls within this period but it occurs earlier on southern Grand Bank than on northern Grand Bank (Hutchings and Myers, 1994). Cod spawning occurs later inshore than offshore (Templeman, 1979). Data from inshore areas suggest that spawning occurs primarily between May and July (Thompson, 1943; Anderson *et al.* 1995; Smedbol and Wroblewski, 1997) but can extend into August and September (Thompson,1943; Pinsent and Methven,1997). Water temperature is thought to influence initiation of spawning (Templeman, 1962) but this relationship may be modified by local oceanographic conditions (Hutchings and Myers, 1994). Oocyte development as a function of water temperature may explain later initiation of spawning inshore relative to offshore (Smedbol and Wroblewski, 1997).

Atlantic cod are broadcast spawners releasing eggs in multiple batches (Scott and Scott, 1988). Healthy eggs rise in the water column during development (Anderson and de Young, 1995) and drift passively near the surface (Page and Frank, 1989). Development rates of eggs increase with temperatures (Pepin *et al.* 1997), hence eggs spawned in colder waters (e.g. during March to May off Labrador) may experience longer periods of drift than those spawned in warmer waters (e.g. during April to July in inshore 3K). Distributions of Atlantic cod eggs have been collected along the coast of Newfoundland (Scott, 1935) and Labrador (Serebryakov, 1968). From sampling on transects across the Northeast Newfoundland shelf during 1991-1992, Pepin and Helbig (1997) found stage I eggs near the shelf-slope break, stage II and III eggs were broadly distributed over the shelf south of Funk Island Bank; only a small number of stage IV eggs were collected but they were near the northeast coast of Newfoundland.

Cod larvae were considered to drift passively from spawning areas on the Northeast Newfoundland Shelf into bays along the northeast coast of Newfoundland where they settle as juveniles into demersal habitats (Lear and Green, 1984). This view was challenged by simulations of particle drift on the continental shelf that suggested appropriate wind forcing would be required for larvae to be transported to coastal areas from the offshore (Helbig *et al.* 1992; Anderson *et al.* 1995; Davidson and de Young, 1995). Modelling also suggested that only a small percentage of the larvae transported inshore are retained there (Pepin and Helbig, 1997). Nevertheless, in the 1990s high numbers of demersal juvenile cod were collected inshore relative to offshore (Dalley and Anderson, 1997). Juvenile cod were observed to recruit to coastal sites in pulses during summer and autumn (Methven and Bajdik, 1994; Grant and Brown, 1998; Gregory *et al.*, 2002) where they settle to the bottom at lengths of 40 to 100 mm (Lomond *et al.* 1998). Genetic analysis of post-settlement cod showed that roughly half of the fish collected inshore during a recruitment period in August were spawned offshore while half originated inshore; more fish collected during October originated inshore (70%) than offshore (30%) (Beacham *et al.* 2000). Conclusions based on particle drift modelling to date are inconsistent with observations on juvenile cod recruitment at coastal sites.

A number of theories have been proposed to explain recruitment pulses of Atlantic cod at coastal sites. Geographic separation of spawning was the basis for two hypotheses.

Temporal separation of spawning between the inshore and offshore (Templeman, 1979) led to the hypothesis (e.g. Methven, 1993) that fish in certain pulses originated offshore while those in other pulses were primarily of inshore origin. Similarly, Beacham *et al.* (2000) investigated whether juvenile cod from different pulses were similar genetically to adults sampled at locations inshore or offshore (banks). Other theories were based on physical oceanography. Tidal stage was postulated to influence arrival or settlement of larvae at coastal sites as movement of tidal fronts has been found to influence the distributions of larval fish, especially near estuaries (Boehlert and Mundy, 1987; Kingsford and Suthers, 1996). There is evidence that upwelling events can interrupt spawning by fish (Kruse and Tyler, 1983) such as Atlantic cod that release eggs over prolonged periods (Scott and Scott, 1988). In this thesis I propose that downwelling determines recruitment timing of cod at coastal sites. This hypothesis was borrowed from the invertebrate literature; Roughgarden *et al.* (1991) proposed that larval barnacles accumulate in an upwelling front off California and are transported to the coast when the front moves shoreward under downwelling conditions. See Chapter 2 for further details.

This thesis is organized into five chapters. In Chapter 2, I document the history of research on juvenile Atlantic cod that has established and focussed on recruitment pulses of fish in Newfoundland coastal waters. Chapter 3 tests whether recruitment pulses are associated with movement of water masses at temporal scales of the tidal amplitude or the upwelling/downwelling cycle. Chapter 4 tests whether seasonal recruitment of juvenile Atlantic cod to Newfoundland coastal waters matches zooplankton abundance nearshore.

Chapter 5 presents conclusions.

1.2. Literature cited

Anderson, J.T., E.L. Dalley and J.E. Carscadden, 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. 52: 115-125.

Anderson, J.T. and B. de Young, 1995. Application of a one-dimensional model to vertical distributions of cod eggs on the northeastern Newfoundland Shelf. Can. J. Fish. Aquat. Sci. 52: 1978-1989.

Bailey, K.M., 1981. Larval transport and recruitment of Pacific hake. Mar. Ecol. Prog. Ser. 6: 1-9.

Beacham, T.D., R.S. Gregory and J. Brattey, 2000. Origins of two recruitment pulses of 0-group Atlantic cod (*Gadus morhua*) in Bonavista Bay, Newfoundland during 1999, determined from genetic variation. Can. Stock. Assessment Secretariat Res. Doc. 2000/093.

Boehlert, G.W., and B.C. Mundy, 1987. Recruitment dynamics of metamorphosing English sole *Parophrys vetulus* to Yaquina Bay, Oregon. Est. Coast. Shelf. Sci. 25: 261-281.

Cushing, D.H., 1969. The regularity of the spawning season of some fishes. J. du Conseil, Cons. Int. Explor. Mer. 33: 81-92.

Cushing, D.H., 1974. The natural regulation of fish populations. In: Sea fisheries research. F.R. Harden Jones (ed) pp 399-412. Wiley, New York.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/ mismatch hypothesis. Adv. Mar. Bio. 26: 249-293.

Dalley, E.G., and J.T. Anderson, 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. 54 suppl 1: 168-176.

Davidson, F.J.M., and B. deYoung, 1995. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. 4: 33-51.

Davis, C.C., 1982. A preliminary quantitative study of zooplankton from Conception bay, insular Newfoundland, Canada. Int. Revue ges. Hydrobiol. 67: 713-747.

Frank, F.T., and W.C. Leggett, 1982. Coastal water mass replacement: its effects on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mattotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991-1003.

Frank, F.T., and W.C. Leggett, 1985. Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? Can. J. Fish. Aquat. Sci. 42: 1841-1849.

Grant, S.M., and J.A. Brown, 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can. J. Fish. Aquat. Sci. 55: 1317-1327.

Gregory, R.S., D.A. Methven, D.C. Schneider and D.W. Ings, 1999. Relative strength of the 1998 year-class, from nearshore surveys of demersal age 0 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Can. Stock. Assessment Secretariat Res. Doc. 99/44.

Gregory, R.S., B.J. Laurel, D.W. Ings, and D.C. Schneider, 2002. Relative strength of the 1999 and 2000 year-classes, from nearshore surveys of demersal age 0 & 1 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Can. Scientific Advisory Secretariat Res. Doc. 2002/087.

Harden Jones, F.R., 1968. Fish Migration. Edward Arnold, London, UK 325 p.

Helbig, J., G. Mertz and P. Pepin, 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. 1: 39-56.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe. Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20: 1-228.

Hutchings, J.A., R.A. Myers and G.R. Lilly, 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2457-2467.

Hutchings, J.A., and R.A. Myers, 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21-31.

Ings, D.W., J. K. Horne and D.C. Schneider, 1997. Influence of episodic upwelling on capelin, *Mallotus villosus*, and Atlantic cod, *Gadus morhua*, catches in Newfoundland coastal waters. Fish. Oceanogr. 6: 41-48.

Kingsford, M.J., and I.M. Suthers, 1996. The influence of tidal phase on patterns of ichthyoplankton abundance in the vicinity of an estuarine front, Botany Bay, Australia. Est. Coast. Shelf Sci. 43: 33-54.

Kruse, G.H., and A,V. Tyler, 1983. Simulation of temperature and upwelling effects on the English sole (*Parophrys vetulus*) spawning season. Can. J. Fish. Aquat. Sci. 40: 230-237.

Lasker, R., 1975. Field criteria for survival of anchovy larvae: the relationship between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453-462.

Lasker, R., 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Reun. CIEM. 173: 212-230.

Lear, W.H., and J.M. Green, 1984. Migration of the "northern" Atlantic cod and the mechanisms involved. In: Mechanisms of migration in fish. JD McCleave, GP Arnold, J Dodson and WH Neill. Eds. Plenum. Pp 159-178.

Leggett, W.C., K.T. Frank and J.E. Carscadden, 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*) Can. J. Fish. Aquat. Sci. 41: 1193-1201.

Lomond, T.M., D.C. Schneider and D.A. Methven, 1998. Transition from pelagic to benthic for age group 0-1 Atlantic cod (*Gadus morhua*) Fish Bull 96:908-911.

Methven, D.A., 1993. Factors contributing to the spatial variation in abundance of juvenile cod from northeast Newfoundland. Report to the Nortern Cod Science Program, Department of Fisheries and Oceans. 24 p.

Methven, D.A., 1994. Temporal variation in size and abundance of juvenile cod at inshore sites along the northeast coast of Newfoundland: preliminary results from 1993. Report to the Nortern Cod Science Program, Department of Fisheries and Oceans. 42 p.

Methven, D.A, and C. Bajdik, 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J.

Fish. Aquat. Sci. 51: 78-90.

Myers, R.A., N.J. Barrowman, G. Mertz, J. Gamble and H.G. Hunt, 1994. Analysis of Continuous plankton recorder data in the northwest Atlantic 1959-1992. Can. Tech. Rep. Fish. Aquat Sci. 1966. 16 p.

Myers, R.A., G. Mertz and C.A. Bishop, 1993. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Oceanogr. 2: 154-165.

Nelson, W.R., M.C. Ingham and W.E. Schaaf, 1977. Larval transport and year-class strength of Atlantic menhaden *Brevoortia tyrannus*. Fish. Bull. 75: 23-41.

Page, F.H., and K.T. Frank, 1989. Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 41 (Suppl. 1): 68-81.

Pepin, P., and J.A. Helbig, 1997. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. 54: 670-685.

Pepin, P., D.C. Orr and J.T. Anderson, 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 54 Suppl. 1: 2-10.

Pinsent, D.L., and D.A. Methven, 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 54 (Suppl.1): 19-24.

Prasad, K.S., 1993. Chlorophyll distribution and primary production on the Grand Banks of Newfoundland investigated by remote sensing. Phd Thesis. Memorial University. 163 p.

Robinson, G.A., J.M. Colebrook and G.A. Cooper, 1973. The continuous plankton recorder survey: plankton in the ICNAF area, 1961 to 1971, with special reference to 1971. ICNAF Res doc 73/78, 19 p.

Rose, G.A., and W.C. Leggett, 1988. Atmosphere-ocean coupling in the northern Gulf of St. Lawrence: effects of wind forced variation in sea temperatures on currents and nearshore distributions and catch rates of *Gadus morhua*. Can J. Fish. Aquat. Sci. 45: 1234-1243.

Roughgarden, J., J.T. Pennington, D. Stoner, S. Alexander, and K. Miller, 1991.

Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. Acta Œcologica 12: 35-51.

Schneider, D.C., 1994. Distribution of capelin (*Mallotus villosus*) in relation to coastal upwelling in the Avalon channel. J. Northw. Atl. Fish. Sci. 17: 23-31.

Schneider, D.C., and D.A. Methven, 1988. Response of capelin to wind-induced thermal events in the southern labrador Current J. Mar.Res. 46: 105-118.

Scott, N., 1935. Some fishes of Newfoundland waters (with notes on the distributions of eggs and larvae) Res. Bull. No. 4. Department of Natural Resources (Newfoundland Government) St. John's Newfoundland. 16 p.

Scott, W.B., and M.G. Scott, 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquatic. Sci. 219: 731 p.

Secor, D.H., 2002. Historical roots of the migration triangle. ICES Mar. Sci. Symp. 215: 329-335.

Serebryakov, V.P., 1968. Cod reproduction in the northwest Atlantic. Fish. Res. Bd. Trans. Ser. No. 1133.

Sinclair, M., 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant. Program, Seattle. 252 p

Sleggs, G.F., 1933. Observations upon the economic biology of the capelin (*Mallotus villosus* O.F. Müller) Rep. Nfld. Fish. Lab. 1: 1-66.

Smedbol, R.K., and J.S. Wroblewski, 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991-1993. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1) 177-186.

Templeman, W., 1948. The life history of capelin (*Mallotus villosus* OF Müller) in Newfoundland waters. Nfld. Gov. Lab. Res. Ser. Bull. 17: 1-151.

Templeman, W., 1962. Divisions of cod stocks in the northwest Atlantic ICNAF Redbook 1962, Part III 79-129.

Templeman, W., 1966. Marine resources of Newfoundland. Bull. Fish. Res. Bd. Can. No. 154, 170 p.

Templeman, W., 1979. Migration and intermingling of stocks of Atlantic cod *Gadus* *morhua* of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Doc. 14: 6-50.

Templeman, W., 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947-1971, and their use for delineating cod stocks. Northw. Atl. Fish. Sci. 2: 21-45.

Thompson, H., 1943. A biological and economic study of cod (*Gadus callarius* L.) in the Newfoundland area. Nfld Dep. Nat. Resour. Res. Bull. No 14.

Whitehead, H., and J.E. Carscadden, 1985. Predicting inshore whale abundance - whales and capelin off the Newfoundland coast. Can. J. Fish. Aquat. Sci. 41: 976-981.

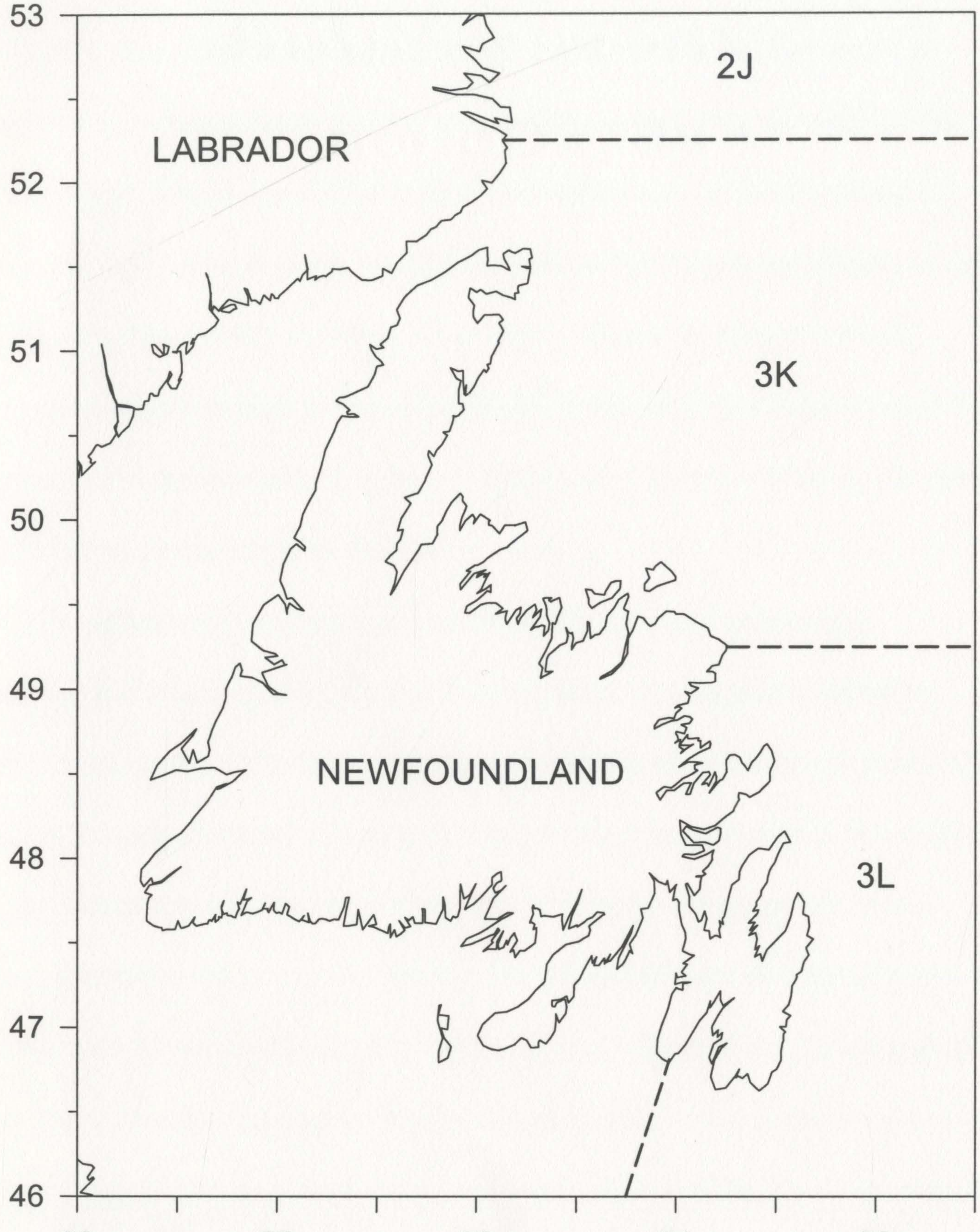


Figure 1.1. Map of Newfoundland showing NAFO subareas 2J, 3K and 3L.

Chapter 2 Recruitment pulses of Atlantic cod in Newfoundland coastal waters

2.1 Background

Pulses of recruitment of juvenile Atlantic cod to benthic habitats were first reported by Methven and Bajdik (1994). Their analysis of data from biweekly seining at one site in Trinity Bay during 1982-1983 and 1989-1990 revealed that the smallest Atlantic cod were collected during two distinct periods, late August-early September and mid to late October, of 1982 and 1989. Also, they noted that the small fish were transparent (similar to pelagic juveniles) and lacked parasites (*Cryptocotyle lingua*) that are typical of fish residing in the nearshore. These findings showed that small Atlantic cod recruited to the nearshore as distinct pulses.

The earliest study on recruitment of juvenile Atlantic cod to nearshore Newfoundland locations (Lear *et al.*, 1980) did not mention these pulses. Based on surveys along the coast of Norway initiated in the late 1800s (e.g. Fromentin *et al.*, 2001), the Fisheries Research Board of Canada developed a beach seine survey for juvenile cod along the northeast coast of Newfoundland. This project was led by the late Alistair Fleming (hereafter referred to as the Fleming Survey) and sampled sites from Placentia Bay in the south to western Notre Dame Bay in the north. During 1958, Fleming and his crew travelled the coast scouting for sample sites and talking to fishermen about their observations on the time and locations of juvenile cod sightings. The Fleming survey began in the autumn of 1959 with 13 sites (Methven, 1993; Schneider *et al.* 1997). Approximately 35-45 sites were sampled in subsequent years until 1964 when the

Fleming survey was discontinued. Results of this work were published by Lear *et al.* (1980) who reported no recruitment signal in the Fleming data. Original field notes obtained from the Department of Fisheries and Oceans make no mention of pulsed recruitment.

The phenomenon reported by Methven and Bajdik (1994) was found to occur all along the northeast coast of Newfoundland. Analysis of data from biweekly seining at sites including Cape Broyle on the southern Avalon Peninsula, Little Mosquito Cove and Trinity, Trinity Bay and Cottlesville and La Scie in Notre Dame Bay showed that Atlantic cod recruited to nearshore sites in distinct pulses over a coast-wide scale (Methven, 1994). While sampling with seines in Trinity Bay during autumn, Grant and Brown (1998) collected newly recruited cod in late-November in addition to those collected during two earlier periods. Newly recruited fish were found during early August and late September-early October 1998 and 1999 in Newman Sound, Bonavista Bay (Gregory *et al.,* 1999; Gregory *et al.,* 2001). However, during 2000 as many as four pulses were detected at the same sites (Gregory *et al.,* 2002).

The number of fish recruiting during the October 1995 pulse was monitored to determine possible enhancement due to the discovery of 10,000 + tonnes of spawning cod in Smith Sound, Trinity Bay (Schneider *et al.*, 1997). However, whether a spawning aggregation occurred there in previous years could not be determined due to lack of data. The Fleming survey, which had been reinitiated by researchers at Memorial University in 1992 (e.g. Schneider *et al.,* 1997), sampled for juvenile cod during autumn. At sites down-current of Smith Sound and at coarser scales, catches of juvenile cod were not higher in 1995 than previous years; offshore drift and dilution of eggs and larvae were thought to explain this negative result (Schneider *et al.*, 1997; Smedbol *et al.,* 1998).

Formal studies on identification of Atlantic cod (*G. morhua*) and Greenland cod (G . *ogac*) were required for investigations on recruitment pulses in Atlantic cod. Both gadids co-occur as juveniles in coastal Newfoundland habitats and are difficult to distinguish at sizes less than 65 mm. Systematic studies distinguishing between adult Greenland cod and Atlantic cod were available during the early 1990s but did not apply to juveniles (Jensen, 1948). Based largely on known differences between adult fish, field techniques for distinguishing between juvenile Greenland cod and Atlantic cod were refined over time (Methven and Bajdik, 1994) and misidentification was thought to be quite low (< 5%) (Methven, 1993). However, lack of formal identification studies plagued researchers. Therefore, two studies on identification of juvenile Greenland cod and Atlantic cod were conducted. Methven and McGowan (1998) found that Greenland cod had a smaller eye diameter, deeper body and greater weight at age than Atlantic cod. Also, they observed that body coloration and shape of the lateral line (more arched for Greenland cod) were useful. Grant (unpublished data) raised egg and larvae of known adult fish in the laboratory and found that Greenland cod had dark pigmentation on the first eight rays of the dorsal fin whereas these rays on juvenile Atlantic cod lacked coloration. These characteristics were then confirmed to apply to field caught specimens (see Appendix 5.1 in Methven, 1997). Improved identification techniques led to research on processes that potentially influence recruitment pulses of Atlantic cod.

2.2 Theories for pulses

2.2.1. Geographic separation of spawning

Variability in spawning time between areas was the basis for early theories on pulse origins. Northern cod have been described as a stock complex (Lear, 1984) with spawning known to vary temporally between inshore and offshore locations and between offshore banks (Templeman, 1979; Myers *et al.,* 1993; Hutchings and Myers,1994). A conceptual diagram (Figure 26 in Methven, 1993) illustrated early views on the origin of pulses. Small Atlantic cod collected in May were thought to be progeny from offshore spawning as winter spawning was not known to occur nearshore (Methven, 1993). Inshore spawning was believed to produce most of the fish recruiting in August-September as an August arrival time for pelagic juveniles was consistent with spawning times (May-June) that Hutchings *et al.* (1993) observed for Trinity Bay. The October pulse was thought to originate from both inshore and offshore spawning (Methven, 1993). Backcalculations using otoliths from juveniles collected nearshore produced estimated spawning dates that varied by as much as a month between years (Pinsent, 1994). Estimated hatch dates and spawning times ranged over longer periods (12 weeks) than were documented previously (Pinsent and Methven, 1997). These results suggested offshore spawning had produced fish collected in May. The relatively high variability in annual spawning time was inconsistent with the view that pulses were due to spawning pulses separated in time or space.

Genetic analysis showed that both inshore and offshore spawning produced fish in the August-September and October pulses. Beacham *et al.* (2000) tested whether juvenile Atlantic cod collected in Newman Sound, Bonavista Bay were similar genetically to adults caught at four offshore and five inshore locations. They found that cod from the August pulse were genetically similar to adults collected either in Bonavista Bay or on Funk Island Bank with approximately 50 % of the fish originating from each location. Approximately 30 % of the October pulse was similar to cod sampled offshore (Funk Island Bank and northern Grand Bank) and 70 % was similar to adults from inshore areas including Notre Dame Bay and Conception Bay in addition to Bonavista Bay. A substantial contribution of offshore spawning to the August pulse did not match the Methven (1993) conceptual diagram with most fish in August produced by inshore spawning. Geographic separation in spawning was eliminated as an explanation for the occurrence of recruitment pulses.

2.2.2 Tidal stage influence

The theory that tidal stage influenced settlement of juveniles nearshore emerged when evidence of multiple pulses during autumn were detected in data from biweekly sampling in Bonavista Bay (Gregory *et al.*, 2001). Tidal processes were known to influence the movement (Boehlert and Mundy, 1987) and distributions (Kingsford and Suthers, 1996) of many larval fish. Tidal stage has also been shown to affect settlement of fish on coral reefs (e.g. Sponaugle and Cowen, 1997). Recruitment of juvenile *Pelates sexlineatus*, for example, occurs during six pulses annually coinciding with full moons / high tides (Smith and Suthers, 2000). I found no evidence that tidal stage influenced fish recruitment to nearshore Newfoundland waters (Chapter Three).

2.2.3. Additional theories from the literature

A literature search for processes known to produce recruitment pulses in marine organisms uncovered two theories in addition to those described previously. The theories were:

1.) Upwelling interrupts spawning. Kruse and Tyler (1983) linked interruptions in spawning of English Sole *Parophrys vetulus* with upwelling related changes in water temperature. Atlantic cod were known to spawn for protracted periods (Myers *et al.*, 1993) similar to English Sole. Water temperature was thought to influence spawning time of Atlantic cod as well (Scott and Scott, 1988). However, actively spawning Atlantic cod in aquaria at the Ocean Sciences Centre with flowthrough seawater were not observed to cease spawning periodically during early summer (JA Brown, pers. comm.) when episodic upwelling occurs (Sleggs, 1933; Templeman, 1948; Schneider and Methven, 1988). I concluded the theory of upwelling interrupted spawning by Atlantic cod was not supported by observations of actively spawning cod from Newfoundland. Therefore, I have not pursued it further in this thesis.

2.) Recruitment occurs during downwelling. Settlement of barnacles, sea urchins and crab in nearshore habitats on the coast of the United States have been linked to downwelling events (Farrell *et al.,* 1991; Roughgarden *et al.,* 1991; Wing *et al.*, 1995; Miller and Emlet, 1997). Schneider and Methven (pers. comm.) considered, then discarded this hypothesis because upwelling events occur more frequently (Schneider and Methven, 1988) than the 2-4 pulses reported for juvenile cod each year. The hypothesis that Atlantic cod recruit to the nearshore during downwelling events was revisited because other explanations failed (Chapter Three).

2.3 Conclusion

Recruitment pulses of Atlantic cod were first discovered at one site in Trinity Bay during the 1980s-early 1990s. Since then, pulses have been observed consistently at nearshore sites all along the northeast coast of Newfoundland. Results from early studies suggested two or three pulses at approximately the same time annually, but more recent studies provided evidence of multiple pulses through autumn. Theories on pulse origins have evolved over time. Original hypotheses were based on spatial and temporal separation of spawning; spawning by Atlantic cod was known to vary temporally between offshore banks and it occurred later inshore than offshore. The geographic separation hypothesis was not supported by annual variability in spawning time or by genetic differentiation of juveniles between recruitment pulses. Observations on actively spawning Atlantic cod held in aquaria did not support the hypothesis that upwelling interrupts spawning. Formal evaluation of two hypotheses may be useful; tidal stage influences pulsed recruitment and downwelling events influence pulsed recruitment.

Literature cited

Beacham, T.D., R.S. Gregory and J. Brattey, 2000. Origins of two recruitment pulses of 0-group Atlantic cod (*Gadus morhua*) in Bonavista Bay, Newfoundland during 1999, determined from genetic variation. Can. Stock. Assessment Secretariat Res. Doc. 2000/093.

Boehlert, G.W., and B.C. Mundy, 1987. Recruitment dynamics of metmorphosing English sole, *Parophorys vetulus*, to Yaquina Bay, Oregon. Est. Coast. Shelf Sci. 25: 261-281.

Farrell, T.M., D. Bracher and J. Roughgarden, 1991. Cross- shelf transport causes recruitment to intertidal populations in central California. Limnol. Oceanogr. 36: 279-288.

Fromentin, J-M., R.A. Myers, O.N. Bjørnstad, N.C. Stenseth, J. Gjøsæter, and H. Christie, 2001. Effects of density-dependent and stochastic processes on the regulation of cod populations. Ecol 82: 567-579.

Grant, S.M., and J.A. Brown, 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can. J. Fish. Aquat. Sci. 55: 1317-1327.

Gregory, R.S., B.J. Laurel, D.W. Ings, and D.C. Schneider, 2002. Relative strength of the 1999 and 2000 year-classes, from nearshore surveys of demersal age 0 & 1 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Can. Scientific Advisory Secretariat Res. Doc. 2002/087.

Gregory, R.S., D.A. Methven, D.C. Schneider and D.W. Ings, 1999, Relative strength of the 1998 year-class, from nearshore surveys of demersal age 0 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Can. Stock. Assessment Secretariat Res. Doc.99/44.

Hutchings, J.A., R.A. Myers and G.R. Lilly, 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2457-2467.

Hutchings, J.A., and R.A. Myers, 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21-31.

Jensen, A.S., 1948. Contributions to the ichthyoplankton of Greenland 8-24. Spolia Zool. Mus. Haun. 9.

Kingsford, M.J., and I.M. Suthers, 1996. The influence of tidal phase on patterns of ichthyoplankton abundance in the vicinity of an estuarine front, Botany Bay, Australia. Est. Coast. Shelf Sci: 43: 33-54.

Kruse, G.H., and A.V. Tyler, 1983. Simulation of temperature and upwelling effects on the English sole (*Parophrys vetulus*) spawning season. Can. J. Fish. Aquat. Sci. 40: 230-237.

Lear, W.H., 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland as inferred from tagging studies. J. Northw. Atl. Fish. Sci. 5: 143-159.

Lear, W.H., A.M. Fleming and R. Wells, 1980. Results of small cod surveys in eastern Newfoundland during 1959-64. North. Atl. Fish. Organ. SCR Doc. 80/IX/144: 1-8.

Methven, D.A., 1993. Factors contributing to the spatial variation in abundance of juvenile cod from northeast Newfoundland. Report to the Nortern Cod Science Program, Department of Fisheries and Oceans. 24 p.

Methven, D.A., 1994. Temporal variation in size and abundance of juvenile cod at inshore sites along the northeast coast of Newfoundland: preliminary results from 1993. Report to the Nortern Cod Science Program, Department of Fisheries and Oceans. 42 p.

Methven, D.A., and C. Bajdik, 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 51: 78-90.

Methven, D.A., and C. McGowan, 1998. Distinguishing small juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*) by comparing meristic characters and discriminant function analysis of morphometric data. Can. J. Zool.

76: 1054-1062.

Miller, B.A., and R.B. Emlet, 1997. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. Mar. Ecol. Prog. Ser 148: 83-94.

Myers, R.A., G. Mertz and C.A Bishop, 1993. Cod spawning in relation to physical and biological cycles of the northern north Atlantic. Fish. Oceanogr 2: 154-165.

Pinsent, D.L., 1994. Hatch date and 0-group growth rate comparisons for cod (*Gadus morhua*) in Newfoundland waters: support for the match hypothesis. MSc. Thesis. Memorial University of Newfoundland. 76 p.

Pinsent, D.L., and D.A Methven, 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 54 (Suppl.1): 19-24.

Roughgarden, J., J.T. Pennington, D. Stoner, S. Alexander, and K. Miller, 1991. Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. Acta Œcologica 12: 35-51.

Ruzzante, D.E., C.T. Taggart, and D. Cook, 1998. A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. Mol. Ecol. 7: 1663-1680.

Schneider, D.C., P. Hennebury, D. Methven, D. Ings, J. Howell, S. White, D. Pinsent and W. Bailey, 1997. Results of the 1995 Fleming Survey of demersal juvenile cod in the coastal zone of eastern Newfoundland. NAFO Sci. Counc. Studies 29: 13-21.

Schneider, D.C., and D.A. Methven, 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. J. Mar. Res. 46: 105-118.

Scott, W.B., and M.G. Scott, 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

Sleggs, G.F., 1933. Observations on the economic biology of capelin (*Mallotus villosus* O.F. Müller). Rep. Newfoundland Fishery Res. Lab 1: 1-66.

Smedbol, R.K., D.C. Schneider, J.S. Wroblewski and D.A. Methven, 1998. Outcome of an inshore spawning event by northern Atlantic cod (*Gadus morhua*) at low stock levels. Can. J. Fish. Aquat. Sci. 55: 2283-2291.

Smith, K.A., and I.M. Suthers, 2000. Consistent timing of juvenile fish recruitment to seagrass beds within two Sydney estuaries. Mar. Freshwater Res. 51: 765-776.

Sponaugle, S., and R.K. Cowen, 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol. Monogr. 67: 177-202.

Templeman, W., 1948. The life history of the capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. Nfld. Gov. Lab. Res. Ser. Bull 17: 1-151.

Templeman, W., 1979. Migration and intermingling of stocks of Atlantic cod *Gadus morhua* of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Doc. 14: 6-50.

Wing, S.R., L.W. Botsford, J.L. Largier and L.E. Morgan, 1995. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. 128: 199-211.

Co-authorship statement

Chapter 3: Physical processes determine daily recruitment of Atlantic cod, Greenland cod and hake to Newfoundland coastal waters.

Danny Ings designed and identified the research proposal, participated in the collection of all field and computational data, performed the data analysis and prepared the manuscript. David C. Schneider and Robert S.Gregory contributed with ideas and methods. Robert S. Gregory coordinated much of the data collection and management; he also participated in data collection. David C. Schneider contributed with statistical analysis. David A. Methven reviewed the manuscript and suggested revisions.

Chapter 4: Seasonal recruitment of Atlantic cod to coastal Newfoundland sites varies with prey requirements of post-recruitment fish and prey availability

Danny Ings designed and identified the research proposal, participated in the collection of all field and computational data, performed the data analysis and prepared the manuscript. Robert S. Gregory coordinated data collection and management; he also participated in data collection. Robert S. Gregory provided zooplankton data from projects funded by the Department of Fisheries and Oceans. David C. Schneider contributed with ideas, methods and statistical analysis. Robert S. Gregory and David A. Methven reviewed the manuscript and suggested revisions.

Chapter 3 Physical processes determine daily recruitment of Atlantic cod, Greenland cod and hake to Newfoundland coastal waters

3.1 Abstract

Recruitment in marine fish is influenced by abiotic and biotic processes operating at many spatial and temporal scales. Annual recruitment has received considerable attention but variation at finer temporal scales can influence biological processes that modify year-class success. I tested the hypothesis that recruitment of marine fish to nearshore areas at a fine temporal scale is determined by downwelling associated with onshore winds. Also, I tested whether fish arrival nearshore was related to tidal stage. During summer and autumn 1998 to 2001 and late spring to autumn 2002, recruitment of Atlantic cod (*Gadus morhua*), Greenland cod (*Gadus ogac*) and hake (*Urophycis tenuis*) to 12 sites in Newman Sound, Newfoundland was monitored every two weeks using seines. Seining was conducted daily at an additional site nearby for approximately two months during 2002. There were sufficient data to identify four to six recruitment pulses of Atlantic cod annually during 1999 to 2002. Greenland cod and hake were found to recruit once annually during 1998 to 2002. Winds were mostly offshore during the periods studied. However, recruitment of Atlantic cod (19 events), Greenland cod (five events) and hake (five events) was estimated to begin on days with onshore winds or following onshore winds (two day lag maximum). Results were consistent with larval transport onshore during downwelling. Recruitment of Atlantic cod, Greenland cod and hake to the nearshore was not associated with tidal stage. Collapse of episodic upwelling fronts may

affect the timing of recruitment of other invertebrate and fish species in the coastal zone of Newfoundland.

3.2 Introduction

Recruitment of marine fish is influenced by abiotic and biotic processes operating at a number of spatial and temporal scales. Hjort (1914) postulated, and it is generally accepted, that level of recruitment is set during the first year of life. Recruitment may be defined as the period at the beginning of a defined stage; in this thesis, recruitment refers to the period at the beginning of the juvenile phase when mortality drops substantially and juvenile fish are considered to have recruited into the population. Biological processes affecting recruitment success in the first year have been studied at relatively fine scales; the focus has been on linking first-feeding larvae with their prey either temporally (Cushing, 1969) or spatially (Lasker, 1975, 1978). In contrast, oceanographic studies on egg and larval drift have tended to consider relatively large spatial scales. High levels of recruitment are thought to occur when eggs or larvae are transported to suitable nursery areas inshore (Nelson *et al.*, 1977; Bailey, 1981) or are retained on banks offshore (Isles and Sinclair, 1982; Sinclair, 1988). Generally, these studies have been conducted relatively far from shore during research cruises of no more than a few weeks duration. However, fine resolution sampling of the nearshore for extended periods was conducted over a century ago (Hjort and Dahl, 1900). Based on results from approximately daily sampling for juvenile fish along the coast of Norway during 1898-99, Hjort and Dahl (1900) postulated that wind induced movements of water masses in autumn determined fish recruitment at the coast.

Off the northeast coast of Newfoundland, Atlantic cod historically ranged over most of the continental shelf from waters near shore to the continental slope. The northeast Newfoundland Shelf extends 150-400 km offshore and encompasses a number of banks including Hamilton, Belle Isle, and Funk Island Banks and the Grand Banks along with St. Pierre Bank off the south coast. Relatively large and deep (> 200 m) bays constitute most of the northeast coast of Newfoundland. The dominant oceanographic feature in this area is the Labrador Current. It begins at the northern tip of Labrador and flows southward with an inshore and an offshore branch. The main branch follows the continental slope with temperatures of 3 to 4 °C while the colder (-1 to 2 °C) inshore branch flows over the shelf (Lazier, 1982). During spring, a warm water layer develops over the core of the Labrador Current, both inshore (Templeman, 1948) and offshore (Helbig *et al.,* 1992).

Episodic upwelling occurs along the northeast coast of Newfoundland in response to prevailing winds from the west and southwest (Sleggs, 1933; Templeman, 1948; Schneider and Methven, 1988). From June to September, strong southwest winds associated with passing storms induce upwelling of cold water (Leggett *et al.,* 1984) and the seasonal thermocline is raised (Templeman, 1948). Consequently, upwelling and downwelling periods in this system can be identified by vertical movements of the thermocline over a few days or less (Schneider and Methven, 1988). For bays wider than the Rossby radius (circa 5 km), longshore winds establish upwelling (Yao, 1987). In small bays and coves (< 5 km wide) where dynamics are irrotational, upwelling is associated with cross-shore wind stress (Taggart and Frank, 1987). Models incorporating wind stress can predict rise of the thermocline (Schneider and Methven, 1988), but upwelling may alsooccur in the absence of local wind events due to propagating internal waves (de Young *et al.*,1993).

The timing of spawning by Atlantic cod differs among locations. Data from research trawling suggests that spawning occurs over most of the continental shelf, but is concentrated over the slopes, particularly off Hamilton Bank (Templeman, 1981) or in areas near shore (Hutchings *et al.,* 1993). Using trawl data, Myers *et al.* (1993) calculated mean peak spawning times that ranged from 7 April for Hamilton Bank to 9 June for NAFO Division 3L. Spawning times are earlier on southern Grand Bank (mid-May) than on northern Grand Bank (early June) (Hutchings and Myers, 1994). Cod on the Flemish Cap are thought to spawn in February (Thompson, 1943). During annual shoreward migrations in May and June, cod continue spawning (Templeman, 1979; Rose, 1993) but finish spawning before reaching the inshore (Rose, 1993). Nevertheless, cod in spawning condition are known to occur inshore (Harvey, 1891; Smedbol and Wroblewski, 1997). Thompson (1943) assumed cod collected during May to June and August to September in Trinity Bay were in spawning condition. Smedbol and Wroblewski (1997) monitored reproductive condition of wild cod from ripening to spawning and spent in Trinity Bay. They estimated peak spawning from mid-June to mid-July. Inshore spawning times have also been estimated indirectly from data on juvenile cod. Anderson *et al.* (1995) estimated peak spawning was during May-June based on back-calculated ages (from otoliths) of pelagic juveniles sampled in Trinity Bay. From post-settled cod collected by beach seine between late May and January (five separate collections), Pinsent and Methven (1997) estimated spawning occurred during mid-January to late-February, late-April to late-May and between mid-August to early-September. However, findings by Gregory *et al.* (1998) suggest that fish collected in May may have been spawned earlier than January. The spawning locations of post-settled fish in these studies are unknown. There are no data on spawning times of Atlantic cod from other areas on the northeast coast.

Numerical simulations using fine scale data suggest that Atlantic cod eggs and larvae are sometimes transported from the northeast Newfoundland Shelf to coastal waters. Particle transport from the shelf into northern bays and from NAFO divisions 3NO into Trinity and Conception Bays was simulated by Helbig *et al.* (1992) when storm passage (10 day frequency) was included in modelling. Davidson and deYoung (1995) added hourly wind data to simulations of vertically averaged flow. They concluded that wind and diffusion can sometimes influence drift of eggs and larvae into bays on the northeast coast of Newfoundland. Using surface currents estimated from drogued satellite-tracked drifters and data on the spatial distribution of eggs and larvae, simulations by Pepin and Helbig (1997) suggested that up to 10 percent of particles seeded on the Hamilton Banks reached bays on the northeast coast of Newfoundland. Only some of these were retained near shore but nearshore processes were not included in models.

Hjort and Dahl (1900) postulated that the arrival time of juvenile cod at the coast of Norway was associated with water mass movements induced by storm events. This hypothesis is supported over 80 years later by evidence that movements of coastal water masses and associated fronts transport fish and invertebrate larvae toward the coast. Peaks in recruitment of English sole (*Prophrys vetulus*) to the coast of Oregon were associated with onshore Ekman transport (Boehlert and Mundy, 1987). Arrival of King George whiting at the coast of Australia was correlated with onshore winds (Jenkins *et al.*, 1997). Settlement of intertidal barnacles (Farrell *et al.*, 1991; Roughgarden *et al.*; 1991), sea urchins and crab (Wing *et al.*, 1995a, b) on the California coast and sea urchins off Oregon (Miller and Emlet, 1997) occurred during periods of increasing water temperatures attributed to downwelling. Aggregations of larval Dungeness crab (Shenker, 1988) and blue crab (Shanks *et al.,* 2000) have been observed in convergent fronts (slicks) associated with shoreward moving internal waves. Accumulations of shrimp, polychaetes and pre-settlement fish have been found in similar convergences (Kingsfort and Choat, 1986; Shanks, 1998; Shanks *et al.*, 2000). Accumulations of larval cod have been observed at relatively stationary fronts on Western Bank off Nova Scotia (Lochmann *et al.*, 1997; McLaren *et al.,* 1997) and in the North Sea (Munk *et al.,* 1995) where the pattern was recurrent during four consecutive years (Munk *et al.,* 1999). Fish and invertebrate larvae may accumulate at fronts that provide a transport mechanism to the nearshore.

Tidal forcing may also influence the distributions of invertebrates and fish. Pineda (1991) found biweekly periodicity in water temperature data from the coast of California and argued that settlement of barnacle and cyphonautes (bryozoan) larvae was associated with tidal bores rather than wind induced events. Outside Botany Bay, Australia, Kingsford and Suthers (1996) found ichthyoplankton were more abundant in an estuarine front at low tide than during other tidal stages. Eggleston *et al.* (1998) observed drifters to accumulate at a front where Dungeness crab megalopae were concentrated, and move with winds into the Grays Harbor estuary, Washington. Larval English sole *(Prophrys vetulus*) were observed to recruit to estuaries on the coast of Oregon during flood tides (Boehlert and Mundy, 1987).

Atlantic cod recruit to sites on the northeast coast of Newfoundland during multiple events annually (Methven and Bajdik, 1994; Grant and Brown, 1998). During late-August to early-September and October of 1982-1983 and 1989-1991, Methven and Bajdik (1994) observed newly recruited Atlantic cod in biweekly seine collections at a coastal site in Trinity Bay. Pinsent and Methven (1997) describe two recruitment pulses during spring-summer at another location in Trinity Bay. However, small fish can be noted in their plot of standard length and date (Figure 2, page 22) from mid-October onward suggesting that at least three events occurred during 1993. Grant and Brown (1998) conducted seining weekly during autumn of 1994-95 in the same cove where Pinsent and Methven (1997) sampled. Grant and Brown (1998) suggested there were three recruitment events during autumn. Further from shore, Anderson *et al.* (1995) observed multiple peaks in length frequency data for pelagic juveniles collected in Conception Bay during September. Atlantic cod may also recruit to other nearshore areas of

Newfoundland in multiple pulses as Robichaud and Rose (1999) observed small Atlantic cod (40-45 mm) during two periods, September-October and December of 1997 and 1998 in Placentia Bay seine data.

I investigated whether recruitment of Atlantic cod, Greenland cod and hake to the coast of Newfoundland was determined by episodic upwelling. Although the life histories of these three fish species differ (Scott and Scott, 1988), all have pelagic larvae (Scott and Scott, 1988) that may respond similarly to wind-induced events or tidal forcing. Greenland cod spawn mostly in shallow waters near shore (Scott and Scott, 1988). This pattern contrasts with widespread spawning by Atlantic cod (Hutchings *et al.*, 1993). Little is known about the spawning time and locations for hake collected off the northeast coast of Newfoundland. Regardless of spawning location, juvenile Atlantic cod, Greenland cod and hake have been collected by seines in shallow water habitats during summer and autumn (Methven *et al.,* 2001). During this study, data from daily beach seining conducted at one location from mid-July to early-September 2002 were used to determine both arrival time of fish and fish size at recruitment. Arrival time is indicated by the first occurrence of small fish in seine collections as tagging studies by Sheppard (2005) showed that juvenile Atlantic cod and Greenland cod remain localized following settlement at sites in Newman Sound. Estimates of fish size at recruitment were used to determine arrival time of fish at 12 sites in Newman Sound, Bonavista Bay sampled biweekly during 1998 to 2002. Water mass movements, as illustrated in Fig 3.1., were estimated by two methods. Water temperature data collected at sites in Newman Sound were analysed to determine movements of the thermocline, hence vertical displacement of the pycnocline (Schneider and Methven, 1988). Also, data on wind speed and direction measured at Gander Airport located approximately 70 km away were used to model onshore and offshore windstress acting on the surface waters near shore. Tidal stage was determined from tables of tidal height produced by the Canadian Hydrographic Service.

I tested two hypotheses. I investigated whether Atlantic cod recruited to the northeast coast of Newfoundland during wind-induced events as hypothesized by Hjort and Dahl (1900) for the coast of Norway. The patterns in recruitment of Atlantic cod, Greenland cod and hake were evaluated relative to influences of onshore winds that produce downwelling. Also, I tested whether fish arrival was associated with tidal forcing as described by Pineda (1991) for invertebrate larvae on the coast of California. Estimated recruitment dates for fish sampled in 1998-2002 were tested against downwelling periods and tidal phases.

3.3 Methods

3.3.1 Biweekly sampling 1998-2002

From 1998-2002, 12 sites in Newman Sound, Bonavista Bay (Fig. 3.2) were sampled by beach seine between mid-July (1998-2001) or late May (2002) to mid-November. Each site was sampled biweekly (once every second week) within two hours of low tide. A 25 m beach seine with 19 mm stretch mesh in the wings and belly and 9 mm stretch mesh in the codend was used to sample 880 m^2 (16 m along shore, 55 m offshore) (Schneider *et al.,* 1997). The seine sampled the bottom two metres of the water column. From SCUBA observations on seine retrieval, Gotceitas *et al.* (1997) estimated that less than five percent of fish escaped. All fish collected were identified to species; juvenile Atlantic cod were distinguished from Greenland cod using pigment and morphometric characteristics (Methven and McGowan, 1998; Grant and Brown, 1998). Fish were measured (mm Standard Length) and released alive at site of capture. A small number of gadids were subsampled from the catch during each collection period and preserved in 95% ethanol for verification of identifications later.

3.3.2 Daily sampling 2002

To determine arrival times of fish and size at recruitment, beach seines were pulled daily from 11 July to 6 September of 2002 and subsequently two to four times per week until 23 October at one location in Newman Sound (Fig. 3.2). A previous study (Hancock, 2000) had located 10 sites (Fig. 3.2) suitable for sampling with beach seines at this location. Also, the bottom type and depth profile were similar among all ten sites. I sampled two sites per day (e.g.,1 and 6, 2 and 7 etc.) within two hours of low tide.

3.3.3. Estimation of size at arrival

Size at arrival of all three fish species was estimated from linear regressions of daily modal length of fish against Julian date at Bermuda Beach. Modal lengths were determined visually from plots of length frequencies (3 mm bins for Atlantic cod and Greenland cod, 5 mm bins for hake) constructed for each sample day. The range of data used in regressions was one day post arrival to the end of linear increase in length (determined visually) or to the end of daily sampling (23 Oct.). Size at arrival was backcalculated from the relationships between modal length and date.

3.3.4. Estimation of arrival time in biweekly data

Arrival times of fish (1998-2002) were also estimated from regressions of modal length of fish and Julian date. Daily plots were constructed to distinguish between recruitment pulses of Atlantic cod. For Greenland cod and hake biweekly plots were used as only one pulse was detected annually. Lengths of each species were binned as above (Section 3.3.3). Recruitment events were identified in length frequency plots by the appearance of small fish on one or two sample days. On subsequent days, a mode in each length frequency plot (when discernable) was assigned to this recruitment pulse based on tracking fish growth visually over time. Assignment of modes to pulses was first conducted forward, beginning with the recruitment event and continuing through all daily plots. Pulse identification was verified by tracking modes backward through time beginning with modes on the later days of sampling and working to recruitment events. Daily modal lengths were averaged when bins were of equal size. When distributions from two pulses overlapped, modal length was adjusted downward and upward for the most recent and earlier pulse respectively. Daily modal length was regressed against

Julian date for the linear portion of the time series. Arrival times (Julian date) were backcalculated by inserting the estimated length of fish at arrival (Section 3.3.3) into the equations obtained from regression of daily modal length of fish and Julian date.

3.3.5. Water temperature data

Water temperatures were monitored at four locations within Newman Sound (Fig. 3.2) by Seamon thermographs placed on the bottom at approximately 3 m depth. Water temperatures were recorded every four hours (1998-2001) or hourly (2002) and averaged over two days (for presentation). Water temperatures varied little between sites; therefore, data from Buckleys Cove were analyzed as this site was monitored during all five years and was near the location seined daily.

3.3.6. Calculation of wind energy

Hourly wind speed and direction data collected during 1998-2002 at Gander airport (Fig. 3.2), located 70 kilometres northwest of Newman Sound, was supplied by Environment Canada. There are no large topographical features near Newman Sound and Gander that would greatly influence local wind patterns. Wind stress relative to the northeast coast of Newfoundland was calculated using equation 5b in Schneider and Methven (1988);

$$W_x = W(-W \cos (A - 50))$$

(1)

where;

W_x is the wind stress component in the offshore direction for one day intervals

W is the observed wind speed (m s^{-1}) averaged over one day

A is the angle from which wind is blowing relative to north (degrees)

The coast is angled 50° east of north

Only the cross-shore component of wind stress was used as Newman Sound is an irrotational bay (< 5 km wide).

3.3.7. Assignment of tidal stage

Influence of tidal stage on fish recruitment was tested using the three days with highest and lowest tidal heights every two weeks to identify spring and neap tides respectively. In all statistical testing, tolerance of type I error was set at $\propto$=0.05. Analysis were performed in SAS (1988).

3.4 Results

3.4.1. Daily sampling

3.4.1.1. Daily collections of Atlantic cod

A total of 401 Atlantic cod were collected in 127 seine hauls between 12 July and 23 October 2002 at Bermuda Beach (Fig. 3.3). The smallest Atlantic cod in the samples were 39 mm SL (n=3). These fish were semi-transparent and lacked external parasites. They were collected on three sample dates; 30 July, 5 August and 4 September (Fig. 3.3).

On 5 August two small Atlantic cod were collected with an average length of 40 mm SL. After 5 August, fish length increased with time until 4 September when a 39 mm fish was sampled. I concluded that during the period of daily sampling at Bermuda Beach in 2002, Atlantic cod recruited to benthic habitats in late July- early August and again in early September.

3.4.1.2 Length of Atlantic cod at recruitment

Daily modal lengths of Atlantic cod was regressed against Julian date ($F_{[1,4]} = 5.33$, p=0.2601; Table 3.1) to estimate the length of cod at recruitment to the nearshore. Using the equation from this regression, I calculated the length of cod at recruitment as 43 mm. This estimate was considered too high because the largest cod collected on the first day of recruitment, for both pulses identified at Bermuda Beach, was only 41 mm. Visual identification of distinct modes in many of the daily length frequency plots was prevented by the relatively small number of Atlantic cod recruiting to Bermuda Beach in 2002 (Fig. 3.3). This may have contributed to the weak relationship between daily modal length of Atlantic cod and Julian date.

I chose 39 mm as the representative length of Atlantic cod at recruitment. For both pulses identified at Bermuda Beach during 2002, only fish measuring 39 mm were collected on the first day of recruitment. This estimate also approximates the size of the smallest newly recruited Atlantic cod (38 mm SL) reported by Grant and Brown (1998). Overall, the pulses I observed at Bermuda beach during 2002 were represented by a small number of fish (Fig. 3.3). I assumed that a relatively small number of cod collected on a particular day closely approximated the modal length of the population on that day.

3.4.1.3. Daily collections of Greenland cod.

A total of 4436 Greenland cod were collected at Bermuda Beach during 2002 (Fig. 3.4). The smallest Greenland cod measured 30 mm SL and was collected on 17 July, the first day Greenland cod recruited to Bermuda Beach during 2002 (Fig. 3.4). The four Greenland cod collected on this day had an average length of 34.25 mm SL. Fish measuring 31-32 mm SL were collected on the following five days; 18-22 July. Length of fish increased with time (Fig 3.4). I concluded there was one recruitment event for Greenland cod at Bermuda Beach during 2002; it began on 17 July.

To determine the length of Greenland cod on the first day of recruitment (Julian date 198), I regressed daily modal length of fish and date for Julian date199 onward (Table 3.1). Modal length of Greenland cod increased with time ($F_{[1,52]} = 3548.94$, $p<0.0001$) according to the equation SL= 0.7884 (Julian date) - 123.72 (Table 3.1). Using this equation, I backcalculated the modal length of Greenland cod on the first day of recruitment (Julian date 198) as 33 mm.

3.4.1.4. Daily collections of hake

I collected a total of 945 hake at Bermuda Beach during 2002 (Fig 3.5). Hake were first collected on 18 July when the smallest fish was 55 mm SL and the average length of hake was 61.75 mm SL. Smaller hake were collected after this date with the smallest hake measuring 46 mm SL on 1 August 2002. Daily ranges in length appeared to be broader for hake (Fig. 3.5) than for Greenland cod (Fig. 3.4). However, modal length of hake increased with time (Fig 3.5). I concluded there was one recruitment event for hake at Bermuda Beach during 2002. Note that three small hake were collected earlier (one measuring 65 mm on 10 July and 69 mm and 75 mm hake on 11 July) at other locations during biweekly sampling (see Fig. 3.8).

To determine the length of hake on the first day of recruitment at Bermuda Beach (Day 199), I regressed daily modal length of fish and date for Julian dates from 200 onward (Table 3.1). Modal length of hake increased with time ($F_{[1,41]} = 384.17$, $p<0.0001$) according to the equation SL= 0.70 (Julian date) - 83.86 (Table 3.1). Using this equation, I backcalculated the modal length of hake on the first day of recruitment (Day 199) as 55 mm.

3.4.2. Biweekly sampling 1998-2002

3.4.2.1 Arrival time estimates

Average catch rates of Atlantic cod sampled during 1999 to 2002 ranged from 9.89 fish per haul in 1999 to 27.09 fish per haul in 1998 (Table 3.2). The average number of Greenland cod per haul ranged from 9.13 in 1998 to 34.88 in 2000 (Table 3.2). Data on Atlantic cod collected during 1998 were not included in analyses because only a small proportion of these fish were sub-sampled and measured. The average number of hake per haul sampled annually between 1998 and 2002 ranged from 7.44 in 1998 to 21.56 in 2000 (Table 3.2).

Size frequencies of Atlantic cod sampled during 1999-2002 and Greenland cod and hake sampled during 1998-2002 were plotted (Appendix 1) to determine recruitment events. Modal lengths of fish in daily size frequency plots were determined visually and regressed against date to track pulses of recruitment through time (e.g. Table 3.3; Appendix 1). All but one regression for Atlantic cod were significant (p-values ranged from < 0.0001 to 0.0661). An event late in 2002 was included although the regression of modal length and Julian date was not significant at the five percent level ($F_{[1,3]} = 13.65$, $p = 0.0661$). The small sample size (n=four) was thought to contribute to a high possibility of type II error. However, explained variance was high ($R^2 = 0.87$; Table 4.3) and the four data records were easily distinguished in daily length frequency plots (Appendix 1). Additional data would not likely change the estimate of recruitment date. Four or five recruitment events for Atlantic cod were identified each year during 1999 to 2001. During these years, recruitment was estimated to begin on dates ranging from 19 July in 2001 to 21 October 1999. During 2002 when sampling began earlier than in previous years, six recruitment pulses were identified; the first event was estimated to begin on 21 May and the last on 20 October (Table 3.3). However, recruitment of the first pulse may have occurred before 21 May during 2002 as modal length of Atlantic cod did not change between Julian dates 144 and 162. There are no seine data prior to 21 May during 2002 to determine whether this pulse originated earlier. All regressions of daily modal length of

Greenland cod and date were significant for 1998 to 2002 (p-values ranged from <0.0001 to 0.0004; Table 3.4). The dates when Greenland cod were estimated to begin recruitment in Newman Sound each year ranged from 5 July (Day 186) in 2000 to 17 July (Day 198) in 2001 and 2002 (Table 3.4). Daily modal length of hake was related to date each year during 1998 to 2002 (p-values ranged from <0.0001 to 0.0006). Hake were estimated to recruit to Newman Sound annually on dates ranging from 22 June (Day 174) in 2000 to 15 July (Day 197) in 2002 (Table 3.5).

3.4.2.2. Summary of physical variables 1998-2002

Winds were mostly offshore during the periods studied (Fig 3.6). From 20 May to 6 December of 1998 to 2002, there were 737 days with offshore winds compared to 268 days with onshore winds. The maximum offshore wind stress in a single day was 2044 $km^2\ hr^{-2}$ (mean wind speed was 50 $km\ hr^{-1}$) calculated for 15 October 1999. Onshore wind stress was never higher than 1130 $km^2\ hr^{-2}$ (mean wind speed was 34 $km\ hr^{-1}$), calculated for 29 October 2000. Daily water temperatures were highly variable, but the seasonal cycle was apparent each year; waters temperatures increased from approximately 3-4 °C in May to 16-17 °C in August and then decreased to 3-4 °C by late November (Fig. 3.6). The plot of water temperature and date for 1999 was distinct from other years because a large decrease in water temperature (from 17.8 °C to 9.2 °C) occurred in early August and temperatures slowly increased through August and most of September, never attaining the levels prior to the decrease. Upwelling occurred episodically in all years. This was indicated by water temperature decreases of 4-5 °C over four to eight days and a subsequent return to predecline levels.

3.4.2.3. Test for wind stress influence on arrival times

I identified 19 recruitment events for Atlantic cod in Newman Sound from 1999 through 2002 (Fig. 3.6). Most (15 of 19) recruitment events were estimated to have begun either on days with onshore winds or one day following onshore winds (Fig. 3.6). For the periods ranging from 29 June (last day with onshore winds prior to the first recruitment event in 1999 to 2001) or 20 May 2002 (first day of sampling in 2002) to the last day of sampling each year, there were 468 days with offshore winds and 159 days with onshore winds. Expected odds of an occurrence during onshore winds was $p/1\text{-}p = (159/627)/(468/627) = 0.34:1$; for offshore winds the odds were $p/1\text{-}p = (15/19)/(4/19) = 3.75:1$. The observed odds for recruitment of Atlantic cod relative to the odds of onshore winds on the same day or the following day was 11.04:1. Estimated recruitment dates occur an improbably high number of times immediately after upwelling ceases ($G=25.10$, $p<0.0001$) (Fig. 3.6; Appendix 2). All 19 recruitment events were estimated to have begun on days with onshore winds or within two days following onshore winds. All recruitment events for Atlantic cod were associated with onshore wind events following upwelling (Fig. 3.6).

Similar to Atlantic cod, estimated recruitment dates of Greenland cod and hake occurred after cessation of offshore winds. During four of five years, estimated recruitment dates of Greenland cod to sites in Newman Sound occurred on days with onshore winds (Fig. 3.7). During 2000, estimated Greenland cod recruitment began two days after a period of onshore winds (Fig. 3.7). In three (1998, 1999, 2002) of five years, estimated dates of hake recruitment occurred on days with onshore winds (Fig. 3.8). During 2000 and 2001, estimated hake recruitment occurred two days and one day, respectively, following the onset of onshore winds (Fig. 3.8).

3.4.2.4. Influence of tidal stage on arrival times

The three days each month with the highest and lowest tides were identified to test whether recruitment of Atlantic cod, Greenland cod and hake to sites in Newman Sound was associated with tidal stage (Fig 3.9). During the study periods, there were 126 days with highest tides and 126 days with lowest tides. The expected odds of recruitment on a day with highest or lowest tides was p/1-p= (126/627)/(501/627) = 0.20:1. Three of 19 events were estimated to have begun on days with the highest tides and three were estimated to have begun on days with lowest tides. The odds for three positives in 19 events is 1.053:1. The dates when recruitment was estimated to have begun were not significantly associated with highest (G= 0.234, p=0.6285; Appendix 2) or lowest tides (G= 0.234, p=0.6285; Appendix 2). On 375 days, tides were intermediate between high and low. The expected odds of recruitment on days with intermediate tides was p/1-p = (375/627)/(252/627)= 0.60:1. There were 13 of 19 events estimated to have begun on days with intermediate tides. The observed odds ratio was 0.786:1 which was not significant

(G=0.622, p=0.4303; Appendix 2). Greenland cod were estimated to recruit to my sites on spring tides only during 1998 and on a neap tide only during 2002 (Fig 3.9). Recruitment of hake to my sites on spring tides was estimated to occur only once, during 1998 (Fig. 3.9). Other recruitment events for Greenland cod and hake were estimated to begin between tidal extremes. Based on Figure 3.9, it is clear that fish recruitment was not associated with tidal phase, even in a general way. I concluded daily recruitment of Atlantic cod, Greenland cod and hake to nearshore Newfoundland waters was not related to the tidal cycle (spring and neap).

3.5 Discussion

Recruitment of Atlantic cod, Greenland cod and hake to sites in Newman Sound occurred an improbably high number of times during onshore winds, supporting the theory that fish recruitment nearshore is associated with cessation of upwelling (Hjort and Dahl, 1900). However, fish did not recruit to the near shore following every onshore wind event. Greenland cod and hake recruited during only one event annually. This may be linked to limited spawning periods and locations, as discussed below. Atlantic cod recruited episodically during the sampling periods which extended from May to November in 2002 and July to November during 1999 to 2001. This pattern is consistent with larval transport during downwelling. I suggest that transport of fish larvae to the coast is a two step process. First, larvae accumulate at an upwelling front (Munk *et al.* 1995; Lochmann *et al.* 1997; McLaren *et al.*1997). Then, following an upwelling event the front moves to the coast (downwelling) and deposits larvae (Farrell *et al.* 1991, Roughgarden *et al.* 1991), which then settle into bottom habitats and take up a juvenile existence. During the next onshore wind event, the front moves toward the coast but does not contain larvae. Concurrent with this downwelling event, larvae that are relatively far from the coast drift shoreward but do not reach the coast. These larvae resupply the next upwelling front that develops and the cycle begins again. There are a number of observations to support this scenario. Recruitment of Atlantic cod to my sites never occurred during two consecutive onshore wind events rather, recruitment was often associated with alternate periods of onshore winds. Upwelling fronts are known to exist off the northeast coast of Newfoundland (Schneider and Methven, 1988). Laprise and Pepin (1995) observed eggs and larvae of a number of species including Atlantic cod were most abundant on the eastern side of Conception Bay when winds were westerly but during a southerly wind event, highest abundance was on the western side, associated with the warmest waters. Episodic recruitment of Atlantic cod occurs simultaneously all along the northeast coast of Newfoundland (Methven, 1996) suggesting that the process generating the pattern operates at large spatial scales. Identifying large scale influences on the recruitment success of Atlantic cod is particularly important now, as stocks off Newfoundland have been reduced to less than two percent of historic levels (Lilly *et al.*, 2003) and have been declared endangered by the Committee On the Status of Endangered Wildlife in Canada (COSEWIC, 2003).

Previous studies conducted near shore identified two to four recruitment events for

Atlantic cod annually whereas I observed at least five events during 2002. Recruitment pulses were thought to originate during late-August to early-September and October (Methven and Bajdik, 1994), May and mid-August (Pinsent and Methven, 1997) and during three or four autumn periods (Grant and Brown, 1998; Gregory *et al.* 2002). There are two potential explanations for variation in the number of annual recruitment events recorded during sampling near shore. First, frequency of onshore wind events during the spawning period may vary among years. During certain years (1998, 2001 and 2002) there were periods of two to three weeks without onshore winds during July or August. Onshore winds were more frequent during the summers of 1999 and 2000. Second, spawning time and duration differs between areas both offshore (Myers *et al.*, 1993; Hutchings and Myers, 1994) and inshore (Thompson, 1943; Smedbol and Wroblewski, 1997). The number of annual recruitment pulses of Atlantic cod on the northeast coast of Newfoundland varies with the timing and number of downwelling events.

Early physical models of egg and larval drift showed offshore movement with prevailing winds, which are from the southwest during summer and west or northwest in autumn and winter. Winds blow from the east during short periods, associated with passing storms. Therefore, models that incorporated storm passage (Helbig *et al.*, 1992) suggested that Atlantic cod recruitment to the coast is small and only occurs after sustained onshore winds, which are rare. Later baroclinic models (Pepin and Helbig, 1997) suggested that more larvae reached coastal areas, but retention was still only 10 %. Nevertheless, roughly half of the small cod Beacham *et al.* (2000) sampled from Newman

Sound during August 1999 were genetically most similar to adults caught on Funk Island Bank; in their October sample, 30 percent of the fish were most similar to offshore cod (Funk Island Bank and northern Grand Bank) while 70 percent originated inshore. Therefore, Atlantic cod larvae may not drift passively. Larvae that maintain their vertical position in the water column (depth-keeping), will collect at an upwelling front, which is convergent at the surface. Accumulations of Atlantic cod larvae have been found at relatively stationary fronts (Lochmann *et al.,* 1997; McLaren *et al.*, 1997; Munk *et al.* 1999). Larvae that accumulate at upwelling fronts near the coast are transported shoreward when upwelling favorable winds subside and the front collapses quickly (Farrell *et al.*,1991; Roughgarden *et al.*,1991).

On a relatively coarse temporal scale, initiation of recruitment by Greenland cod to the nearshore may be determined by the location and timing of spawning and development rates of eggs and larvae. Greenland cod recruited to Newman Sound once in each of the five years, 1998 to 2002. This species spawns during February and March primarily in shallow waters (Scott and Scott, 1988). Greenland cod eggs are demersal (Cohen *et al.*, 1990) which prevents loss from offshore drift. Generally, both adult and juvenile Greenland cod inhabit coastal areas. Only low numbers have been collected further from shore (Nielsen and Andersen, 2001). With winds offshore on most days prior to settlement, a relatively high proportion of Greenland cod larvae may be lost from waters nearshore in the absence of a retention mechanism. Larvae that drift away from the coast may be retained in an upwelling front if they have a behavioural response (to light, temperature, or salinity) that results in maintaining position in the water column. Greenland cod recruited to Newman Sound after the seasonal thermocline was established and I found that arrival times near shore were associated with onshore winds. During the period from late-July to mid-August, onshore wind events are sometimes rare (e.g.1998, when mean catch was lowest of the five years studied). Therefore, delayed development of eggs or larvae may result in poor recruitment at the coast. Annual recruitment of Greenland cod to the northeast coast of Newfoundland may be influenced by environmental (wind and water temperature) conditions during early summer.

Little is known about hake reproduction in Newfoundland waters. Hake are thought to spawn during winter or early spring (Scott and Scott, 1988), but the locations are not known. Local fishers in Bonavista Bay report catching hake during winter in shallow water habitats similar to those where Greenland cod spawn. Populations of hake have been documented on the southern Grand Banks (Kulka and Simpson, 2002), but not closer to my sites. Hake have pelagic eggs (Scott and Scott, 1988), which are subject to drift, unlike demersal eggs of Greenland cod. Hake recruited to Newman Sound in early summer, similar to Greenland cod and the arrival times were also associated with onshore winds. Although there were a number of similarities between recruitment of hake and Greenland cod, which mostly originate near shore, my data do not indicate whether the hake I collected originated from spawning offshore or near shore.

Recruitment of Atlantic cod, Greenland cod and hake was not associated with tidal stage. In contrast, settlement of invertebrate spat and cyprids in the California Bight occurred during periods of increasing water temperatures associated with internal tidal bores (Pineda, 1991). Perhaps tidal forcing influences larval recruitment to estuarine areas rather than to more open areas of the coast. Larval English sole recruit to Oregon estuaries on the highest tides every two weeks but arrival at coastal sites is associated with onshore winds (Boehlert and Mundy, 1987). Similarly, recruitment of *Rhabdosargus sarba* and *Pelates sexlineatus* to Australian estuaries depends on tidal stage but wind induced advection may be required for transport to the coast (Smith and Suthers, 2000). I can not rule out the possibility that tidal forcing influences movement of fish larvae into estuaries on the northeast coast of Newfoundland. However, for the three species of fish that I investigated, there was no association of recruitment events in Newman Sound with tidal stage.

Fine scale data were required to detect associations between fish recruitment at the coast and wind stress. Using daily catch data for Atlantic cod permitted tracking of multiple length frequency modes through time. My results showed that daily recruitment of Atlantic cod, Greenland cod and hake is associated with onshore winds. Typically, winds were onshore for no more than two or three consecutive days. Previous studies on the influence of wind on larval transport were conducted at coarser resolutions. Results of these studies were inconsistent. Modelling of particle drift using a resolution of no more than ten days (captures storm tracks) simulated particle drift from offshore banks to the near shore only during prolonged onshore winds, which are rare (Helbig *et al.* 1992; Davidson and deYoung). Simulations using data at the monthly scale (Anderson *et* *al.*,1995) predicted particles drift to the coast only occasionally. The average movement of larvae is offshore, but onshore movement occurs occasionally.

In conclusion, recruitment of Atlantic cod, Greenland cod and hake to near shore bottom habitats was associated with onshore wind events following upwelling. I observed Atlantic cod recruited to near shore sites during multiple (four to six) events annually during 1999 to 2002. Recruitment events occurred episodically during the summer and autumn periods studied. Greenland cod and hake recruited to my sites only once annually, during June or July. During daily seining at one location in Newman Sound during 2002, Greenland cod and hake were first collected during a period of increasing water temperatures and onshore winds as predicted. Analysis of data collected biweekly at 12 sites during 1998 to 2002 verified that the annual recruitment events for Greenland cod and hake were associated with onshore winds. Similarly, 19 of 19 estimated recruitment events for Atlantic cod during 1999 to 2002 occurred within one day following onshore winds. Results were consistent with larval transport to my sites during onshore movements of convergent fronts following upwelling. Retention at an upwelling front depends on behavioural responses of larvae, which was beyond the scope of my study. Upwelling fronts may play an important role in retention and recruitment of a number of fish and invertebrate species in Newfoundland coastal waters.

3.6. Acknowledgements

I would like to thank all the students, technicians and volunteers who participated in beach seining; Erin Alcock, Jessica Anderson, Louise Copeman, Dave Cote, Katie Dalley, Peter Frampton, Doug Gibson, Ann Marie Gorman, Janelle Hancock, Ben Hammond, Brianna Hookey, Chris Howell, Robyn Jamieson, Terra Lynn Lander, Ben Laurel, Janice Linehan, Mike Norris, Miriam O, Adam Ogilvie, Melissa Pink, Dan Porter, Andrea Powell, Heather Reid, Mark Renkawitz, Philip Sargent, Lee Sheppard, Dave Sterling, Steve Sutton, Christine Vickers, Nadine Wells, Richard Wong, and Kimberly Young. Lee Sheppard is thanked for producing Figure 3.2.

3.7 Literature cited

Anderson, J.T., E.L. Dalley and J.E. Carscadden, 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. 52: 115-125.

Bailey, K.M., 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1-9.

Boehlert, G.W., and B.C. Mundy, 1987. Recruitment dynamics of metamorphosing English sole, *Parophorys vetulus*, to Yaquina Bay, Oregon. Est. Coast. Shelf Sci. 25: 261-281.

Cohen, D.M., T. Inada, T. Iwamoto and N. Scialabba, 1990. Gadiform fishes of the world. FAO species catalogue FIR/S125 vol. 10.

COSEWIC, 2003. COSEWIC assessment and update status report on the status of Atlantic cod *Gadus morhua* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa xi + 76 pp.

Cushing, D.H., 1969. The natural regulation of fish populations. In: Sea fisheries research.

FR. Harden Jones (ed), pp. 399-412. Wiley, New York.

Davidson, F.J.M. and B. deYoung, 1995. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. 4: 33-51.

de Young, B., T. Otterson and R.J. Greatbatch, 1993. The local and nonlocal response of Conception Bay to wind forcing. J. Phys. Oceanogr. 23: 2636-2649.

Eggleston, D.B., D.A. Armstrong, W.E. Elis and W.S. Patton, 1998. Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae. Mar. Ecol. Prog. Ser. 164: 73-82.

Frank, K.T., and W.C. Leggett, 1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Can. J. Fish. Aquat Sci. 38: 215-223.

Farrell, T.M., D. Bracher and J. Roughgarden, 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnol. Oceanogr. 36: 279-288.

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

Grant, S.M., and J.A. Brown, 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can. J. Fish. Aquat. Sci. 55: 1317-1327.

Gregory, R.S., J.A. Brown and C. Mercer, 1998. Implications of interspecific competition between demersal juvenile Atlantic cod and Greenland cod on the recovery of Atlantic cod stocks. Final Report to Canadian Centre for Fisheries Innovation. 37p.

Hancock, J.K., 2000. Along shore movement rate of juvenile cod (*Gadus* spp.) determined by mark-recapture. Honours thesis. Memorial University of Newfoundland. 48 p.

Harvey, A.W., 1891. Operations at Dildo. p. 5-12. In: Annual report of the Newfoundland Fisheries Commission for the year 1890. JW. Withers, St. John's Nfld.

Helbig, J., G. Mertz and P. Pepin, 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. 1: 39-56.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe. Rapp P.-v. Reun Cons. Int. Exp. Mer 20:1-228.

Hjort, J., and K. Dahl, 1900. Fishing experiments in Norwegian fjords. In: Report on Norwegian fishery and marine investigations. J. Hjort [ed]. Vol 1: 1-215.

Hutchings, J.A., R.A. Myers and G.R. Lilly, 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2457-2467.

Hutchings, J.A. and R.A. Myers, 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21-31.

Jenkins, G.P., K.P. Black, M.J. Wheatley and D.N. Hatton, 1997. Temporal and spatial variability of a temperate seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. Mar. Ecol. Prog. Ser. 148: 23-35.

Isles, T.D. and M. Sinclair, 1982. Atlantic herring: stock discreteness and abundance. Science 215: 627-633.

Kingsford, M.J., and J.H. Choat, 1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. 91: 161-171.

Kingsford, M.J., and I.M. Suthers, 1996. The influence of tidal phase on patterns of ichthyoplankton abundance in the vicinity of an estuarine front, Botany Bay, Australia. Est. Coast. Shelf Sci: 43: 33-54.

Kulka, D.W., and M.R. Simpson, 2002. The status of white hake (*Urophycis tenuis*), in NAFO Division 3L, 3N, 3O and Subdivsiion 3Ps. Can. Stock. Assess. Sec. Res. Doc. 2002/055.

Laprise, R., and P. Pepin, 1995. Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. Mar. Ecol. Prog. Ser. 122: 73-92.

Lasker, R., 1975. Field criteria for survival of anchovy larvae: the relationship between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453-462.

Lasker, R., 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Reun. CIEM. 173: 212-230.

Lazier, J.R.N., 1982. Seasonal variability of temperature and salinity in the Labrador Current. J. Mar. Res. 40: 341-356.

Leggett, W.C., K.T. Frank and J.E. Carscadden, 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*) Can. J. Fish. Aquat. Sci. 41: 1193-1201.

Lilly, G.R., P.A. Shelton, J. Brattey, N.G. Cadigan, B. P. Healey, E. F. Murphy, D. E. Stansbury and N. Chen, 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL in February 2003. Can. Scientific Advisory Secretariat Res. Doc. 2003/023.

Lochmann, S.E., C.T. Taggart, D.A. Griffin, K.R. Thompson, and G.L. Maillet, 1997. Abundance and condition of larval cod (*Gadus morhua*) at a convergent front on Western Bank, Nova Scotia. Can. J. Fish. Aquat. Sci. 54: 1461-1479.

McLaren, I.A., P. Avendaño, C.T. Taggart and S.E. Lochman, 1997. Feeding by larval cod in different water-masses on Western bank, Scotian Shelf. Oceanogr. 6: 25-265.

Methven, D.A., 1996. Early life history of juvenile Atlantic cod (*Gadus morhua*): spatial and temporal variability and variability due to gear. Final report to Northern Cod Science Program. 132 p.

Methven, D.A., and C. Bajdik, 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 51: 78-90.

Methven, D.A., R.L. Haedrich and G.A. Rose, 2001. The fish assemblage of a Newfoundland estuary: diel, monthly and annual variation. Est. Coast. Shelf Sci. 52: 669-687.

Methven, D.A., and C. McGowan, 1998. Distinguishing small juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*) by comparing meristic characters and discriminant function analysis of morphometric data. Can. J. Zool. 76: 1054-1062.

Miller, B.A., and R.B. Emlet, 1997. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. Mar. Ecol. Prog. Ser. 148: 83-94.

Munk, P., P.O. Larsson, D.S. Danielssen and E. Moksness, 1995. Larval and small juvenile cod *Gadus morhua* in the highly productive areas of a shelf break front. Mar. Ecol. Prog. Ser. 125: 21-30.

Munk, P., P.O. Larsson, D.S. Danielssen and E. Moksness, 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. Mar. Ecol. Prog. Ser. 177: 221-233.

Myers, R.A., G. Mertz and C.A. Bishop, 1993. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Oceanogr. 2: 154-165.

Nelson, W.R., M.C. Inghan and W.E. Schaaf, 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 75: 23-41.

Nielsen, J.R., and M. Andersen, 2001. Feeding habits and density patterns of Greenland cod, *Gadus ogac* (Richardson 1836), at west Greenland compared to those of the coexisting Atlantic cod, *Gadus morhua* L. J. Northw. Atl. Fish. Sci. 29:1-22.

Pepin, P., and J.A. Helbig, 1997. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. 54: 670-685.

Pineda, J., 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253: 548-551.

Pinsent, D.L., and D.A. Methven, 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 54 (Suppl.1): 19-24.

Robichaud, D., and G.A. Rose, 1999. Distribution of 0 and 1 group cod in nearshore waters of Placentia Bay (NAFO Subdivision3Ps), 1997-1998. Can. Stock Assess. Sec. Res. Doc. 99/66.

Rose, G.A., 1993. Cod spawning on a migration highway in the northwest Atlantic. Nature (Lond.) 366: 458-461.

Roughgarden, J., J.T. Pennington, D. Stoner, S. Alexander and K. Miller, 1991. Collisions of upwelling fronts with intertidal zones: the cause of recruitment pulses in barnacle populations of central California. Acta. Œcol. 12: 35-51.

SAS 1988. SAS/STAT Release 6.03. SAS Institute Inc., Cary, North Carolina.

Schneider, D.C., and D.A. Methven, 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. J. Mar. Res. 46: 105-118.

Schneider, D.C., D.A. Methven and E.L. Dalley, 1997. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 187-199.

Scott, W.B, and M.G. Scott, 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

Shanks, A.L., 1998. Abundance of post-larval *Callinectes sapidus*, *Penaeus* spp., *Uca* spp. and *Libinia* spp. collected at an outer coastal site and their cross-shelf transport. Mar. Ecol. Prog. Ser. 168: 57-69.

Shanks, A.L., 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. 45: 230-236.

Shenker, J.M., 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopea off Oregon. Fish. Bull. 86: 299-317.

Sheppard, G.L., 2005. Natural mortality and movement of juvenile cod (Gadus spp.) inhabiting eelgrass (*Zostera marina*) in Newfoundland waters. Msc thesis, Department of Biology, Memorial University of Newfoundland. 147 p.

Sinclair, M.., 1988. Marine populations: an essay on population regulation and speciation. Washington sea Grant. Program, Seattle. 252 p.

Sleggs, G.F., 1933. Observations on the economic biology of capelin (*Mallotus villosus* O.F. Müller). Rep. Newfoundland Fishery Res. Lab 1: 1-66.

Smedbol, R.K., and J.S. Wroblewski, 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991-1993. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 177-186.

Smith, K.A., and I.M. Smith, 2000. Consistent timing of juvenile fish recruitment to seagrass beds within two Sydney estuaries. Mar. Freshw. Res. 51: 765-776.

Taggart, C.T., and K.T. Frank, 1987. Coastal upwelling and *Oikopleura* occurrence ('slub'): a model and potential applications to inshore fisheries. Can. J. Fish. Aquat. Sci. 44: 1729-1736.

Templeman, W., 1948. The life history of capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. Nfld. Gov. Lab. Res. Ser. Bull. 17: 1-151.

Templeman, W., 1979. Migration and intermingling of stocks of Atlantic cod *Gadus morhua* of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Doc. 14: 6-50.

Templeman, W., 1981. Vertebral numbers in Atlantic cod *Gadus morhua* of the Newfoundland and adjacent areas, 1947-1971, and their use for delineating cod stocks. Northw. Atl. Fish. Sci. 2: 21-45.

Thompson, H.,1943. A biological and economic study of cod (*Gadus callarius* L.) in the Newfoundland area. Nfld Dep. Nat. Resour. Res. Bull. No 14.

Wing, S.R., L.W. Botsford, J.R. Largier and L.E. Morgan, 1995a. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. 128: 199-211.

Wing, S.R., J.L. Largier, L.W. Botsford and J.F. Quinn, 1995b. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. 40: 316-329.

Yao, T., 1987. The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmos. Ocean. 24: 235-252.

Table 3.1. Length of Atlantic cod, Greenland cod and hake on the first day of recruitment at Bermuda Beach, 2002 estimated from regressions of modal length of fish and Julian date. Data were collected daily by beach seine between 12 July and 23 October.

Fish	β_o	F	p-value	α	R^2	n	First day of recruits	Estimated length of recruits (mm)
Atlantic cod	0.316	5.33	0.2601	-27.00	0.84	3	247 (4 Sept.)	43
Greenland cod	0.788	2927.57	< 0.0001	-123.72	0.98	52	198 (17 July)	33
Hake	0.700	384.17	<0.0001	-83.86	0.91	41	199 (18 July)	55

Table 3.2. Number of Atlantic cod, Greenland cod and hake per haul collected by beach seine at 12 sites in Newman Sound during 1998 to 2002.

Year	Atlantic cod (# $haul^{-1}$)	Greenland cod (# $haul^{-1}$)	Hake (# $haul^{-1}$)	Number of seine hauls
1998	27.09	9.13	7.44	118
1999	9.89	19.91	10.14	119
2000	14.14	34.88	21.56	120
2001	11.29	34.65	20.39	102
2002	12.62	28.26	9.59	159

Table 3. 3. Estimated initiation dates for recruitment of Atlantic cod during 1999 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained from regression of daily modal length of cod (mm SL) against Julian date. Fish were collected by beach seine.

Year	Event	β_o	F	p-value	α	R^2	n	Estimated date of event
1999	1	0.703	128.04	<0.0001	-109.58	0.96	8	30 July
1999	2	0.670	188.13	<0.0001	-116.88	0.97	7	21 Aug.
1999	3	0.522	175.37	<0.0001	-89.87	0.97	8	4 Sept.
1999	4	0.594	40.66	0.0078	-122.39	0.93	6	29 Sept.
1999	5	0.391	55.42	0.0017	-76.03	0.93	6	21 Oct.
2000	1	0.506	281.25	<0.0001	-66.33	0.98	9	26 July
2000	2	0.439	365.09	<0.0001	-58.92	0.98	9	10 Aug.
2000	3	0.257	38.02	0.0035	-23.46	0.91	6	30 Aug.
2000	4	0.436	145.91	0.0003	-83.92	0.97	6	8 Oct.
2001	1	0.503	542.88	<0.0001	-61.53	0.99	8	19 July
2001	2	0.701	236.19	0.0001	-127.57	0.98	6	28 Aug.
2001	3	0.528	178.88	0.0002	-93.67	0.98	6	8 Sept.
2001	4	0.573	79.25	0.0030	-117.08	0.96	5	29 Sept.
2002	1	0.544	31.79	0.0013	-37.63	0.84	8	21 May
2002	2	0.723	506.53	0.0002	-79.28	0.99	5	13 June
2002	3	0.425	20.98	0.0195	-50.60	0.88	5	30 July
2002	4	0.340	15.68	0.0288	-43.03	0.84	5	29 Aug.
2002	5	0.645	32.46	0.0047	-135.23	0.89	6	27 Sept.
2002	6	0.336	13.65	0.0661	-59.34	0.87	4	20 Oct.

Table 3.4. Estimated initiation dates for recruitment of Greenland cod (33 mm) during 1998 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained by regression of daily modal length (mm SL) of Greenland cod against Julian date. Fish were collected by beach seine.

Year	β_o	F	p-value	α	R^2	n	Estimated date of event
1998	0.640	257.49	<0.0001	-88.82	0.99	6	10 July
1999	0.685	120.91	0.0004	-94.21	0.97	6	5 July
2000	0.690	557.04	<0.0001	-100.25	0.99	6	14 July
2001	0.651	1372.22	<0.0001	-95.60	0.99	7	17 July
2002	0.740	366.08	<0.0001	113.60	0.99	7	17 July

Table 3.5. Estimated initiation dates for recruitment of hake (55 mm) during 1998 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained by regression of daily modal length of hake against Julian date. Fish were collected by beach seine.

Year	$ß_o$	F	p-value	α	R^2	n	Estimated date of event
1998	0.605	99.72	0.0006	-61.05	0.96	6	11 July
1999	0.607	322.50	0.0004	-57.79	0.99	5	5 July
2000	0.377	703.50	<0.0001	-10.69	0.99	6	22 June
2001	0.454	404.55	<0.0001	-26.42	0.99	6	28 June
2002	0.484	151.60	0.0002	-40.42	0.97	6	15 July

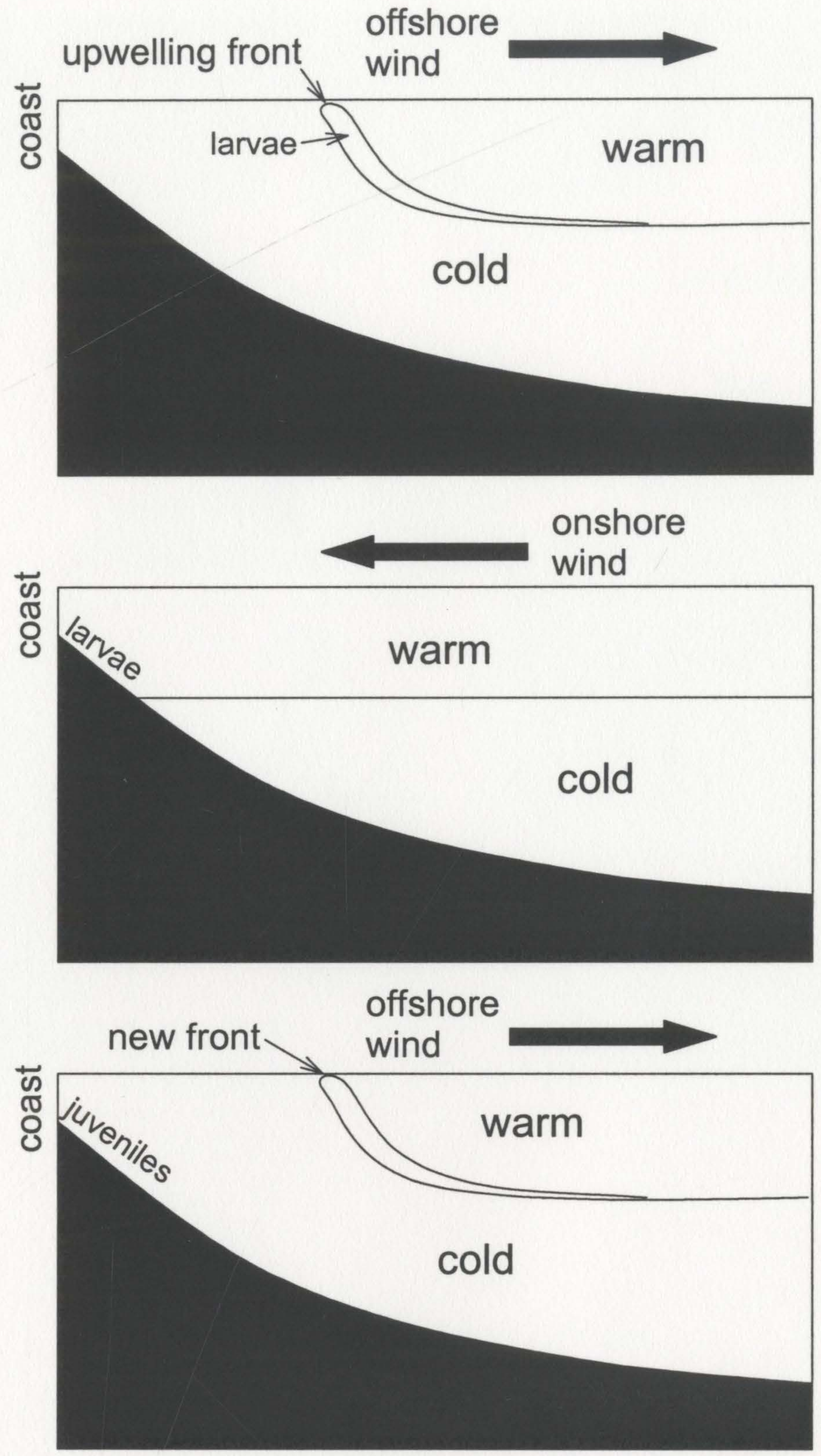


Figure 3.1. Diagram illustrating water mass movements occurring during upwelling and relaxation in confined bays along the northeast coast of Newfoundland. In the top panel, winds are offshore, an upwelling front exists a few kilometers from the coast where larval and pelagic juvenile fish accumulate. In the middle panel, the winds have reversed to onshore, the front has moved to the coast and larval or juvenile fish are deposited. In the bottom panel, winds switch to offshore again and another upwelling front is established away from the coast. Larvae have made the transition to the demersal juvenile stage.

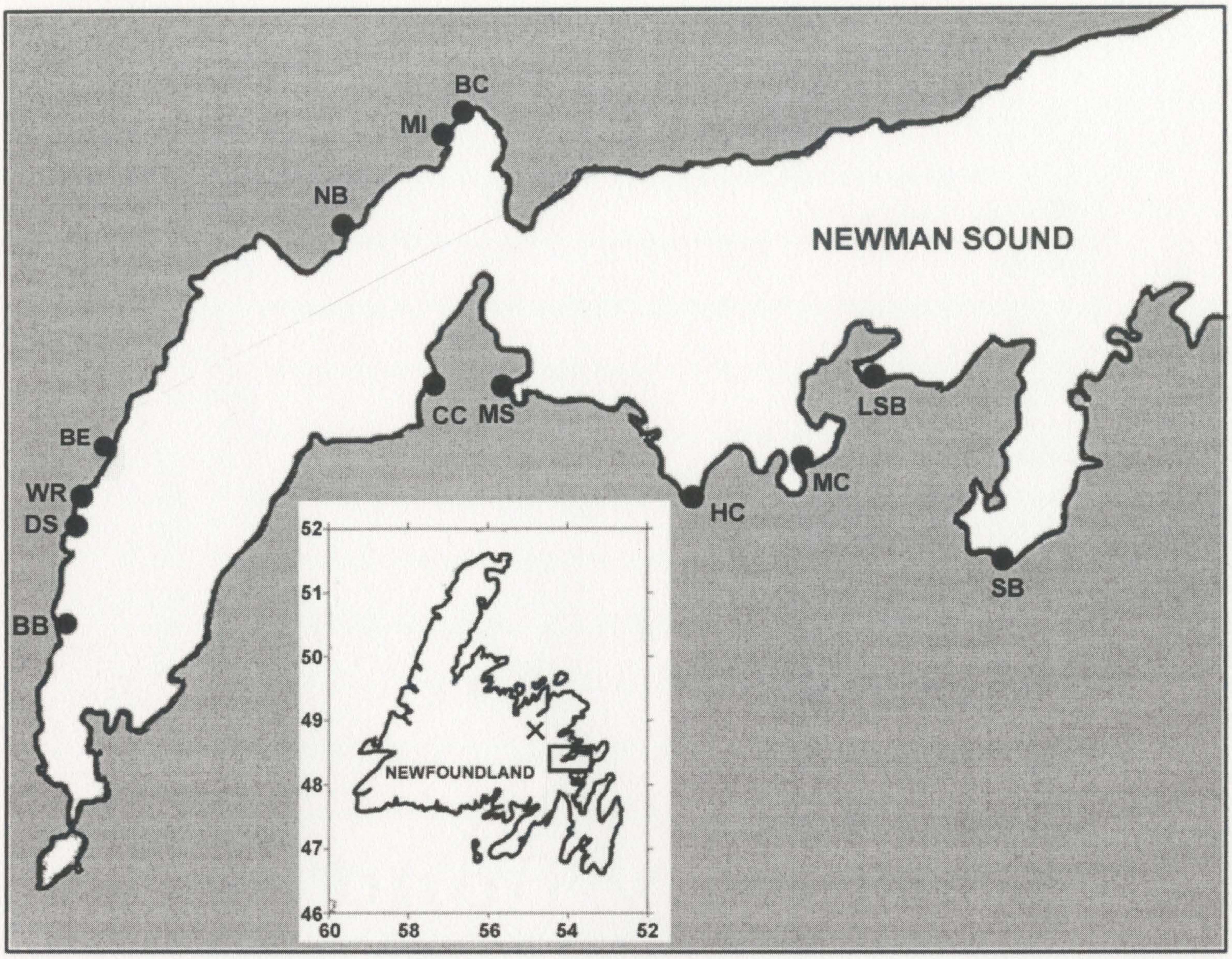


Figure 3.2. Map of Newfoundland showing sites in Newman Sound sampled by beach seine for Atlantic cod, Greenland cod and hake during 1998 to 2002. Sites were South Broad Cove (SB), Little South Broad Cove (LSB), Minchins Cove (MN), Hefferns Cove (HC), Mount Stanford Cove (MS), Buckleys Cove (BC), Mistaken Cove (MI), Newbridge Cove (NB), White Rock (WR), Dockside (DS) and Big Brook (BB). Daily seining was conducted at Bermuda Beach (BE). Wind data were recorded at Gander Airport indicated by an X.

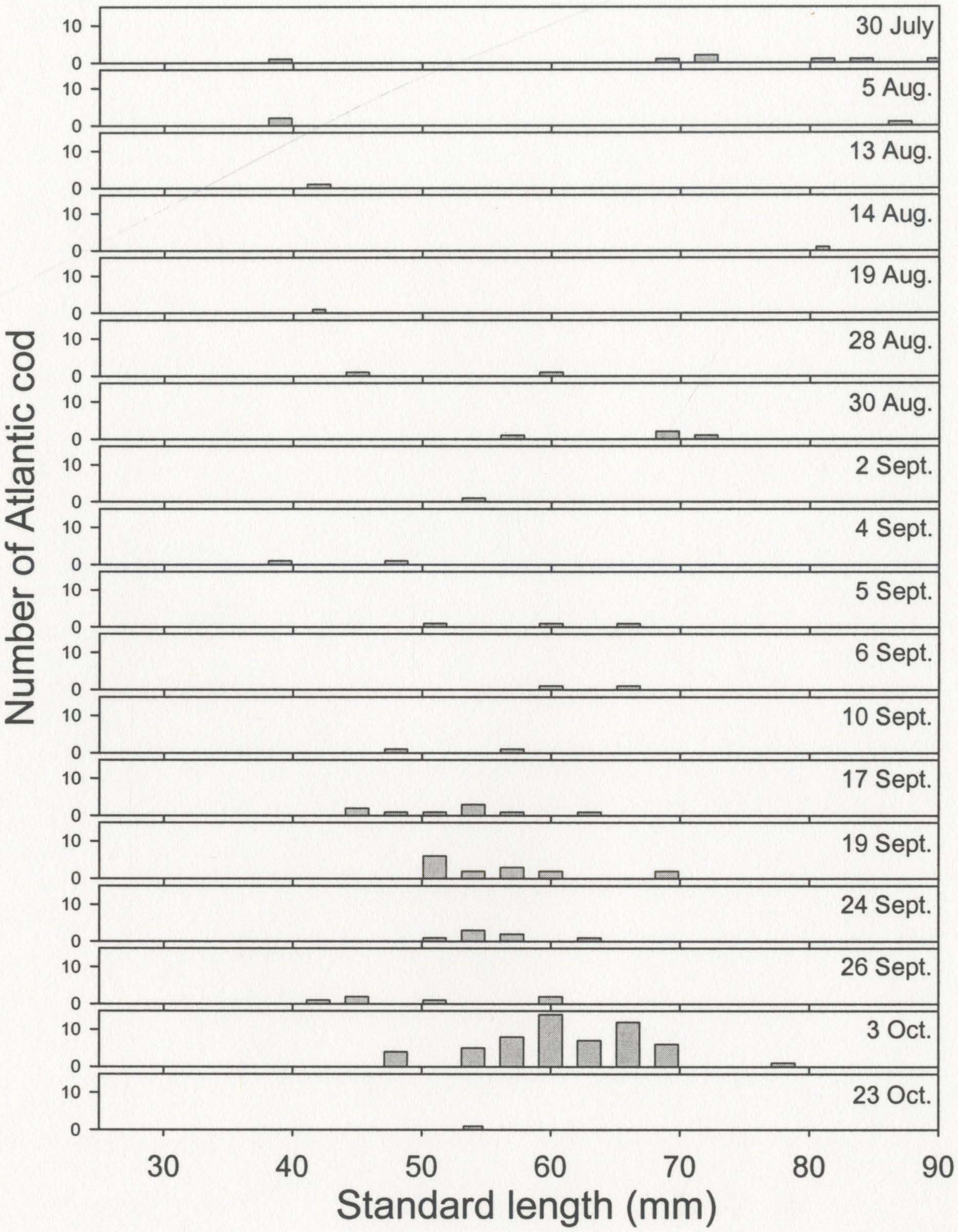


Figure 3.3. Daily length frequency plots for Atlantic cod collected by beach seine at Bermuda Beach between 12 July and 23 October 2002. Newly recruited Atlantic cod were not observed before 30 July so data between12-29 July were not presented.

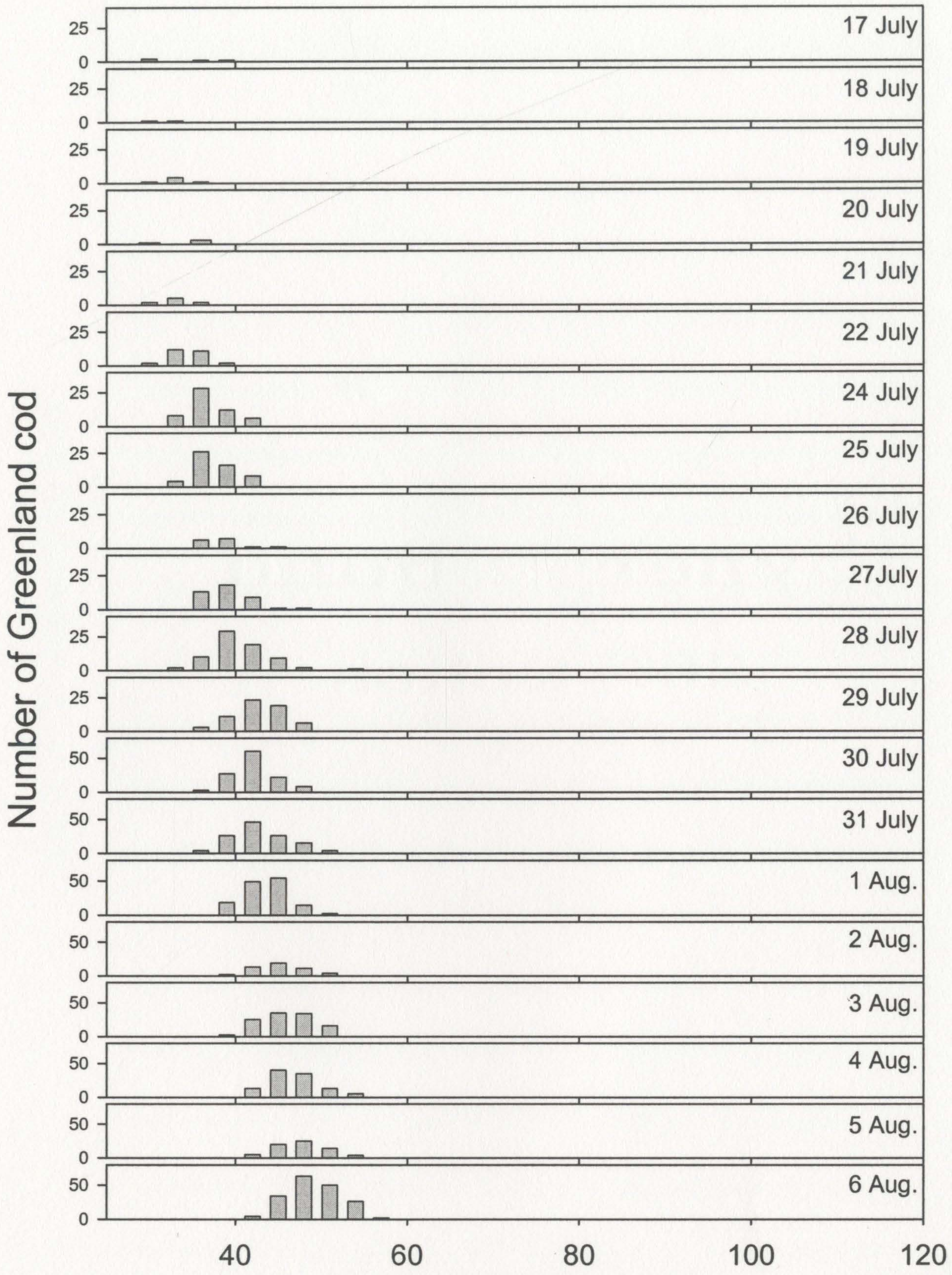


Figure 3.4. Daily length frequency plots for Greenland cod collected by beach seine at Bermuda Beach between 12 July and 23 October 2002. Newly recruited Greenland cod were not observed before 17 July so data between12-16 July were not presented.

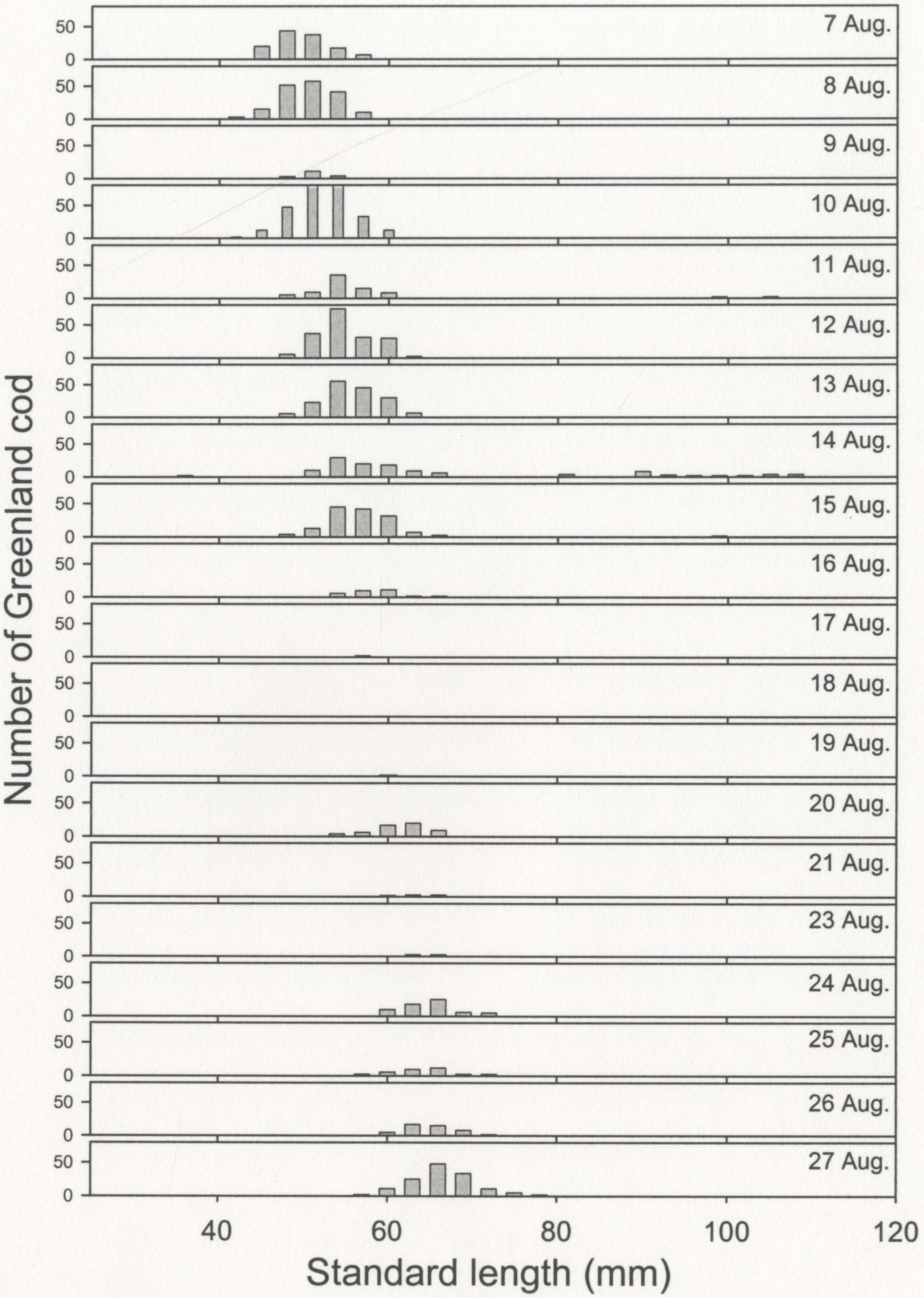


Figure 3.4 continued.

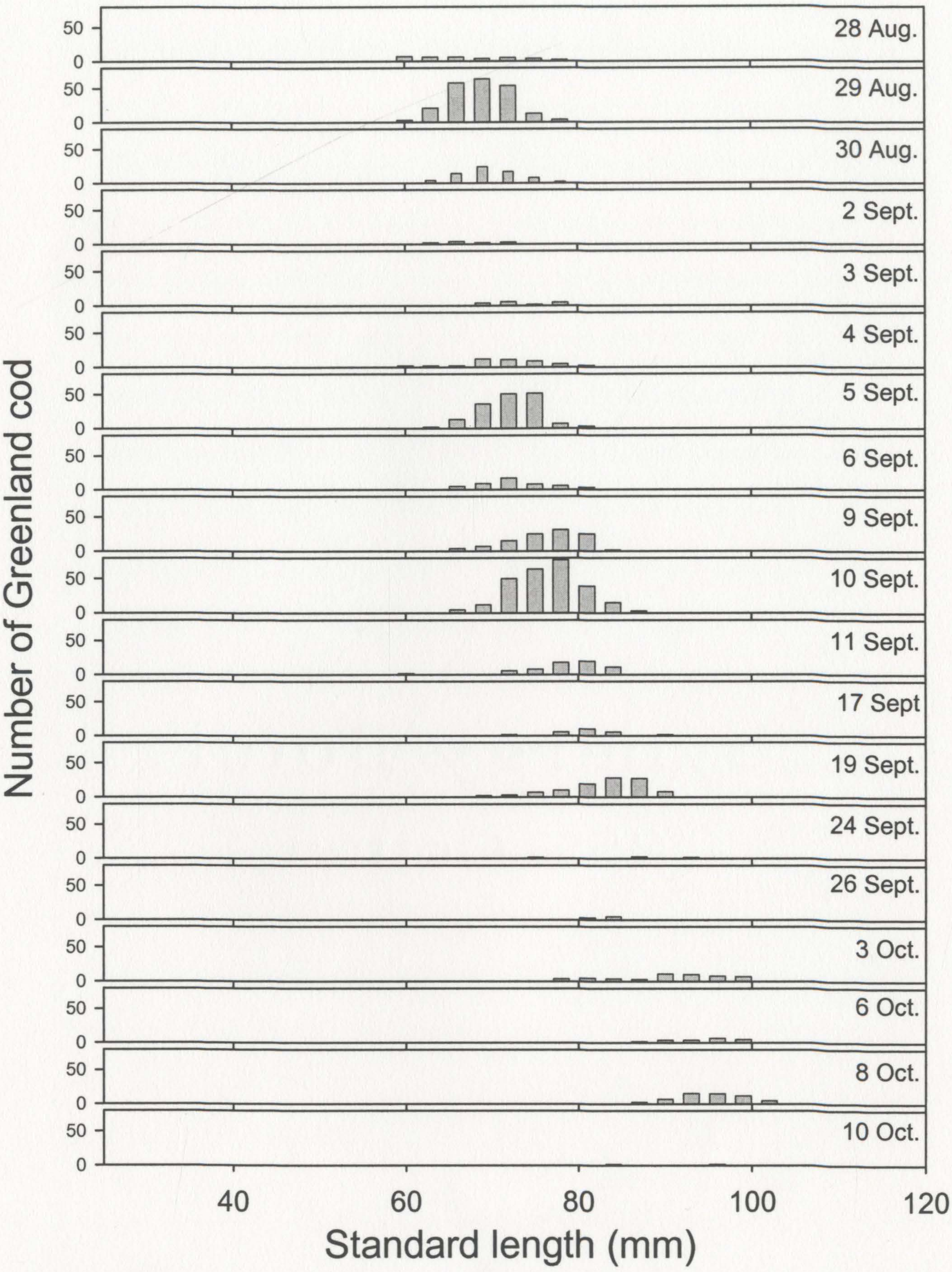


Figure 3.4 continued.

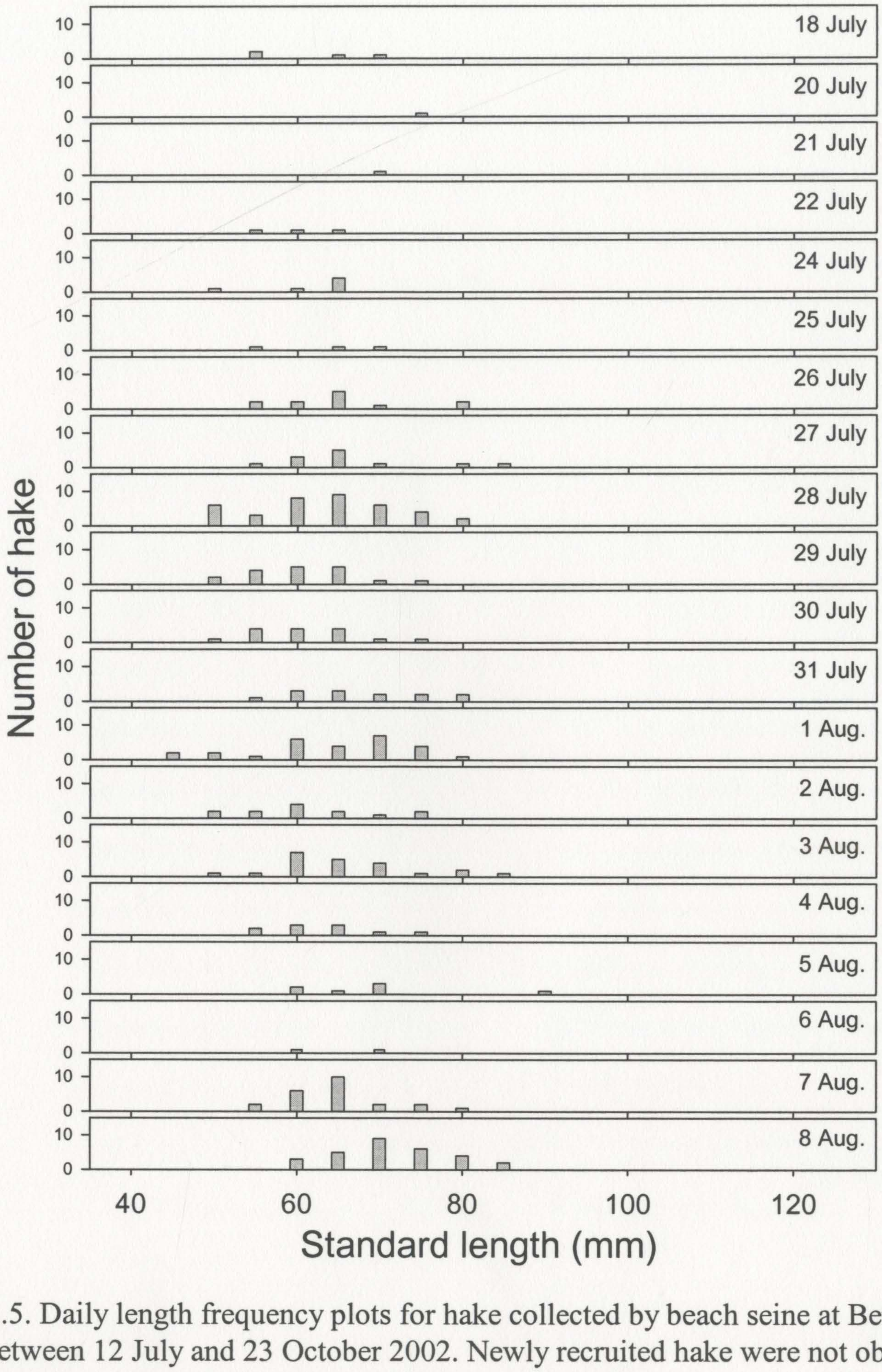


Figure 3.5. Daily length frequency plots for hake collected by beach seine at Bermuda Beach between 12 July and 23 October 2002. Newly recruited hake were not observed before 18 July so data between12-17 July were not presented.

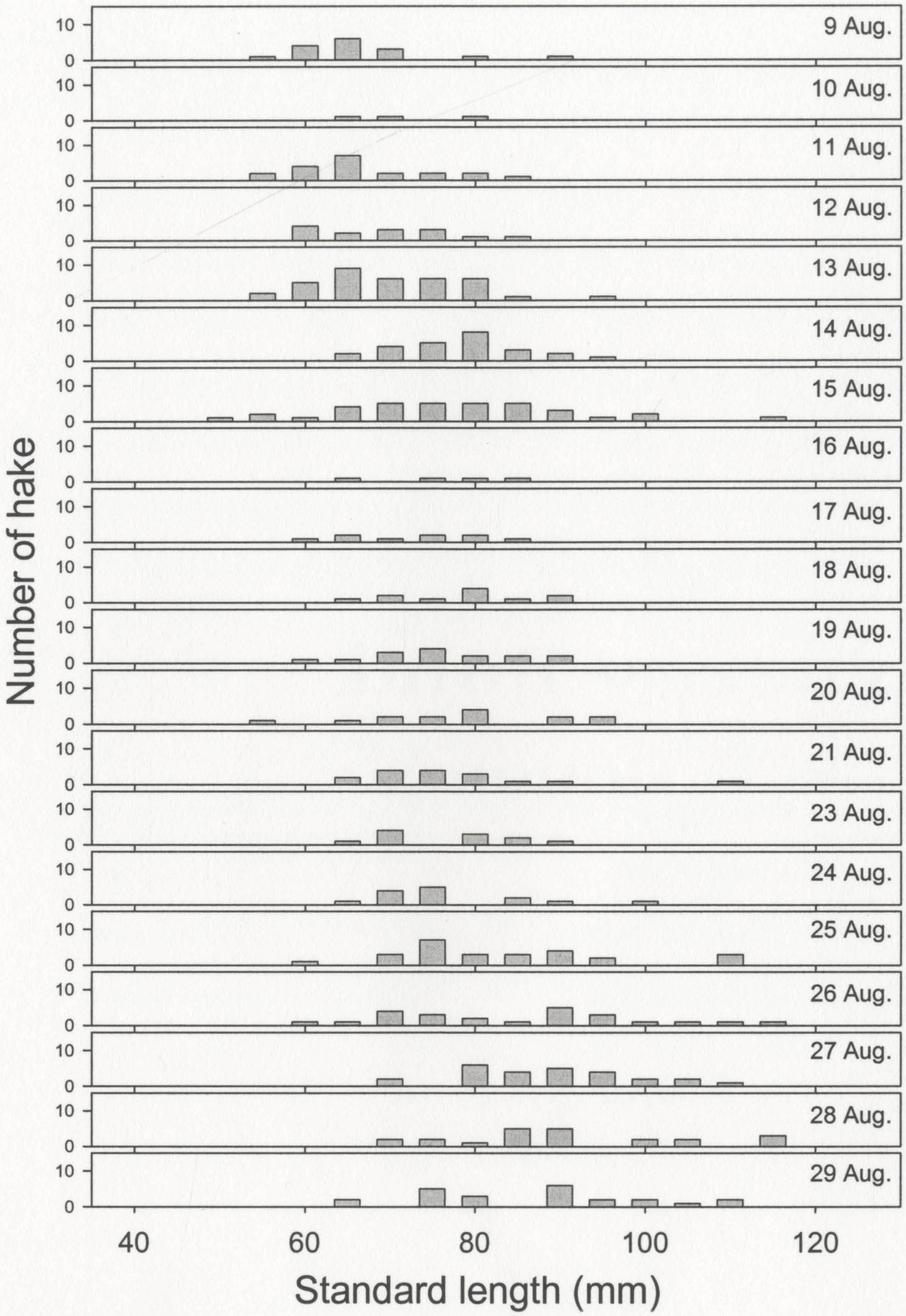


Figure 3.5 continued.

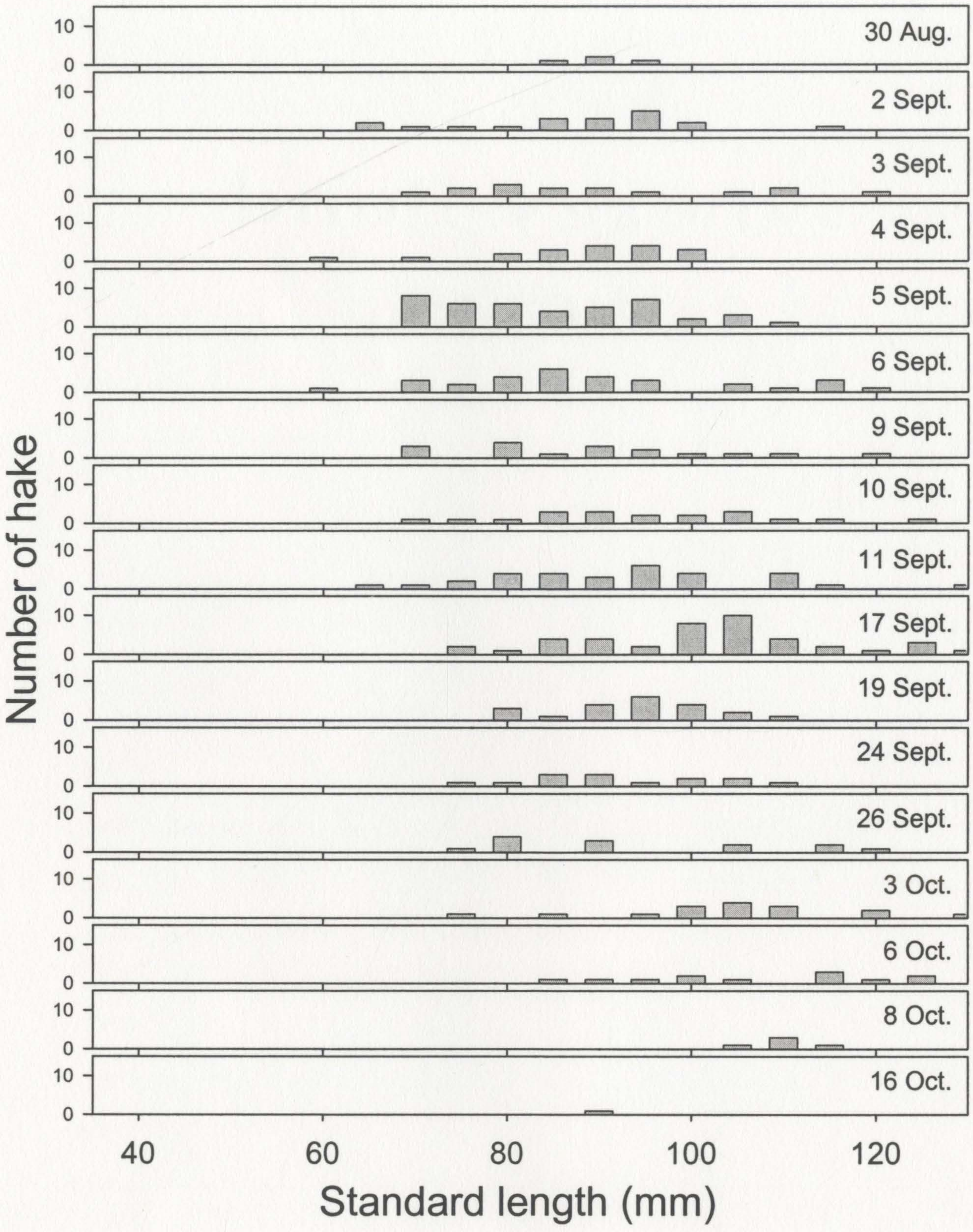


Figure 3.5. continued.

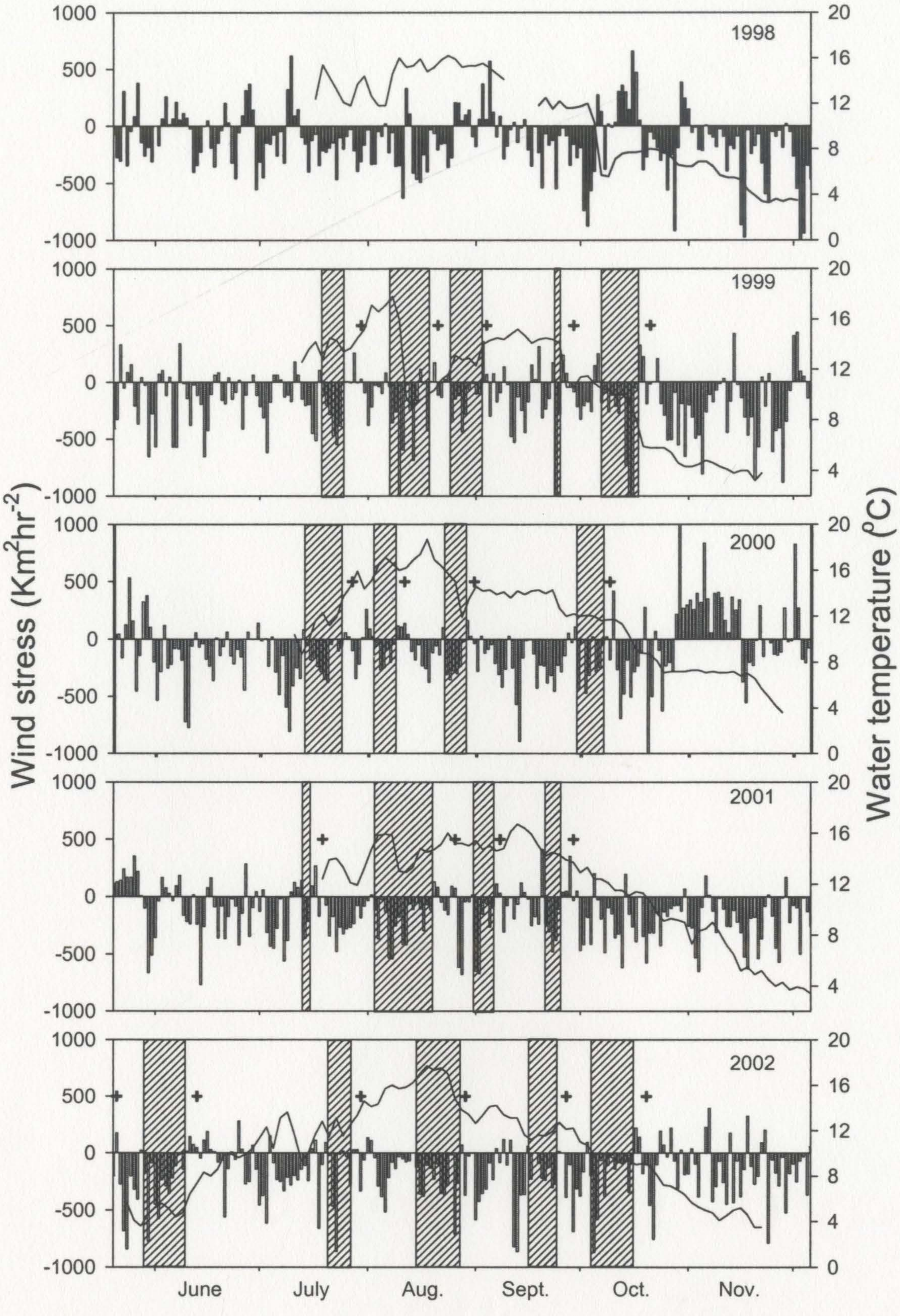


Figure 3.6. Estimated dates recruitment of Atlantic cod began at Newman Sound during July to November, 1999 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling favourable winds prior to arrival of Atlantic cod. + indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress.

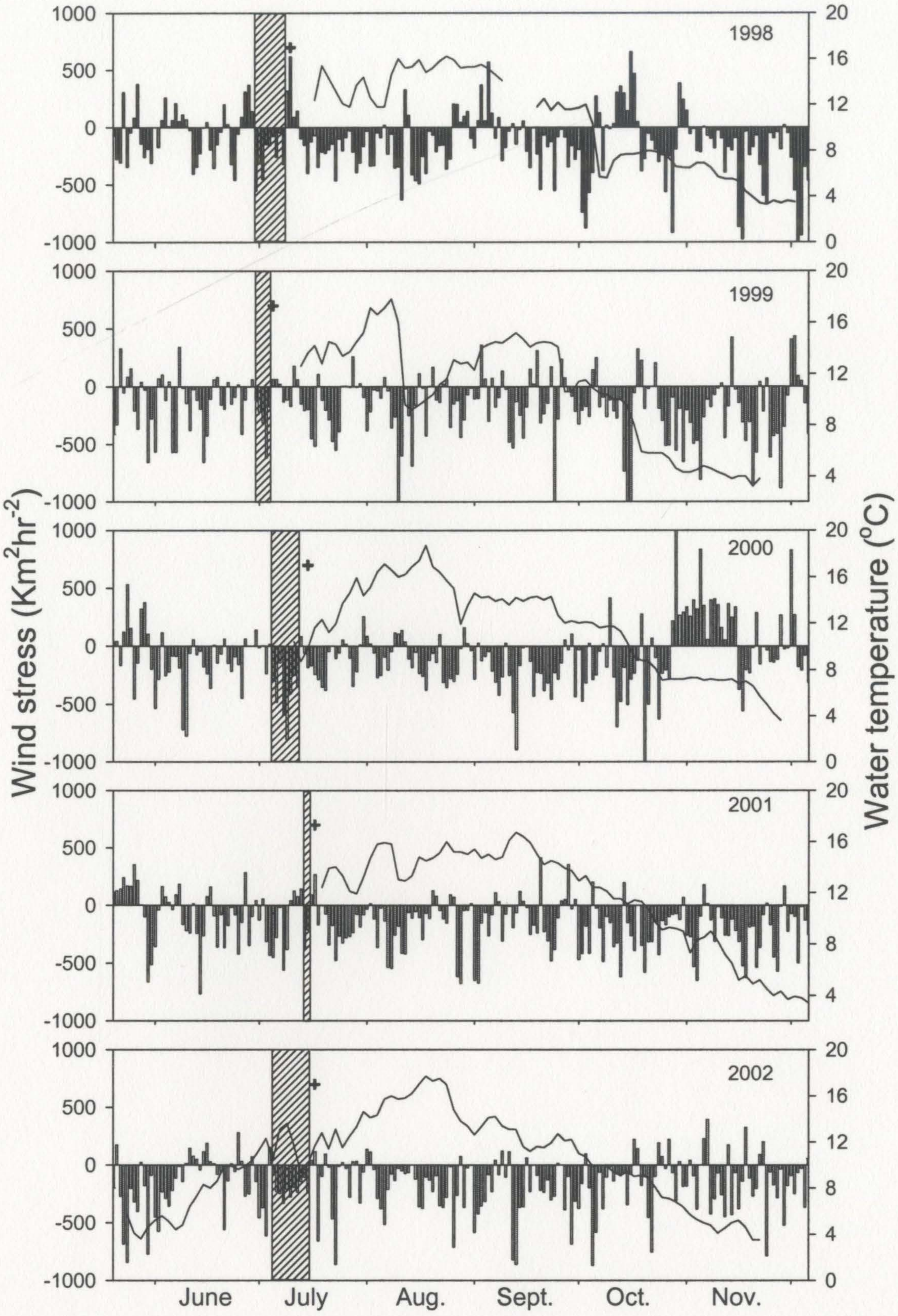


Figure 3.7. Estimated dates recruitment of Greenland cod began at Newman Sound during July to November, 1999 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling favourable winds prior to arrival of Greenland cod. + indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress.

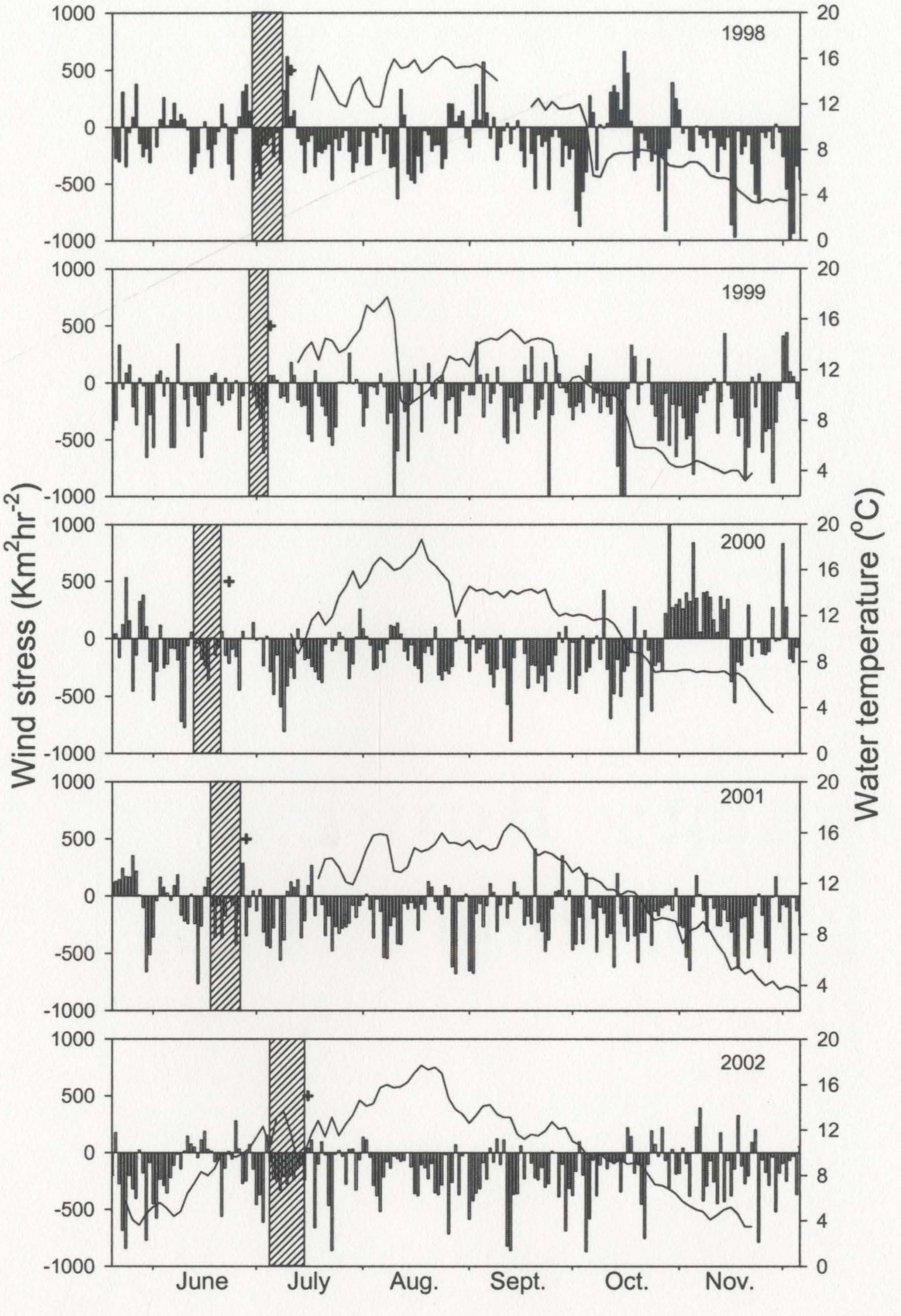


Figure 3.8. Estimated dates recruitment of hake began at Newman Sound during July to November, 1998 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling favourable winds prior to arrival of hake.+ indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress.

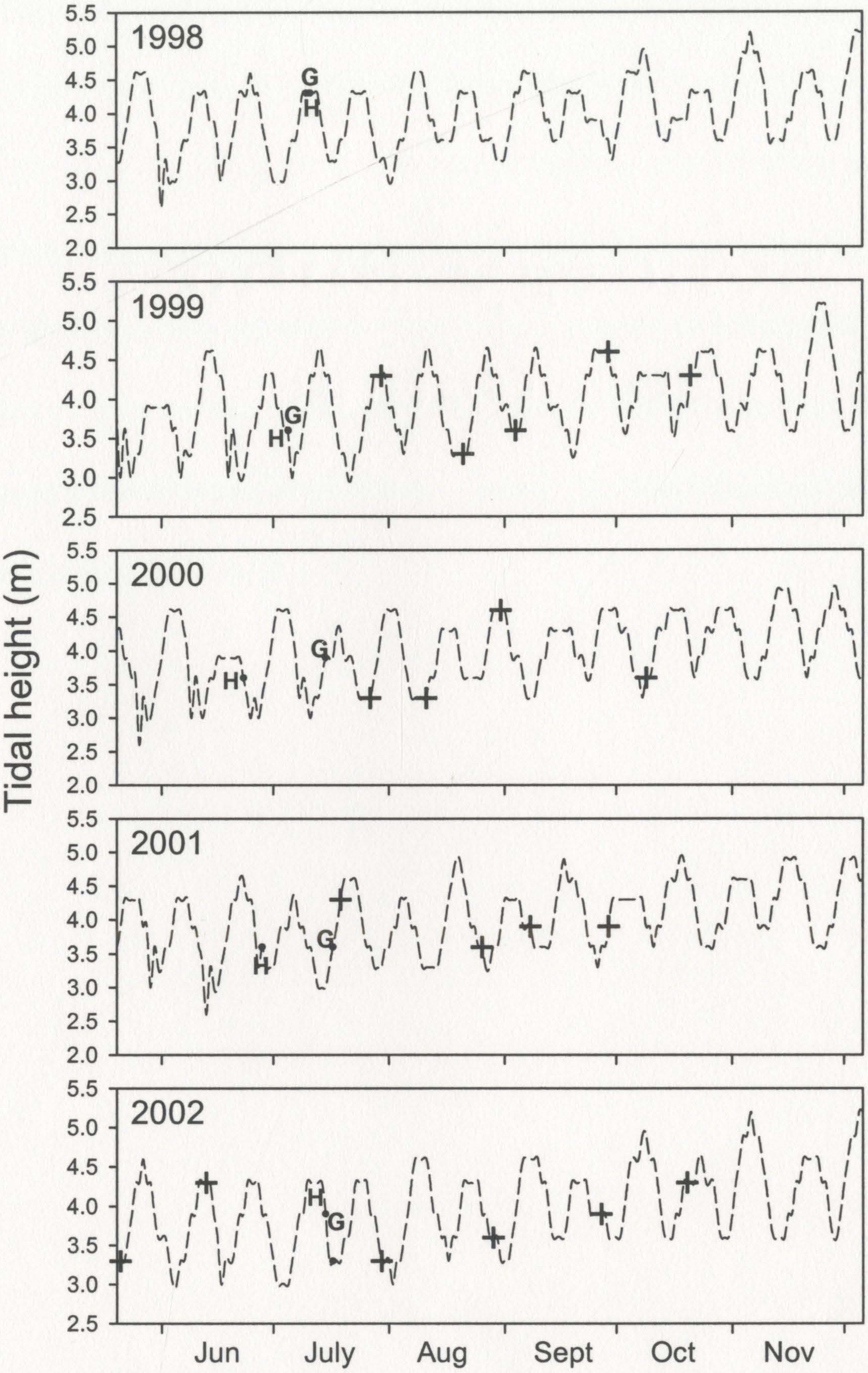


Figure 3.9. Estimated dates recruitment of Atlantic cod, Greenland cod and hake began at Newman Sound during July to November, 1998 to 2001 and May to November 2002 plotted with daily tidal heights. G indicates Greenland cod arrival, H indicates hake arrival and + indicates Atlantic cod arrival.

Connecting text

As described in chapter 3, the timing of recruitment of Atlantic cod to benthic habitats near shore was associated with onshore winds following upwelling. Level of recruitment refers to the number of individuals that enter a defined stage such as the free drifting egg stage, pelagic larval stage, benthic juvenile stage or adult stage. I have defined recruitment as the period at the end of the larval phase when mortality drops substantially and juveniles are considered to have recruited into the population. In Chapter 4, I investigate influences on the number of Atlantic cod recruiting to benthic habitats in the nearshore at a seasonal scale.

Chapter 4. Seasonal recruitment of Atlantic cod to coastal Newfoundland sites varies seasonally with prey requirements of newly-recruited fish and prey availability.

4.1. Abstract

Recent evidence suggests that year-class strength of some marine fish can be modified during the juvenile stages. Survival during the juvenile stages is thought to be influenced mostly by predation which is generally higher on smaller size classes. Hence, recruitment success may be positively related to growth rates of juvenile fish. I investigated whether Atlantic cod recruit to sites on the coast of Newfoundland during periods when post-recruitment fish grow quickly. I tested whether seasonal abundance of Atlantic cod newly recruited to nearshore sites was associated with water temperature and prey availability, factors known to influence growth rate of fish. Abundance of Atlantic cod recruiting to Newman Sound during July to November of 2000-2001 and May to November of 2002 was monitored at 12 sites every two weeks with seines. Instantaneous growth rates of post-recruitment Atlantic cod were calculated from modal lengths of fish sampled from 14 recruitment pulses observed in the seine data. Water temperatures were recorded on the bottom at a sample site in Newman Sound during 2000-2002. The seasonal abundance of zooplankton in Newman Sound was monitored by pump sampling near the surface during June to August of 2001 and September to November of 2002. This was compared to data from Logy Bay during 1979 and station 27 (off St. John's) during 2000-2002. I found that in Logy Bay (1979) and Newman Sound (2001-2002)

zooplankton abundance was relatively low from April to July and high during August to November, similar to the pattern previously reported at station 27 during 2000-2002. Generally, there was a positive association between abundance of newly-recruited Atlantic cod nearshore and prey availability during 2000 to 2002. Also, there was a positive association between abundance of newly-recruited Atlantic cod and growth rate of post-recruited fish during autumn; growth rates peaked in October each year during 2000-2002. Taken together, data on zooplankton abundance, Atlantic cod abundance and water temperature suggest that both prey availability and water temperature influence growth rates of post-recruitment Atlantic cod and hence recruitment to the nearshore.

4.2. Introduction

Survival during the first year of life is thought to determine the number of marine fish recruiting to adult populations (Hjort, 1914). Critical periods within this first year have been debated for some time. Hjort (1914) postulated that level of recruitment is determined by prey availability to larvae during the period following initiation of exogenous feeding. The "match / mismatch" hypothesis (Cushing 1969, 1982, 1990) extended the critical period concept to a longer period by relating year-class success to prey availability during the period up to metamorphosis. Subsequent studies have found that recruitment level can be modified substantially during the period between the larval stage and the age 1 juvenile stage (Peterman *et al.*, 1988; Fromentin *et al.*, 2001). Predation is thought to be the most important factor contributing to mortality of both larvae and juvenile fish (Cushing and Harris, 1973; Sheppard and Cushing, 1980; Sissenwine, 1984). Mortality of pre-recruited fish due to predation may be related to prey availability through three nonexclusive mechanisms (Hare and Cowan, 1997): 1) larger prey (Leggett and DeBlois, 1994) 2) faster growing prey (Shepard and Cushing, 1980; Campana, 1996; Nordeide *et al.*, 1994) and 3) faster developing prey (Houde, 1989) have higher survival rates relative to other prey.

The match / mismatch hypothesis has influenced much research on recruitment variability during the past few decades but it may not apply to Atlantic cod in waters around Newfoundland (Brander, 1994). The "match / mismatch" hypothesis has two components; (1) spawning time varies little between years, occuring at the mean timing of peak zooplankton abundance and (2) temporal overlap between abundance of first feeding larvae and the peak abundance of their prey determines year-class success. Brander (1994) concluded the "match / mismatch" hypothesis may not apply to Atlantic cod on the Northeast Newfoundland Shelf because spawning occurs over an extended period. Also, spawning times of Atlantic cod vary spatially; depending on location offshore peak spawning occurs between April and June (Hutchings and Myers, 1994; Myers *et al.*, 1994). Atlantic cod are known to spawn later inshore than offshore (Templeman, 1989). Cod in spawning condition have been collected inshore as early as April (Brattey, 1997) and as late as September (Thompson, 1943). Arrival of juvenile cod at sites on the northeast coast of Newfoundland from summer through autumn (Pinsent and Methven, 1997; Grant and Brown, 1998; Chapter 3) is further evidence that spawning time is not related to an annual peak in zooplankton production. Also, Grant and Brown (1998) showed that zooplankton are not limiting nearshore as small fish continued to grow throughout late summer and autumn. Prey availability to larvae may not determine recruitment of Atlantic cod off Newfoundland.

Year-class success of Atlantic cod may be set during the early juvenile stages rather than during the larval stage. Recruitment of Atlantic cod on Georges Bank was influenced more by changes in survival of post-larval fish than by variation in larval survival (Perry and Neilson,1988). Year-class strength of Atlantic cod was modified during the demersal juvenile (age 0) stage in populations of post-settlement Atlantic cod on the coast of Norway at sites that were monitored for 44 to 73 years (Fromentin *et al.*, 2001). Also at these sites, Buehler (2001) observed year-class strength of Atlantic cod was correlated with survival during the first few months post-settlement. The period immediatedly following settlement may be critical for survival of Atlantic cod (Tupper and Boutilier, 1995; Gotceitas *et al.* 1997) and other fish species (Sale and Ferrell, 1988) .

Predation is thought to be the most important factor influencing survival of Atlantic cod post-settlement (Sissenwine, 1984; Houde, 1989). High rates of predation on juvenile fish have been observed in a number of species including Atlantic cod (Tupper and Boutilier, 1995; Borg *et al.*, 1997, Steele and Forrester, 2002). Most of the production of post-larval fish on Georges Bank is consumed by larger fish (Sissenwine, 1984). In marine fish, mortality from predation can be density-dependent (Anderson and Gregory, 2000; Anderson, 2001). Density-dependent mortality occurs in populations of Atlantic cod (Myers and Cadigan, 1993; Fromentin *et al.*, 2001).

Survival of fish during juvenile stages that are vulnerable to predation is influenced indirectly by growth rates during those stages (Houde, 1989). Year-class success of Atlantic cod off Nova Scotia was found to be positively related to growth rates of pelagic juveniles (Campana, 1996). Ottersen and Loeng (2000) found that recruitment of Atlantic cod (and haddock, *Melanogrammus aeglefinus*, and herring, *Clupea harengus*) at age three in the Barents Sea was correlated with length at the post-larval and demersal stages of 0 group fish. Tupper and Boutilier (1995) observed growth rate of post-settlement Atlantic cod was important for survival, as was shelter from predation. Analysis of data on recruitment of Atlantic cod off Norway by Nordeide *et al.*, (1994) showed that the strongest year-class (1987) during 1985 to 1990 had the fastest growth rate during three to five months after settlement to demersal habitats.

Growth rate of juvenile Atlantic cod is influenced by prey availability over a number of temporal scales. Growth of post-larval Atlantic cod (from otolith measurements) over a period of days was positively related to abundance of zooplankton in nearby waters (Suthers *et al.*, 1989). Low prey abundance, in addition to low water temperatures, may contribute to slow growth rates of Atlantic cod during winter (Hawkins *et al.*, 1985). Survival of Atlantic cod during the post-settlement period has been found to be positively related to prey availability (Buehler, 2001). Prey availability was found to determine size distributions of populations of demersal Atlantic cod along the coast of Norway; distributions were more highly skewed toward larger sizes (indicating competition) at sheltered sites where presumably prey abundance was relatively low (Lekve *et al.*, 2002).

Laboratory studies show a parabolic relationship between growth rate of juvenile Atlantic cod and water temperature. Tat'yankin (1974) found that juvenile Atlantic cod from the Barents Sea prefer water temperatures of 9.5 ºC during summer. Peck *et al.* (2003) monitored growth rates of age 0 Atlantic cod at 5, 8, 12 and 15 ºC; they found highest growth rates at 12 ºC. Brown *et al.* (1989) observed that growth rates of age 0 Atlantic cod from Newfoundland decreased with water temperature in the range 8.3-0.6 ºC. Soofiani and Hawkins (1982) estimated the energy costs associated with feeding by juvenile Atlantic cod collected off Scotland was lowest in tanks at 10 ºC and greater in 7, 15, and 18 °C treatments. These findings show a temperature optimum for growth of juvenile Atlantic cod around 9.0-11.0 °C.

Atlantic cod recruit to demersal habitats during autumn when post-recruitment fish experience high growth rates. Along the northeast coast of Newfoundland, juvenile Atlantic cod recruit to shallow water sites in multiple pulses during summer and autumn (Methven and Bajdik, 1994; Grant and Brown, 1998; Chapter 3). Settlement to demersal habitats occurs when juvenile fish are 40 to100 mm standard length (Lomond *et al.* 1998; Hüssey *et al.* 2000). Juvenile Atlantic cod remain localized for at least several weeks post-settlement (Tupper and Boutilier, 1995; Grant and Brown, 1998) but continue to consume pelagic prey (Lomond *et al.,* 1998; Grant and Brown, 1998). The most common species of zooplankton in the diet of juvenile Atlantic cod varies daily and seasonally (Grant and Brown, 1998). Indices of condition for recently-settled Atlantic cod were highest (early to mid-October) when abundance of these fish was also highest at a Trinity Bay site sampled by Grant and Brown (1999); however, recently-settled cod increased in length regardless of condition. The seasonal pattern of growth rates of newly-recruited Atlantic cod is not known.

I tested whether the seasonal abundance of Atlantic cod newly recruited to sites in Newman Sound, Bonavista Bay matched the seasonal pattern of zooplankton abundance at the same sites. I used seines to monitor density of newly recruited Atlantic cod at 12 sites from July to November of 2000-2001 and from May to November of 2002. I also investigated whether Atlantic cod recruited to the nearshore during periods of high growth of fish nearshore. I tested seasonal abundance of newly recruited Atlantic cod against growth rates of Atlantic cod sampled from recruitment pulses observed during 2000-2002. I determined instantaneous growth rate of Atlantic cod during the three week period immediately following their recruitment to demersal habitats. Growth rate of marine fish is influenced by water temperature and prey availability (Brett, 1979). Therefore, I tested whether growth rate of Atlantic cod was related to mean water temperature (parabolic relationship) and zooplankton abundance.

4.3 Methods

4.3.1. Newman Sound zooplankton sampling

To determine the seasonal abundance of zooplankton in Newman Sound, pump sampling was conducted at two sites, Dockside and Mistaken Cove (Fig. 4.1) during June-August of 2001 and September-November of 2002. Two samples were taken monthly at each site on one day or two consecutive days. For each 2 minute collection, 35.5 l of water was pumped from 0.5 m below the surface. A 220 micron filter collected organisms. Samples were preserved in 5% formalin. In the laboratory, samples were sorted and counted. Zooplankton were identified to the lowest taxonomic level possible but nauplii were grouped. The principal text used for identification was Gosner (1971). Data were reported as counts per litre filtered.

4.3.2. Logy Bay zooplankton sampling

The seasonal abundance of zooplankton in relatively open coastal areas was determined by analyzing data from Kendaris (1980) collected at Logy Bay in 1979 (Fig. 4.2). Six stations within the bay were visited once monthly between April and September (no sampling at two sites in May and August). Vertical tows were conducted using a 70 cm diameter net with a 210 micron mesh. This net was pulled from depths that varied between sites (constant within site); consequently different water masses were sampled depending on site. Data were reported as counts per meter of the water column sampled. For my analysis, sites were categorized as either inshore (relatively shallow with seasonal warm water layer only) or offshore (deeper with sampling seasonally through both the colder bottom layer and the warm surface layer). Specimens were preserved in 5 % formalin and seawater (Kendaris, 1980). Nauplii were not identified to species or stage (Kendaris, 1980).

4.3.3 Atlantic cod recruitment

The seasonal pattern of juvenile cod recruitment was determined by sampling 12 sites in Newman Sound (Fig. 4.1) using a 25 m seine. During the periods from July to November of 2000-2001 and late-May to late-November of 2002, sampling was conducted once every two weeks. The seine had 19 mm stretch mesh in the wings and belly and 9 mm stretch mesh in the codend. It swept an area of 880 m^2 (16 m alongshore, 55 m offshore). The seine sampled the bottom two metres of the water column. Further details are reported in Schneider *et al.* (1997).

4.3.4 Water temperature data

Water temperatures were monitored at a site in Buckleys Cove in Newman Sound (Fig. 4.1) by a Hugrun thermograph placed on the bottom at approximately 3 m depth. Water temperature were recorded every four hours (2000-2001) or hourly (2002). Mean daily water temperatures were used for presentation and analyses.

4.3.5. Analysis

Number of zooplankton per litre at each site in Newman Sound during 2001-2002 was plotted against month to determine the patterns of abundance seasonally. Similarly, total number of zooplankton per vertical meter at Logy Bay, 1979 (Kendaris, 1980) were plotted against month to determine seasonal patterns at inshore and offshore sites. Trends were determined by visually inspecting plots. Results were compared with DFO (2003) which summarizes monthly zooplankton abundance at station 27 (Fig. 4.1); station 27 is located 7 km off from St. Johns and is considered to represent oceanographic conditions on the Newfoundland Shelf.

Cod less than 101 mm were considered newly-recruited fish (Lomond *et al.* 1998). Number of newly-recruited cod per seine haul was plotted with month to determine seasonal patterns in abundance of recruiting cod.

Growth rates were estimated for Atlantic cod sampled from14 recruitment pulses observed during 2000-2002 (Appendix 1). These pulses were identified visually from the modal lengths of fish in plots of length frequencies (3 mm bins) constructed for each sample day. Recruitment events were identified in length frequency plots by the appearance of small fish (approximating 39 mm) on one or two sample days. On subsequent days, a mode in each length frequency plot (when discernable) was assigned to this recruitment pulse based on tracking fish growth visually over time, as follows. Assignment of modes to pulses was first conducted forward, beginning with the recruitment event and continuing through all daily plots. Pulse identification was verified by tracking modes backward through time beginning with modes on the later days of sampling and working toward recruitment events (see Chapter 3).

Estimates of growth rates were calculated for approximately three week periods (15 to 28 days). I standardized data on growth rates to November 2002 data which permitted calculation of fish growth for only 19 days. The formula for instantaneous growth rate was:

$$G=(\ln (L_2 / L_1)) / \Delta t \qquad (1)$$

where, G= growth rate in percent day^{-1}

L_2=modal length at end of period (mm)

$L_{1=}$ modal length at beginning of period (mm)

Δt=change in time (days)

SAS (1988) was used for all analyses. The generalized linear model procedure

(GENMOD) of SAS was used to test for a parabolic relationship between growth rate of newly-recruited Atlantic cod and water temperature. The formula was:

$$G = ß_o + ß_T T + ß_{T2} T^2 + \varepsilon \qquad (2)$$

where, T=mean water temperature during three weeks post-recruitment (°C)

ε=error term

4.4. Results

4.4.1. Atlantic cod abundance during 2000-2002

A total of 1501 newly-recruited cod (< 101 mm standard length) were collected in 120 seine hauls at 12 sites in Newman Sound during July to November of 2000. During July to November of 2001, 756 newly-recruited cod were collected in105 seine hauls at the same sites; 1905 newly-recruitment cod were collected in 137 seine hauls during May to November of 2002. Overall, monthly catch of newly-recruitment cod per haul ranged from 2.58 in August of 2002 to 35.00 in May of 2002 (Fig. 4.3). The general trend in catch of recruiting cod per month was that catches were high during May, relatively low during June to August, high in September-October and slightly lower in November. (Fig. 4.3).

4.4.2. Growth rates during 2000-2002

Instantaneous growth rates of newly-recruited Atlantic cod estimated from daily modal lengths of fish sampled from 14 recruitment pulses observed in data from Newman Sound during 2000-2002 ranged from 0.0036 (May 2002) to 0.018 % day^{-1} (Oct. 2001) (Fig. 4.4). Generally, growth rate increased from low values in August to a peak in October (Fig. 4.4).

4.4.3. Water temperatures at Newman sound during 2000-2002

4.4.3.1. Seasonal pattern

Mean daily water temperatures at Newman Sound ranged from 2.9 °C on 28 May of 2002 to 19.0 °C on 17 August 2000 (Fig. 4.4). The seasonal pattern was that water temperatures increased from low values in May to a peak in August then decreased through November of 2000-2002 (Fig. 4.4).

4.4.3.2. Water temperature and growth rate

Growth rate of newly-recruited Atlantic cod sampled from 14 recruitment pulses observed in data from Newman Sound during 2000-2002 was related to mean water temperature (Fig. 4.5) according to the parabolic relationship:

$$\ln G = -6.14 + 0.367 * T - 0.0184 * T^2 \qquad (4.1)$$

Where G= growth rate (% day^{-1}) and T = mean water temperature (°C) (see Appendix 3). The highest growth rates of fish occurred when mean water temperatures were approximately 10 °C (Fig. 4.5). At higher and lower mean water temperatures, growth rates of Atlantic cod were lower.

4.4.4. Seasonal abundance of zooplankton

4.4.4.1. Logy Bay sampling during 1979

Pseudocalanus minutus, *Oithonia nana* and nauplii were collected both inshore and offshore on all sample dates (Table 4.1). *Calanus finmarchicus* were represented in all inshore samples and in five of six offshore samples (Table 4.1). *Temora longicornus* were present offshore on all sample days; they were collected inshore on five of six days. *Euterpina* spp., *Hyperia* spp. and *Microsetella* spp. were rare, collected only inshore on one day. *P. minutus* were most abundant with an overall mean of 177.276 individuals m^{-1}.

The general pattern of zooplankton abundance with time at both inshore and offshore sites in Logy Bay during 1979 was that of relatively low abundance of zooplankton during April to late-June and high abundance during August and September (Fig 4.6).

4.4.4.2 Newman Sound sampling during 2001-2001

There were 19 taxa present in samples from Newman Sound (Table 4.2). Four taxa (*Microsetella spp.*, *O. nana*, *Acartia* spp. and *T. longicornis*) were present at both sites on all collection days (Table 4.2). Nauplii were present at Mistaken Cove on all sample days, but at Dockside on only four of six days (Table 4.2). *Acartia* spp. were most abundant with an overall mean of 2.246 individuals l^{-1}. *Calanus* spp., *Centropages* spp.

and Cnidarians were rare, collected only at one site on one day (Table 4.2).

The general pattern of zooplankton abundance with time suggested by data from Dockside and Mistaken Cove in Newman Sound during 2001-2002 was that of relatively low abundance during June and July and high abundance during August through November (Fig. 4.7).

4.5. Discussion

Seasonal abundance of newly-recruited Atlantic cod near shore is similar to the pattern of monthly zooplankton abundance at near shore and offshore locations on the northeast Newfoundland Shelf. Data from sampling sites in Logy Bay (1979) and Newman Sound (2001-2002) showed that abundance of zooplankton was relatively low during April to July and comparatively high during August to November. This pattern is similar to the seasonal pattern of abundance of a dominant zooplankton species (*T. longicornis*) at station 27 (Fig.5 in DFO (2003)); abundance of *T. longicornis* increased from low values in spring to consistently high values from August to November of 2000-2002. The same pattern was observed for total zooplankton abundance (DFO, 2003). These findings suggest that on the northeast Newfoundland Shelf, the seasonal pattern of zooplankton abundance is similar both offshore and near shore. Densities of newly-recruited Atlantic cod in Newman Sound were relatively high in May (2002), low during June to August, high during September and October and slightly lower during November of 2000 to 2002. Therefore, from June to November of 2000-2002, seasonal abundance of newly-recruited Atlantic cod in Newman Sound was similar to zooplankton abundance both near shore and offshore. During September and October of 2001, abundance of Atlantic cod in Newman Sound was low compared to the same months of 2000 and 2002. During September and October of 2001, zooplankton abundance at station 27 was also relatively low compared to 2000 and 2002 (DFO, 2002). The abundance of newly-recruited Atlantic cod in Newfoundland coastal waters was positively associated with prey availability during summer and autumn.

The seasonal abundance of zooplankton on the Northeast Newfoundland Shelf and other shelf systems leaves little opportunity for recruitment variation according to the match-mismatch hypothesis (Cushing 1969, 1974, 1990). The central tenent of the match- mismatch hypothesis is that prey are available to larval fish only during a relatively short period annually. However, based on data from Newman Sound (2001-2002) and Logy Bay (1979), zooplankton abundance near shore is relatively high over an extended period from August through November. At station 27 during 2000 to 2002, the observed seasonal pattern was that zooplankton abundance increased from low values in spring to relatively high values in autumn (DFO, 2003). This pattern is due to the annual production of three to four non-synchronous generations of the dominant zooplankton species (Davis, 1982). Therefore, the primary prey of larval fish, copepod nauplii, are abundant during extended periods annually (April-June and August-November, this study). Similar results were found elsewhere. In the Bay of Fundy, abundance of the dominant zooplankton species was also found to increase from low values in spring to high values in summer and autumn (Corey, 1988). Similarly, zooplankton abundance is high through autumn but low during spring in fjords on the coast of Norway (Salvanes *et al.*, 1995). Zooplankton biomass in the upper waters of the Bering Sea is relatively high from May through November (Rudjakov *et al.*, 1995). The seasonal pattern of zooplankton abundance observed on the northeast Newfoundland Shelf is similar to that of other coastal systems. These patterns of extended periods of zooplankton abundance suggest that the match-mismatch hypothesis (Cushing 1969, 1974, 1990) does not apply near shore.

Extended recruitment of Atlantic cod to benthic habitats on the northeast coast of Newfoundland is influenced by spawning time and duration. Some of the Atlantic cod recruiting to the nearshore are spawned on offshore banks while others originate near shore (Beacham *et al.* 2000). At offshore areas on the Northeast Newfoundland Shelf, Atlantic cod spawning occurs primarily between April and June (Myers *et al.*,1993; Hutchings and Myers, 1994). Spawning also occurs over many months inshore. Data from inshore areas suggest that spawning occurs primarily between April and July but extends into August and September (Thompson, 1943; Brattey, 1997; Pinsent and Methven, 1997; Smedbol and Wroblewski, 1997). This prolonged spawning by Atlantic cod results in the production of juvenile fish during summer and autumn (Pinsent and Methven, 1997) when they are transported to the coast episodically during periods of downwelling (Chapter 3).

Newly-recruited Atlantic cod were abundant at sites in Newman Sound during autumn of 2000 to 2002 when newly-recruited fish experienced high growth rates. In my three year study, I observed the abundance of newly-recruited Atlantic cod at Newman Sound was generally highest during September-October. This was consistent with findings by Grant and Brown (1998) in Trinity Bay. The seasonal pattern of growth rate of newly-recruited Atlantic cod sampled during 2000 to 2002 was that growth rate was low in August and increased to a peak in October, similar to the pattern of monthly fish abundance. However, abundance of newly-recruited Atlantic cod did not match growth rate of newly-recruited fish during May and June of 2002. This may be explained by the influence of water temperature on the food requirements of individual fish as discussed below. Annual recruitment of Atlantic cod is correlated with growth rate of fish during the three to five month (or longer) period after recruitment (Nordeide *et al.* 1994; Ottersen and Loeng, 2000). From an evolutionary point of view, fast growth during the period immediately following recruitment to demersal habitats is more important than growth rates during later periods if predation is high on small compared to large juvenile Atlantic cod, which is well known for other fish species (Miller *et al.* 1988; Sogard, 1997). Shelter from predation is critical for survival of Atlantic cod during the period post-recruitment to demersal habitats (Tupper and Boutilier, 1995). Newly-recruited Atlantic cod are abundant near shore seasonally when fish grow quickly.

Water temperature and prey availability are the most important factors influencing growth rates of fish (Brett, 1979). I found a parabolic relationship between growth rate of newly-recruited Atlantic cod and water temperature, consistent with laboratory studies

(Tat'yankin, 1974; Soofiani and Hawkins, 1982) which show that Atlantic cod grow optimally at water temperatures near 10 °C. These temperatures were observed twice annually (June of 2002 and October of 2000-2002). During the same period, growth rates of Atlantic cod were also highest. High growth rates of Atlantic cod coincided with high zooplankton abundance during October of 2000-2002 but not during June of 2002. However, the ratio of juvenile cod to their prey (zooplankton) may have been similar during these two periods. Density of newly-recruited Atlantic cod was low during June of 2002 and high during October (2000-2002), similar to the pattern in zooplankton abundance in data from Logy Bay during 1979, station 27 during 2000-2002 (DFO, 2003) and Newman Sound during 2001-2002. Growth rates of juvenile Atlantic cod are influenced by water temperature and prey availability.

Predation influences survival of newly-recruited Atlantic cod directly whereas growth rate of fish influences survival indirectly (Tupper and Boutilier, 1995). I suggest that high growth rate of newly-recruited Atlantic cod may be less important for survival during periods when risk of predation is relatively low. This may explain the comparatively high abundance of newly-recruited Atlantic cod that I observed during May of 2002 when fish grew slowly. There are at least four reasons why predation risk to juvenile Atlantic cod may be reduced during May. First, low water temperatures can result in slow growth rates of predatory fish; hence, predators near shore may require relatively few prey during May. Elliot and Leggett (1997) observed that temperature influenced the size-selective predation of piscovorous fish. Second, some species of fish are seasonally absent or inactive during May; therefore, juvenile Atlantic cod are at a low risk of predation from these species during May. Methven *et al.* (2001) found seasonal patterns of use by fish species at a nearshore site in Trinity Bay; the number of species and number of fish collected at the site was correlated with water temperature. Third, there may be less competition for shelter from predation during periods when use of nearshore sites by fish is relatively low. Fourth, slow growth by juvenile Atlantic cod during May suggests that they require relatively little prey at that time; therefore, juvenile cod may exhibit less risk-taking behaviour while feeding during May than while feeding during summer and autumn. Increased survival from relaxation of predation pressure may explain the occurrence of juvenile Atlantic cod nearshore during spring when growth rates of newly-recruited fish are low.

At sites away from the coast, zooplankton abundance is not consistently high during autumn. Davis (1982) sampled open water stations in Conception Bay and observed zooplankton abundance was highest from May to July of 1978 but variable during August-September of 1978 and 1979. Mertz and Myers (1994) plotted Continuous Plankton Recorder data (offshore sampling) from Robinson *et al.* (1975) showing that *Calanus* abundance is consistently high during May-June in NAFO Region 3, often low during August and variable during September to December. Myers *et al.* (1994) found that seasonal trends in zooplankton abundance in the Continuous Plankton Recorder data for the period 1959-1992 were variable between years.

In conclusion, seasonal recruitment of Atlantic cod to the nearshore varies with conditions that influence survival of newly-recruited Atlantic cod near shore. Between June and November of 2000-2002, the pattern of monthly abundance of newly-recruited Atlantic cod observed at sites in Newman Sound was similar to the monthly abundance of zooplankton in data from Logy Bay (1979), station 27 and Newman Sound (2001-2002). Together, data from these three sources suggest that the seasonal trend in zooplankton abundance near shore is that of relatively low abundance during April to July and high abundance during August to November. Similarly, abundance of newly-recruited Atlantic cod in Newman Sound during 2000-2002 was generally low during June to August and high during September to November. During autumn of 2000-2002, growth rates of newly-recruited Atlantic cod were also highest, with peak values in October. The highest growth rates of age 0 Atlantic cod occurred during periods with mean water temperatures near 10 ºC. I found a parabolic relationship between growth rate of newly-recruited Atlantic cod and water temperature consistent with previous studies. Collectively, data from June to November suggest that water temperature and prey availability interact to influence growth rates of newly-recruited fish, and hence survival of Atlantic cod. High abundance of newly-recruited Atlantic cod during May when growth rates were low and prey abundance was low, together with previous findings on seasonal use of the nearshore by potential predators of juvenile cod, suggest that achieving a high growth rate may be less important for survival of young cod when predation risk is low. The seasonal level of recruitment of Atlantic cod to the nearshore may be determined by multiple factors influencing survival of newly-recruited fish.

4.6. Acknowledgements

Zooplankton data were collected during Department of Fisheries and Oceans sponsored projects by Robert Gregory, Robyn Jamieson and Ben Laurel. I would like to thank Jessica Anderson and Laura Fudge for sorting, counting and identifying zooplankton. I thank Janice Linehan for coordinating field activities. Thanks are also extended to all the field crew and volunteers; Erin Alcock, Louise Copeman, Katie Dalley, Ben Hammond, Brianna Hookey, Robyn Jamieson, Melissa Pink, Andrea Powell, Heather Reid, Mark Renkawitz, Lee Sheppard, David Sterling, Steve Sutton, Christine Vickers and Kimberly Young. Lee Sheppard is thanked for producing Fig 4.1.

4.7. Literature cited

Anderson, J,T., and R.S. Gregory, 2000. Factors regulating survival of northern cod (NAFO 2J3KL) during their first three years of life. ICES J. Mar. Sci 57: 349-359.

Anderson, T.W., 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecol 82: 245-257.

Beacham, T.D., R.S. Gregory and J. Brattey, 2000. Origins of two recruitment pulses of 0-group Atlantic cod (*Gadus morhua*) in Bonavista Bay, Newfoundland during 1999, determined from genetic variation. Can. Stock. Assessment Secretariat Res. Doc. 2000/093.

Beuhler, V., 2001. Mechanisms that regulate selective mortality on larval and juvenile cod: fine tuning between growth and survival. ICES CM 2001/V04.

Brander, K., 1994. Spawning and life history information for North Atlantic cod stocks. ICES Coop. Res. Rep. No. 205 150 p.

Brander, K., and P. Hurley, 1992. Distribution of early-stage cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus),* and witch flounder (*Glyptocephalus cynoglossus*) eggs on the Scotian Shelf: a reappraisal of evidence on the coupling of cod spawning and plankton production. Can J. Fish. Aquat. Sci. 49: 238-251.

Brattey, J. Biological characteristics of Atlantic cod (*Gadus morhua*) from three inshore areas of northeastern Newfoundland. NAFO Sci. Coun. Studies 29: 31-42.

Brett, J.R., 1979. Environmental factors and growth. In: Fish Physiology.Vol. 8. Edited by WS Hoar, DJ Randall, and JR Brett. Academic Press. London UK. Pp 599-675.

Brown, J.A., P. Pepin, D.A. Methven and D.C. Somerton, 1989. The feeding, growth and behaviour of juvenile cod , *Gadus morhua* L., in cold environments. J. Fish. Biol. 35: 373-380.

Borg, A., L. Pihl and H. Wennhage, 1997. Habitat choice by juvenile Atlantic cod (*Gadus morhua* L.) on sandy bottoms with different vegetation types. Helg. Meers. 51: 197-212.

Campana, S.E., 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 135: 21-26.

Corey, S., 1987. Quantitative distributional patterns and aspects of the biology of the Mysidacea (Crustacea: Peracarida) in the zooplankton of the Bay of Fundy region. Can. J. Zool. 66: 1545-1552.

Cushing, D.H., 1969. The regularity of the spawning season of some fishes. J. du Conseil, Cons. Int. Explor. Mer. 33: 81-92.

Cushing, D.H., 1974. The natural regulation of fish populations. In: Sea fisheries research. FR Harden Jones (ed), pp. 399-412. Wiley, New York.

Cushing, D.H., 1982. Climate and fisheries. Academic Press, London. 373 p.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update on the match/mismatch hypothesis. Adv. Mar. Bio. 26: 249-293.

Cushing, D.H., and J.G.K. Harris, 1973. Stock and recruitment and the problem of density dependence. Rapp. P.-v. Reun. Cons. int. Explor Mer. 164: 142-155.

Davis, C.C., 1982. A preliminary quantative study of the zooplankton from Conception Bay, insular Newfoundland, Canada. Int. Revue ges. Hydrobiol. 67: 713-747.

DFO, 2003. 2002 State of the ocean: chemical and biological oceanographic conditions in the Newfoundland and Labrador region. DFO Can. Sci. Advis. Sec. Status Rep.: Eco. Over. 2003/001.

Elliot, J.K., and W.C. Leggett, 1997. Influence of temperature on size-dependent predation by a fish (*Gasterosteus aculeatus*) and jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). Can. J. Fish Aquat. Sci. 54: 2759-2766.

Fromentin, J-M., R.A. Myers, O.N. Bjørnstad, N.C. Stenseth, J. Gjøsæter and H Christie, 2001. Effects of density-dependent and stochastic processes on the regulation of cod populations Ecol. 82: 567-579.

Gosner, K.l., 1971. Guide to identification of marine and estuarine invertebrates Cape Hatteras to the Bay of Fundy. John Wiley & Sons, Inc. New York, 693 p.

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

Grant, S.M., and J.A. Brown, 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Can.

J. Fish. Aquat. Sci. 55: 1317-1327.

Grant, S.M., and J.A. Brown, 1999. Variation in coastal Newfoundland 0-group Atlantic cod (*Gadus morhua)*: field and laboratory studies using simple condition indices. Mar. Biol. 133: 611-620.

Hare, J.A., and R.K. Cowan, 1997. Size, growth, development and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78: 2415-2431.

Hawkins, A.D., N.M. Soofiani and G.W. Smith, 1985. Growth and feeding of juvenile cod (*Gadus morhua* L.). J. Cons. Int. Explor. Mer. 42: 11-32.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe. Rapports Proces-verbaux Reunion du Conseil International pour l'Exploration de la Mer 20: 1-228.

Houde, E.D., 1989. Subtleties and episodes in the early life of fishes. J. Fish Biol. 35 (Suppl. A): 29-38.

Hüssey, K., M.A. St. John and U. Böttcher, 1997. Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? Mar. Ecol. Prog. Ser. 155: 199-208.

Hutchings, J.A., and R.A. Myers, 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21-31.

Kendaris, T.A., 1980. Physical and biological oceanographic observations in Logy Bay, Newfoundland: April- September 1979. Can. Man. Rep. Fish. Aquat. Sci. 1569. 60p.

Leggett, W.C., and E. DeBlois, 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. 32: 119-134.

Lekve, K., G., Ottersen, N.C. Stenseth and J. Gjøsæter, 2002. Length dynamics in juvenile coastal Skagerrak cod: effects of biotic and abiotic processes. Ecol. 86: 1676-1688.

Lomond, T.M., D.C. Schneider and D.A. Methven, 1998. Transition from pelagic to benthic prey for age 0-1 Atlantic cod *Gadus morhua*. Fish Bull. 96: 908-911.

Mertz, G., and R.A. Myers, 1994. Match/mismatch predictions of spawning duration versus recruitment variability. Fish. Oceanogr. 3: 236-245.

Methven, D.A., and C. Bajdik, 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 51: 78-90.

Methven, D.A., R.L. Haedrich and G.L. Rose, 2001. The fish assemblage of a Newfoundland estuary: diel, monthly and annual variation. Estuar. Coast. Shelf Sci. 52: 669-687.

Miller, T.J., L.B. Crowder, J.A. Rice and E.A. Marchall, 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657-1670.

Myers, R.A., N.J. Barrowman, G. Mertz, J. Gamble and H.G. Hunt, 1994. Analysis of Continuous Plankton recorder Data in the northwest Atlantic 1959-1992. Can. Tech. Rep. Fish. Aquat. Sci. 1966. 16 p.

Myers, R.A., and N.G. Cadigan, 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50: 1576-1590.

Myers, R.A., G. Mertz and C.A. Bishop, 1993. Cod spawning in relation to physical and biological cycles of the northern North-West Atlantic. Fish. Oceanogr. 2: 154-165.

Nordeide, J.T. JH. Fosså, A.G.V. Salvanes and O.M. Smedstad, 1994. Testing if year-class strength of coastal cod, *Gadus morhua* L., can be determined at the juvenile stage. Aquac Fish Man. 25 (Suppl. 1): 101-116.

Otterson, G., and H. Loeng, 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. ICES J. Mar. Sci. 57: 339-348.

Peck, M.A., L.J. Buckley, E.M. Calderone and D.A. Bengtson, 2003. Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Mar. Ecol. Prog. Ser. 251: 233-243.

Perry, R.I., and J.D. Neilson, 1988. Vertical distributions and trophic interactions of age 0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Mar. Ecol. Prog. Ser. 49: 199-214.

Peterman, R.M., M.J. Bradford, N.C.H. Lo and R.D. Methot, 1988. Contribution of early life stages to interannual variability in recruitment of Northern Anchovy (*Engraulis mordax*). Can. J. Fish Aquat. Sci. 45: 8-16.

Pinsent, D.L., and D.A. Methven, 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 54 (Suppl.1): 19-24.

Robinson, G.A., J.M. Colebrook and G.A. Cooper, 1975. The continuous plankton recorder survey: plankton in the ICNAF area, 1961 to 1971, with special reference to 1971. ICNAF RES. DOC. 73/78. 19 p.

Rudjakov, J.A., V.B. Tseitlin and V.J. Kitain, 1995. Seasonal variations of mesoplankton biomass in the upper layer of the Bering Sea; understanding biomass oscillations in the ocean. ICES J. Mar. Sci. 52: 747-753.

Sale, P.F., and D.J. Farrell, 1988. Early survivorship of juvenile coral reef fishes. Coral Reefs 7: 117-124.

Salvanes, A.G.V., D. Aksnes, J.H. Fosså and J. Giske, 1995. Simulated carrying capacities of fish in Norwegian fjords. Fish. Oceanogr. 4: 17-32.

Schneider, D.C., and D.A. Methven, 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. J. Mar. Res. 46: 105-118.

Sheppard, J.G., and D.H Cushing, 1980. A mechanism for density dependent survival of larval fish as a basis for a stock-recruitment relationship. J. Cons. Int. Explor. Mer 39: 160-167.

Sissenwine, M.P., 1984. Why do fish populations vary? In: Exploitation of marine communities. RM May [ed] pp 59-94. Springer-Verlag, Berlin.

Smedbol, R.K., and J.S. Wroblewski, 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991-1993. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1):177-186.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129-1157.

Soofiani, N.M., and A.D. Hawkins, 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua* L. J. Fish Biol. 21: 577-592.

Steele, M.A., and G.E. Forrester, 2002. Early postsettlement predation on three reef species: effects on spatial patterns of recruitment. Ecol 83: 1076-1091.

Suthers, I.M., K.T. Frank and S.E. Campana, 1989. Spatial comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 113-124.

Tat'yankin, Y.V., 1974. The distribution of juvenile cod (*Gadus morhua morhua* (L.)), pollock (*Pollachius virens* (L.)) and haddock (*Melanogrammus aeglefinus* (L.)) under temperature gradient conditions. J. Ichthyol. (Engl. Trans) 114: 1002-1009.

Templeman, W., 1989. Variation of vertebral numbers with fish length in Atlantic cod (*Gadus morhua*) of the eastern Newfoundland area, 1947-71. J. Northw. Atl. Fish. Sci. 9: 45-52.

Thompson, H.,1943. A biological and economic study of cod (*Gadus callarias*, L.) in the Newfoundland area. NFLD. Dep. Nat. Resour. Res. Bull. No. 14.

Tupper, M., and R.G. Boutilier, 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Mar. Ecol. Prog. Ser. 118: 295-300.

Walsh, W.J., 1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Envir. Biol. Fish. 18: 257-276.

Table 4.1. Presence and range in mean number of zooplankton at six sites in Logy Bay during April-September 1979 (Kendaris, 1980). Presence is the number of collections, out of a total of six, that contain a particular species.

Species / group	Inshore		Offshore	
	range (# m^{-1})	presence	range (# m^{-1})	presence
Acartia clausi	0-23.7	4	0-8.25	2
Acartia discaudata	0-7.09	2	0	0
Calanus finmarchicus	1.10-32.8	6	0-61.7	5
Calanus hamatus	0-35.4	3	4.78-18.7	6
Centropage typicus	0-42.0	4	0-14.3	5
nauplii	28.6-482	6	22.0-208	6
Euterpina spp.	0-1.10	1	0	0
Fritillaria borealis	0-37.3	5	1-21.5	4
Hyperia spp.	0-2.36	1	0	0
Isias clavipes	0-23.7	2	0-6.59	2
Metridia lucens	0-6.07	3	0-7.88	5
Microsetella spp.	0-0.360	1	0	0
Oithona nana	20.9-426	6	19.8-337	6
Parathemisto spp.	0-1.10	2	0	0
Podocryne spp.	0-5.39	1	0-6.59	3
Podon spp.	0-6	1	0-6.59	1
Pseudocalanus minutus	9.90-828	6	10.1-230	6
Rathkea octopunctata	0-1.71	1	0-6.59	1
Sagitta spp.	0-10.8	4	0-4.39	5
Temora longicornus	0-781	5	0.530-230	6

Table 4.2. Presence and range in number of zooplankton in pump samples taken near the surface at two sites in Newman Sound during June-August 2001 and September-October 2002. Presence is the number of collections, out of a total of six, that contain a particular species.

Species / group	Dockside		Mistaken Cove	
	range (l^{-1})	presence	range (l^{-1})	presence
Calanus spp.	0	0	0-0.0141	1
Centropage spp.	0-0.0282	1	0	0
Cnidaria spp.	0-0.0282	1	0	0
Fritillaria borealis	0-0.0986	3	0-0.1408	5
harpacticoids	0-0.0704	3	0-0.0423	4
Microsetella spp.	0.620-3.25	6	0.0986-1.94	6
nauplii	0-0.632	4	0.0141-0.211	6
Oithonia dioica	0-0.239	2	0-0.169	1
Oithonia nana	0.169-3.42	6	0.0282-1.77	6
Onceaca spp.	0-0.0845	4	0-0.0423	1
Pseudocalanus minutus	0	0	0-0.0423	5
Tisbe spp.	0-0.916	4	0-0.0141	1
trochopores	0-0.0845	2	0-0.113	3
Acartia spp.	0.197-9.24	6	0.439-1.37	6
Temora longicornis	0.0282-8.18	6	0.0141-0.380	6
Evadne spp.	0-0.254	5	0-0.0563	5
Podon spp.	0-0.0845	4	0-0.0563	1
bivalves	0-1.37	5	0-3.817	5
gastropods	0-0.127	4	0-0.0704	5

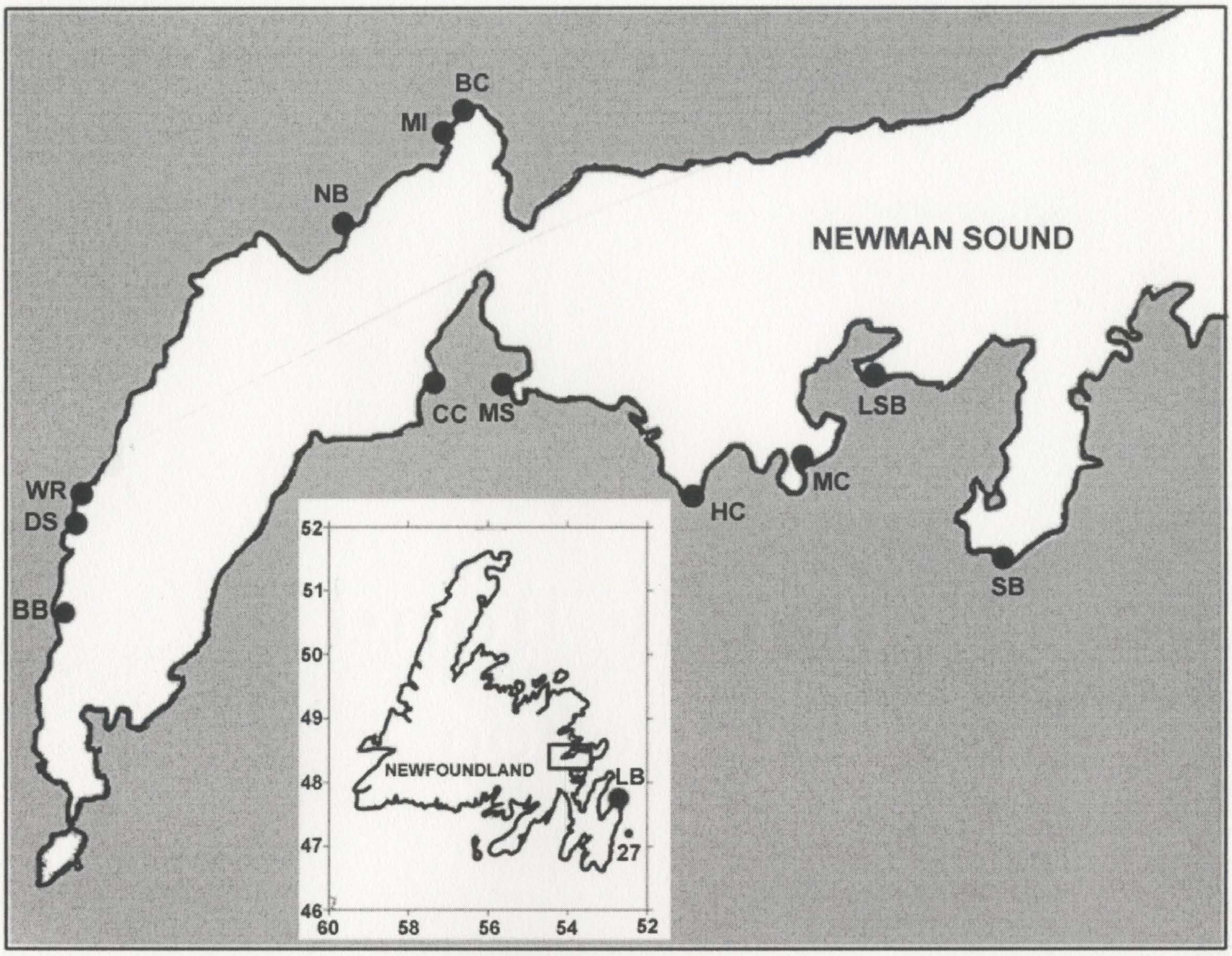


Figure 4.1. Map of Newman Sound showing the locations of 12 sites sampled for newly recruited Atlantic cod during May to November 2002. Zooplankton samples were collected at Dockside (DS) and Mistaken Cove (MI) during June - August 2001 and September-November of 2002. Zooplankton samples were also collected at Logy Bay (LB) by Kendaris (1980). Station 27 is indicated by 27.

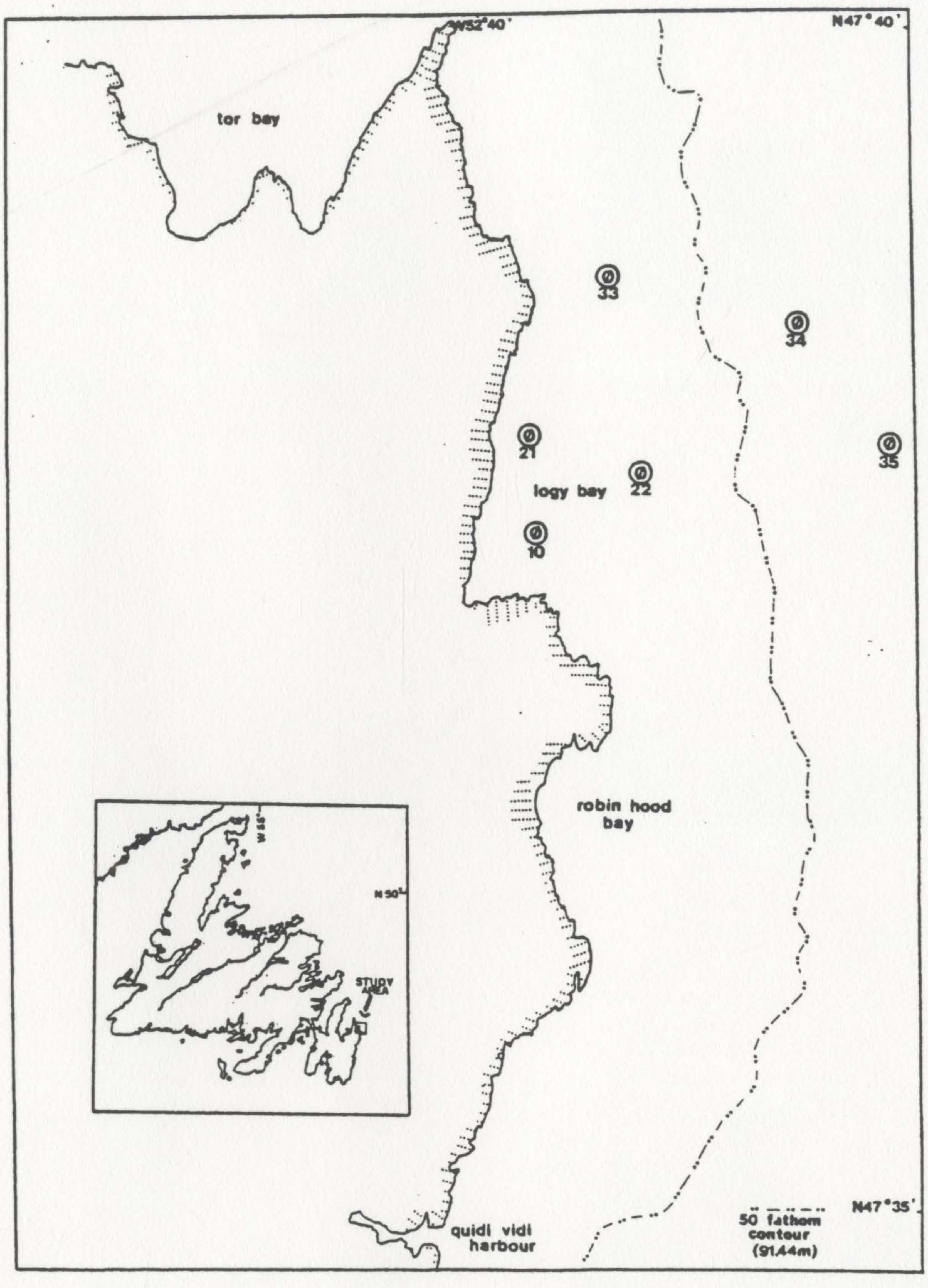


Figure 4.2. Map of Logy Bay reproduced from Kendaris (1980) showing the locations of six sites sampled for zooplankton during April to September 1979. Each site has a unique symbol.

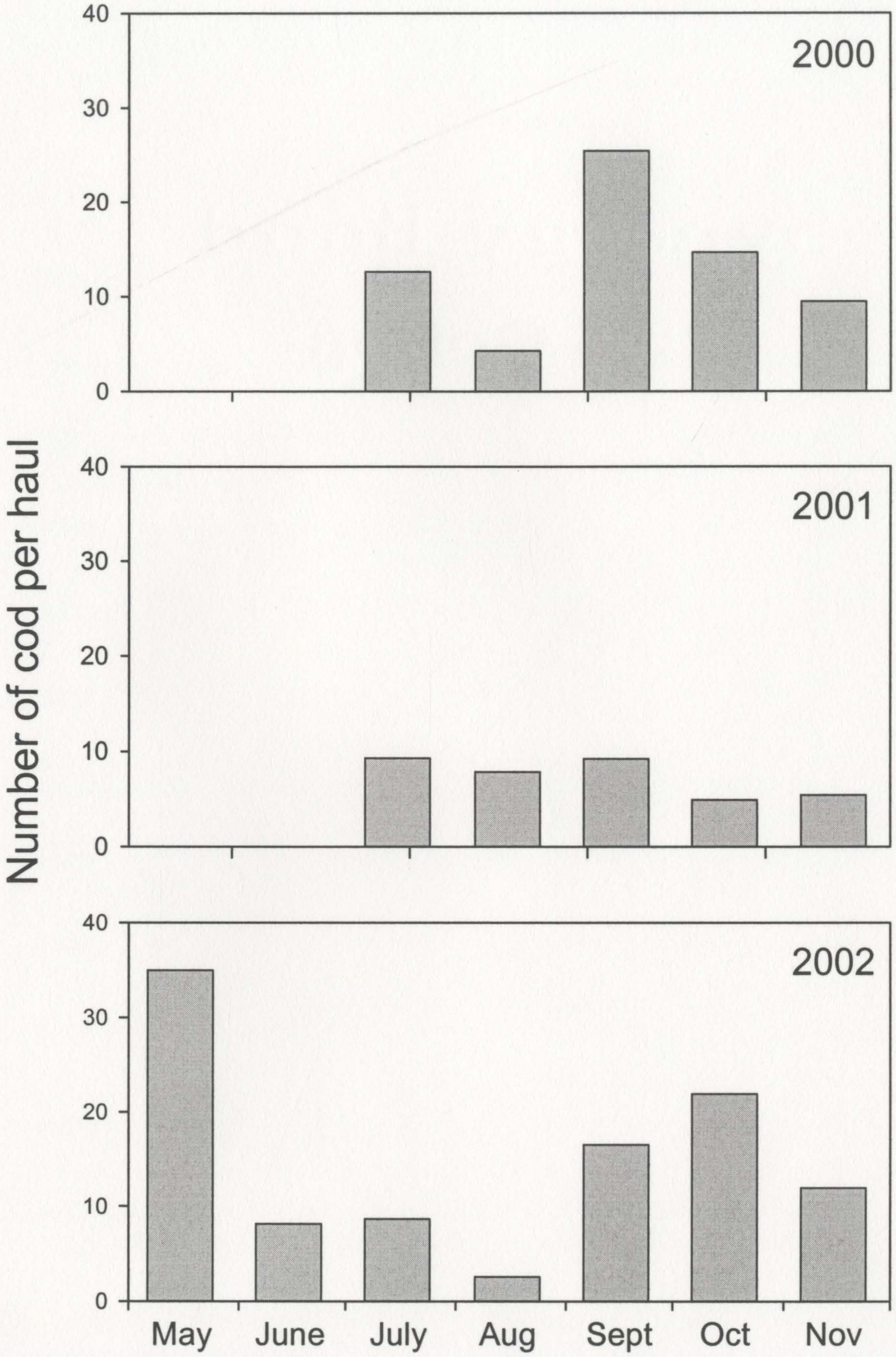


Figure 4.3. Mean number of Atlantic cod (< 101 mm) collected monthly at 12 sites in Newman Sound during July to November of 2000 and 2001 and May to November of 2002.

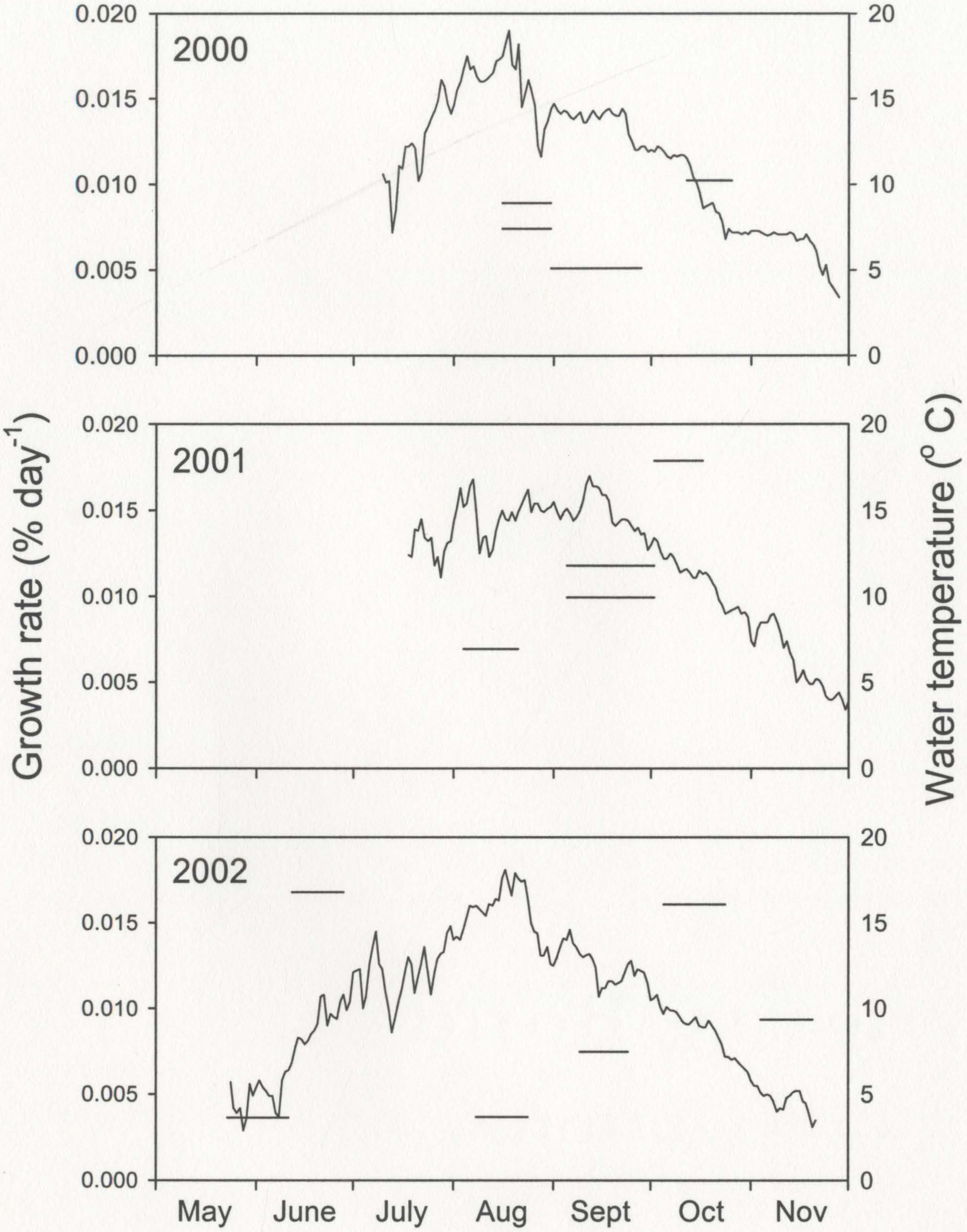


Figure 4.4. Growth rates of newly-recruited Atlantic cod sampled from 14 recruitment pulses observed at Newman Sound during 2000-2002 plotted at three week intervals (horizontal bars) and mean daily water temperature at 3 m depth in Newman Sound (continuous line).

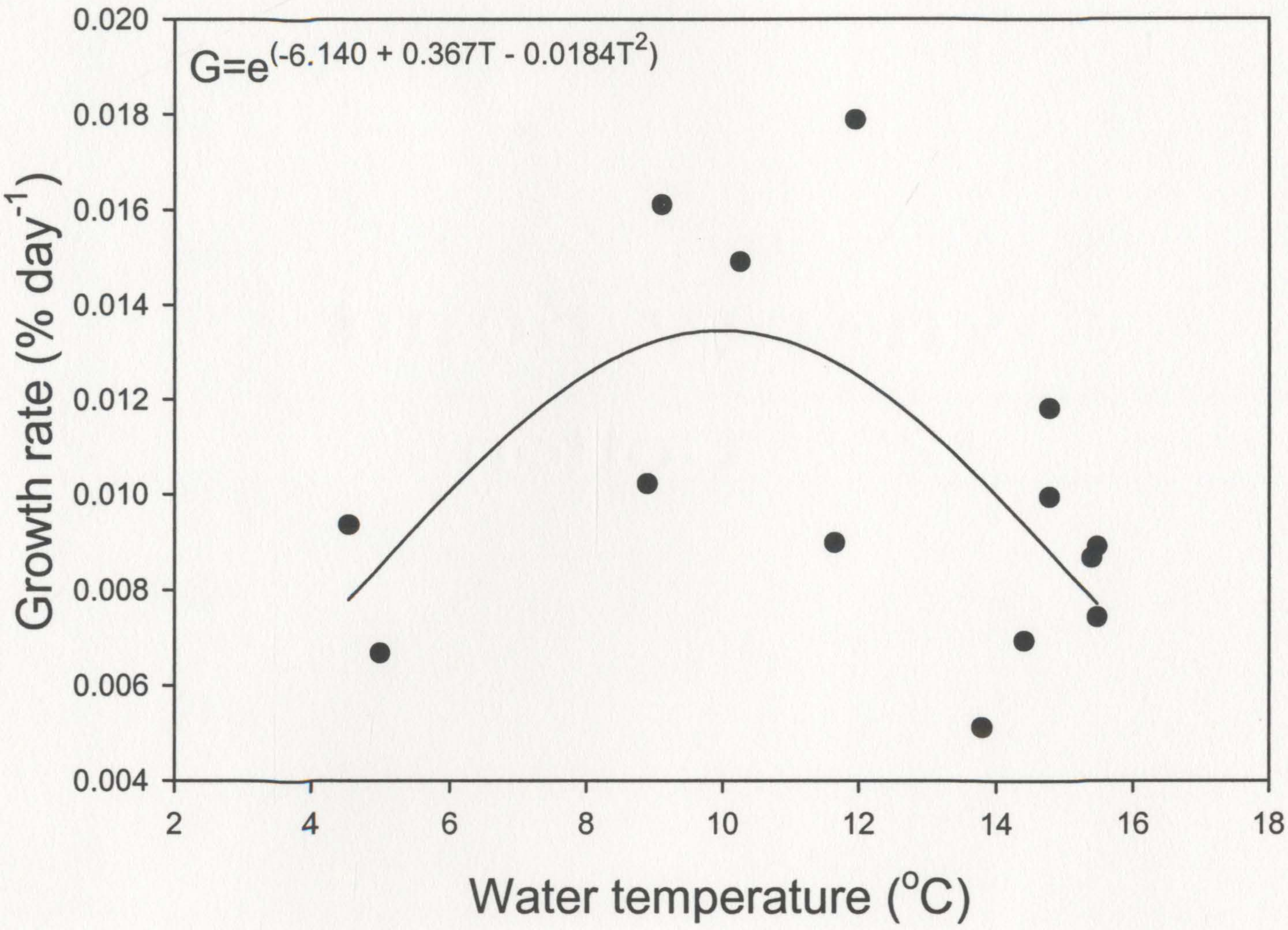


Figure 4.5. Growth rate of Atlantic cod sampled from 14 recruitment pulses observed in Newman Sound during 2000-2002 and mean water temperature during the measurement period showing a parabolic relationship.

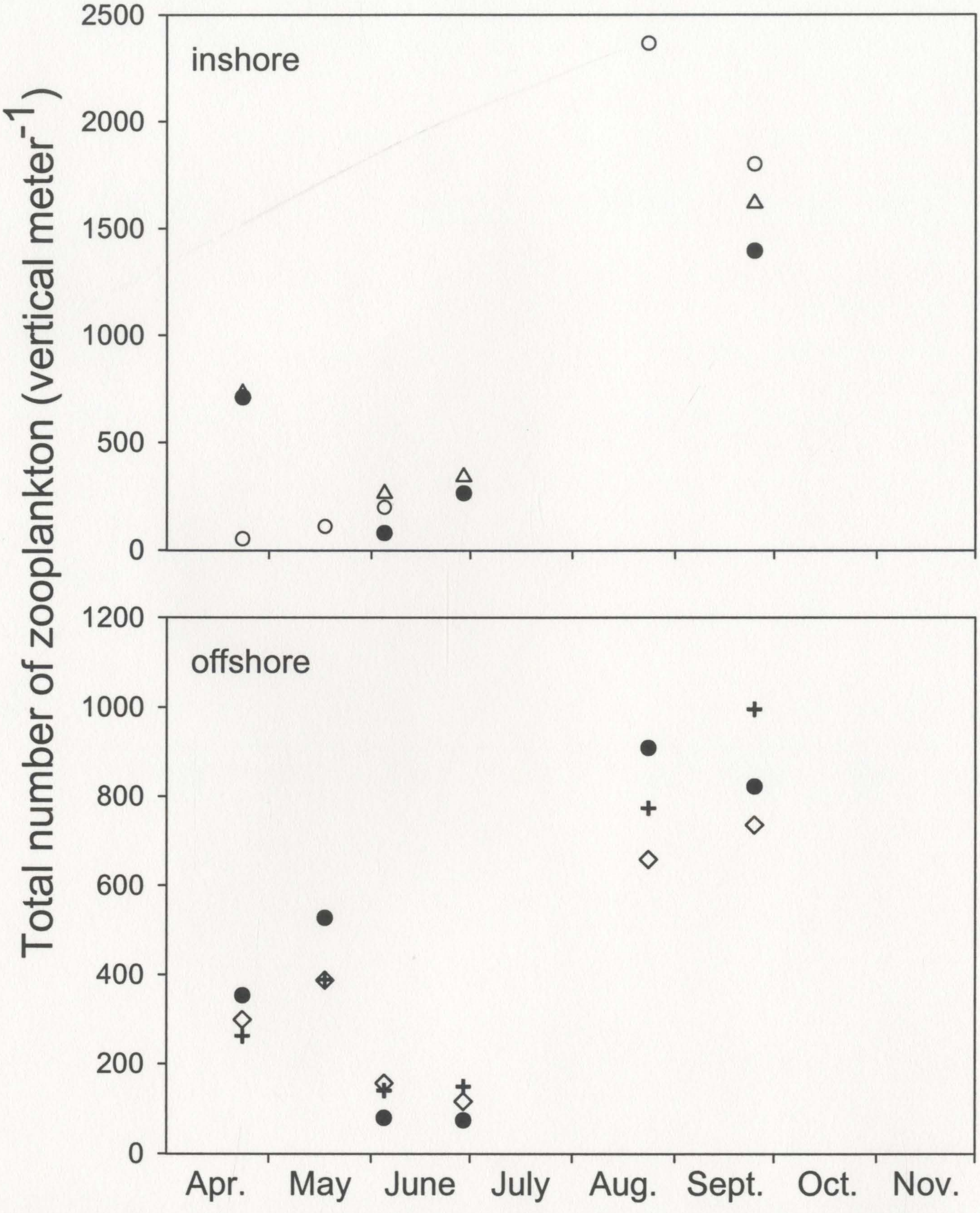


Figure 4.6. Total number of zooplankton per vertical metre at inshore and offshore stations in Logy Bay during 1979 taken from Kendaris (1980).

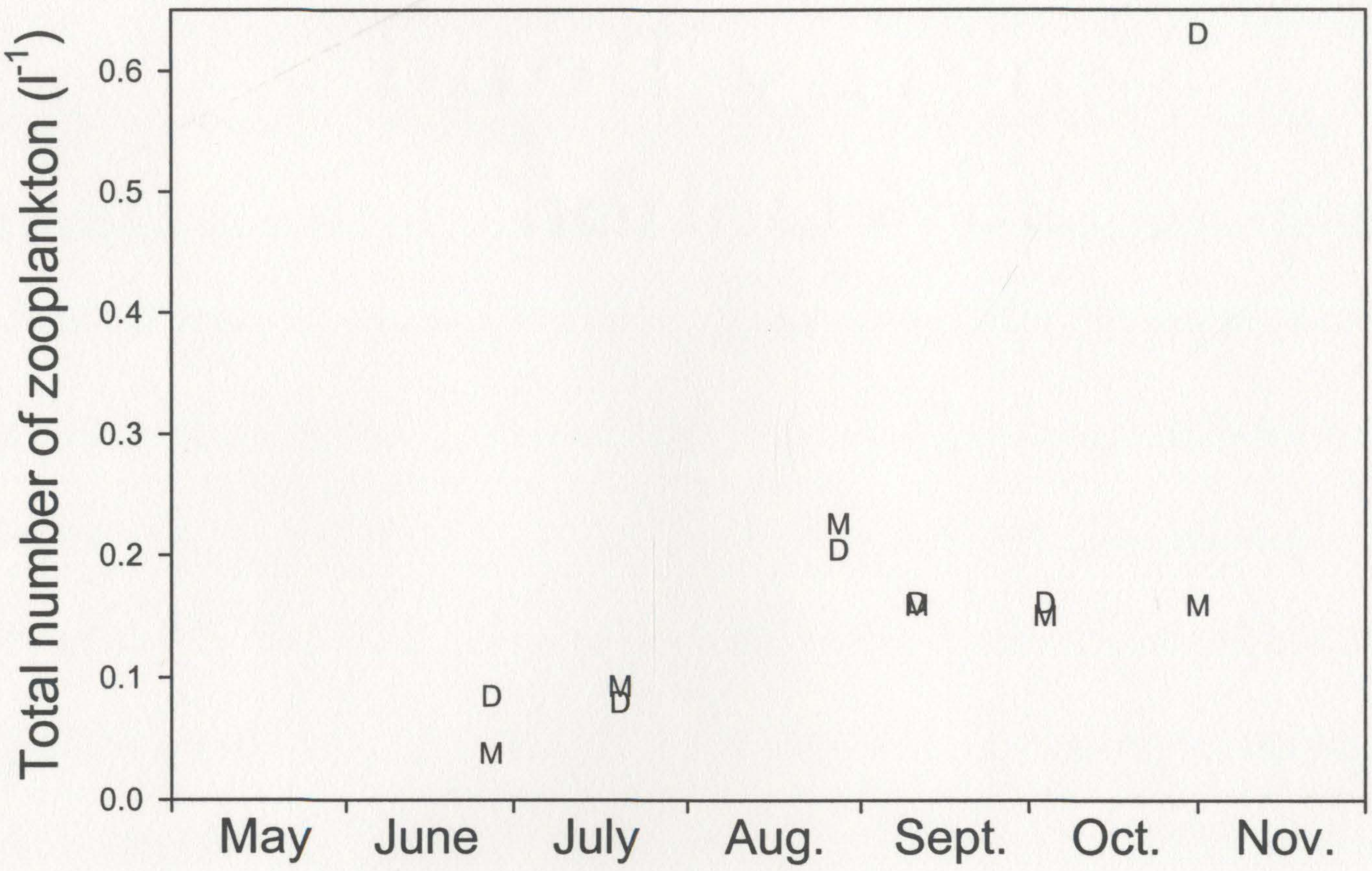


Figure 4.7. Total number of zooplankton per litre in near surface samples collected at Dockside (D) and Mistaken Cove (M) in Newman Sound during June-August 2001 and September-November 2002.

Chapter 5. Summary

5.1. Recruitment theories

5.1.1 Theories for pulses

I found that recruitment of Atlantic cod, Greenland cod and hake to coastal sites was associated with onshore winds following upwelling (Chapter 3). This finding supported the hypothesis that larval fish are transported to the nearshore during downwelling. Other theories were not supported. Data were inconsistent with the hypothesis that recruitment of fish was associated with tidal stage (Chapter 3). Also, observations that Atlantic cod held in aquaria (J. Brown, pers com) continued to spawn during periods of upwelling did not support the theory that upwelling interrupts spawning by Atlantic cod. The theory that geographic separation of spawning contributes to recruitment pulses, was not formally tested in this thesis because genetic analysis from juvenile Atlantic cod collected in Newman Sound (Beacham *et al.*, 2000) provided strong evidence against it. Beacham *et al.* (2000) found that roughly half of the juvenile Atlantic cod sampled from an August recruitment pulse were genetically similar to offshore fish and half were similar to inshore fish ; 30 and 70 percent originated offshore and inshore respectively during October. Similarly, my findings did not support the geographic separation of spawning hypothesis. If spawning occurs both far from and near the recruitment area, pulses will be wide and narrow in time respectively. A recruitment pulse originating far away will arrive over a prolonged period because lateral mixing will spread the pulse spatially. I observed that Atlantic cod, Greenland cod and hake recruited to the nearshore during periods of only a few days.

5.1.2 Annual recruitment theories

My findings are consistent with the theory that episodic advection events influence level of recruitment for fish (Hjort, 1914). I observed that recruitment of Atlantic cod, Greenland cod and hake to nearshore sites was associated with onshore wind events following upwelling (Chapter 3). This is consistent with retention of larvae at an upwelling front and shoreward transport during downwelling. D. Schneider proposed (Fig. 5.1) that in an upwelling favorable wind regime, depth-keeping fish that swim downward will be carried shoreward and collect at an upwelling front. On the landward side of the upwelling front, depth-keeping fish will swim upward, converging at the front. Models of larval drift that do not incorporate retention at an upwelling front suggest that most of the larvae transported to coastal areas are subsequently advected offshore (Pepin and Helbig, 1997). Advection of high numbers of larvae to coastal sites contributes to high year-class success in some species (Bailey, 1981). For fish such as Greenland cod, which spawns nearshore during winter-early spring (Scott and Scott, 1988) and recruits to shallow water habitats during summer when winds are mostly offshore (Chapter 3), a retention mechanism that counters advection offshore may be critical for year-class success.

Hjort (1914) also hypothesized that level of recruitment is determined by the availability of prey to larvae during the period immediately following exogenous feeding. This may not apply to the northeast Newfoundland Shelf. Brander (1994) found that variability in spawning times by Atlantic cod was inconsistent with hypotheses relating recruitment success to the fine temporal match between larvae and their prey (e.g. match - mismatch (Cushing 1969, 1974, 1990)). I observed that zooplankton were available nearshore from April through October (Chapter 4), rather than during a brief period annually. I also observed that Atlantic cod recruited to the nearshore through this extended period during 2000-2002 (Chapter 4). Together, data on prey abundance and recruitment of larval fish, along with known spawning times for Atlantic cod, suggests that the theory that prey availability to larvae during a relatively brief period determines year-class success does not apply to continental shelf systems.

5.2. Views on Atlantic cod recruitment inshore

Inshore areas may contribute more to the annual production of Atlantic cod than previously believed. Hutchings *et al.* (1993) reviewed spawning by Atlantic cod on the Northeast Newfoundland Shelf and concluded that coastal spawning may be important for recruitment along the northeast coast of Newfoundland. Spawning offshore also contributes to recruitment inshore (Beacham *et al.* 2000). Cod eggs (up to stage IV) that were presumably spawned offshore have been found to be distributed progressively closer to the coast with development (Pepin and Helbig, 1997). Modelling of egg and larval distributions based on passive drifters had been interpreted to suggest that a small proportion of the larvae spawned offshore are transported inshore (Helbig *et al.* 1992) and retained there (Pepin and Helbig, 1997). However, behaviour of larvae which results in accumulation at fronts (Chapter 3) was not incorporated into these simulations. Therefore, retention of larvae inshore may be higher than modelling has suggested. Data on distributions of juvenile fish are inconsistent with passive drift. Distributions of pelagic juveniles have been found to extend from bays on the northeast coast of Newfoundland to areas further offshore (Anderson *et al.* 1995). This spatial distribution does not support the conjecture that larvae are transported from offshore areas to the bays only during rare events. Dalley and Anderson (1997) observed an ontogenetic distribution of juvenile Atlantic cod with the highest densities of age 0 fish nearest the coast showing that a relatively large number of juvenile Atlantic cod use nearshore habitats. Genetic analysis has shown that roughly half of the juveniles arriving at coastal sites during August are from offshore spawning and half are from inshore spawning; during October, 30 % originate offshore and 70 % are from the nearshore (Beacham *et al.*, 2000). The importance of the nearshore for production of Atlantic cod may explain why a recruitment signal in post-settlement Atlantic cod at the coast carries through to the overall stock (Schneider *et al.* 1995; Ings *et al.,* 1998).

5.3. Future research

Accumulation of larvae at upwelling fronts is dependant on behavioural mechanisms. Upwelling fronts are well known as convergent areas where bouyant objects collect on the landward side. However, relatively small objects (zooplankton and larvae) would be displaced from frontal areas without depth-keeping movements. While such a mechanism may exist for larval Atlantic cod, rock cod and hake (Chapter 3), determining the stimulus was beyond the scope of this thesis. I suggest that depth-keeping by cod larvae may be stimulated by light. Cod larvae are visual feeders (Ellertsen *et al.* 1981) and undergo diel migrations under natural light regimes (Skiftesvik, 1994). Therefore, the response of cod larvae to light may determine depth-keeping at upwelling fronts.

The process of upwelling / downwelling may have a large influence on recruitment of invertebrates and fish to inshore communities. I found that recruitment of juvenile Atlantic cod, Greenland cod and hake at coastal sites was associated with onshore wind events following upwelling (Chapter 3). Previously, capelin emergence from beaches on the northeast coast was found to occur during onshore winds (Frank and Leggett, 1982). Year-class strength of capelin is positively related to onshore wind frequency (Leggett *et al.,* 1984). Elsewhere, onshore winds or downwelling has been found to influence nearshore settlement of a wide variety of invertebrates and fish (Farrell *et al.,* 1991; Roughgarden *et al.,* 1991; Wing *et al.*, 1995a, b; Jenkins *et al.* 1997). I predict that many species of invertebrates and fish recruit to the northeast coast of Newfoundland during onshore wind events (downwelling) similar to the three gadid species in this study.

This thesis dealt with recruitment at daily and seasonal scales but estimates of annual recruitment are often most desirable. An annual survey (Fleming) for Atlantic cod along the northeast coast of Newfoundland during autumn found a recruitment signal in the post-settlement stages (Schneider *et al.,* 1995; Ings *et al.*, 1997) similar to findings along the coast of Norway (Tveite, 1971; 1984). Unfortunately, the Fleming survey has not been conducted since 2001. However, data from annual monitoring of cod abundance over a smaller area (Newman Sound) but at a finer temporal resolution (biweekly between July and November), is available for some of the years when the Fleming survey was conducted (Gregory *et al.* 2002). The influence of variation in the seasonal abundance of fish and upwelling frequency on annual recruitment of Atlantic cod is not known. Analysis of data from both Newman Sound and the Fleming survey may provide insight into this question. A better understanding of the influences on recruitment success of Atlantic cod is particularly important now as stocks off Newfoundland are severely reduced (< 2% of historical biomass (Lilly *et al.* 2003)) and have been declared endangered by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC, 2003).

5.3. Literature cited

Anderson, J.T., E.L. Dalley and J.T. Carscadden, 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. 52: 115-125.

Bailey, K.M., 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1-9.

Beacham, T.D., R.S. Gregory and J. Brattey,. 2000. Origins of two recruitment pulses of 0-group Atlantic cod (*Gadus morhua*) in Bonavista Bay, Newfoundland during 1999, determined from genetic variation. Can. Stock. Assess. Sec. Res. Doc. 2000/093. 10 p.

Brander, K., 1994. Spawning and life history information for North Atlantic cod stocks. ICES Coop. Res. Rep. No. 205 150 p.

Cushing, D.H., 1969. The regularity of the spawning season of some fishes. J. du Conseil, Cons. Int. Explor. Mer. 33: 81-92.

Cushing, D.H., 1974. The natural regulation of fish populations. In: Sea Fisheries Research. FR Harden Jones (ed), pp. 399-412. Elek Science, London.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update on the match/mismatch hypothesis. Adv. Mar. Bio. 26: 249-293.

COSEWIC, 2003. COSEWIC assessment and update status report on the status of Atlantic cod *Gadus morhua* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa xi + 76 pp.

Dalley, E.L. and J.T. Anderson, 1997Age-dependent distribution of demersal juvenile cod (*Gadus morhua*) in inshore / offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 168-176.

Ellertsen, B., E. Moksness, P. Solemdal, T. Stroemme, S. Tilseth, T. Westgard, and V. Oeiestad, 1981. Some biological aspects of cod larvae (*Gadus morhua* L.). The early life history of fish: recent studies. Rapp. P. -V. Reum. Ciem. 178. 316 p.

Farrell, T,M.., D. Bracher and J. Roughgarden, 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnol. Oceanogr. 36: 279-288.

Frank, K.T. and W.C. Leggett, 1981. Wind regulation of emergence times and early larval survival in capelin (*mallotus villosus*). Can. J. Fish. Aquat Sci. 38: 215-223.

Gregory, R.S., B.J. Laurel, D.W. Ings, and D.C. Schneider, 2002. Relative strength of the 1999 and 2002 year-classes, from nearshore surveys of demersal age 0 Atlantic cod in 3KL and in Newman Sound, Bonavista Bay. Can. Scientific Advisory Secretariat Res. Doc. 2002/087.

Helbig, J., G. Mertz and P. Pepin, 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. 1: 39-56.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe. Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20: 1-228.

Hutchings, J.A., R.A. Myers and G.R. Lilly, 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2457-2467.

Ings, D.W., D.C. Schneider and D.A. Methven, 1997. Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 25-29.

Jenkins,G.P., K.P. Black, M.J. Wheatley, and D.N. Hatton, 1997. Temporal and spatial variability in recruitment of a temperate, sea-grass associated fish is largely determined by physical variables in the pre- and post-settlement phases. Mar. Ecol. Prog. Ser. 148: 23-35.

Leggett, W.C., K.T. Frank and J.E. Carscadden, 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*) Can. J. Fish. Aquat. Sci. 41: 1193-1201.

Lilly, G.R., P.A. Shelton, J. Brattey, N.G. Cadigan, B. P. Healey, E. F. Murphy, D. E. Stansbury and N. Chen, 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL in February 2003. Can. Scientific Advisory Secretariat Res. Doc. 2003/023.

Pepin, P. and J.A. Helbig, 1997. Distribution and drift of cod eggs and larvae on the northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. 54:

Roughgarden, J. J.T. Pennington D. Stoner, S. Alexander and K. Miller, 1991. Collisions of upwelling fronts with intertidal zones: the cause of recruitment pulses in barnacle populations of central California. Acta. Œcol 12: 35-51.

Schneider, D.C. and D.A. Methven, 1988. Response of capelin to wind-induced thermal events in the southern Labrador Current. J. Mar. Res. 46: 105-118.

Schneider, D.C., D.A. Methven and D. Ings, 1995. Distribution and recruitment of demersal cod (ages 0+, 1+ and 2+) in the coastal zone, NAFO divisions 3K and 3L. DFO Atlantic Fisheries Res. Doc. 95/68. 9 p.

Scott, W.B. and M.G. Scott, 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

Skiftesvik, A.B., 1994. Impact of physical environment on behaviour of cod larvae. In: Cod and climate change. Proceedings of a symposium held in Reykjavik, 23-27August 1993. ICES Mar. Sci. Symp. 198: 646-653.

Smedbol, R.K., and J.S. Wroblewski, 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991-1993. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 177-186.

Templeman W., 1979. Migration and intermingling of stocks of Atlantic cod *Gadus morhua* of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Doc. 14: 6-50.

Tveite, S., 1971. Fluctuations in yearclass strength of cod and pollack in southeastern Norwegian coastal waters during 1920-1969. FiskeriDir. Skr. HavUnders 16: 65-76.

Tveite, S., 1984. 0-group cod investigations on the Norwegian Skagerrak coast. In: The propagation of cod *Gadus morhua* L. Edited by E. Dahl, D.S. Danielssen, E. Mokness and P. Solemdal. Flod. Rapp. 1: 581-590.

Wing, S.R., L.W. Botsford, J.R. Largier and L.E. Morgan, 1995a. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. 128: 199-211.

Wing, S.R., J.L. Largier, L.W. Botsford and J.F. Quinn, 1995b. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. 40: 316-329.

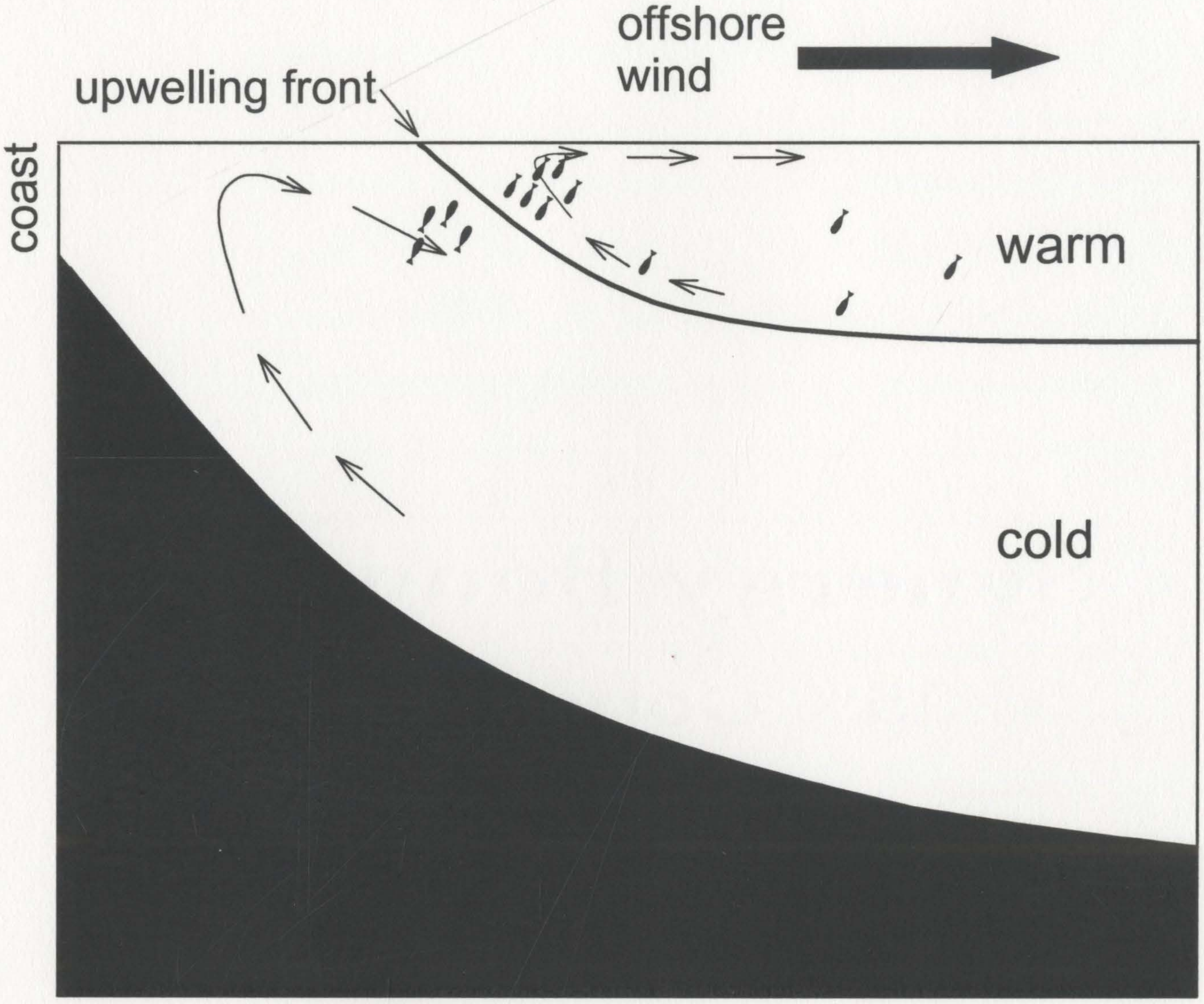
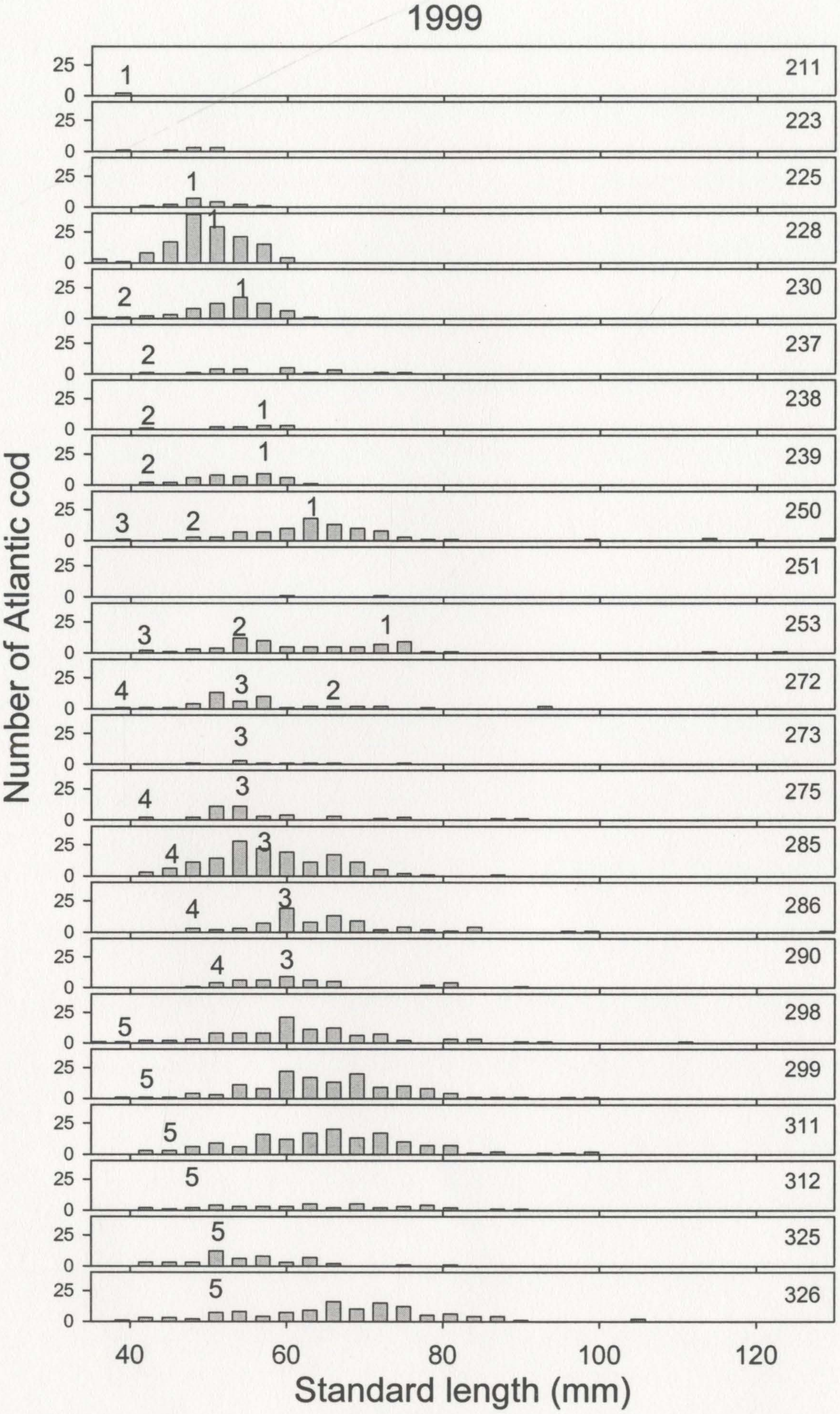
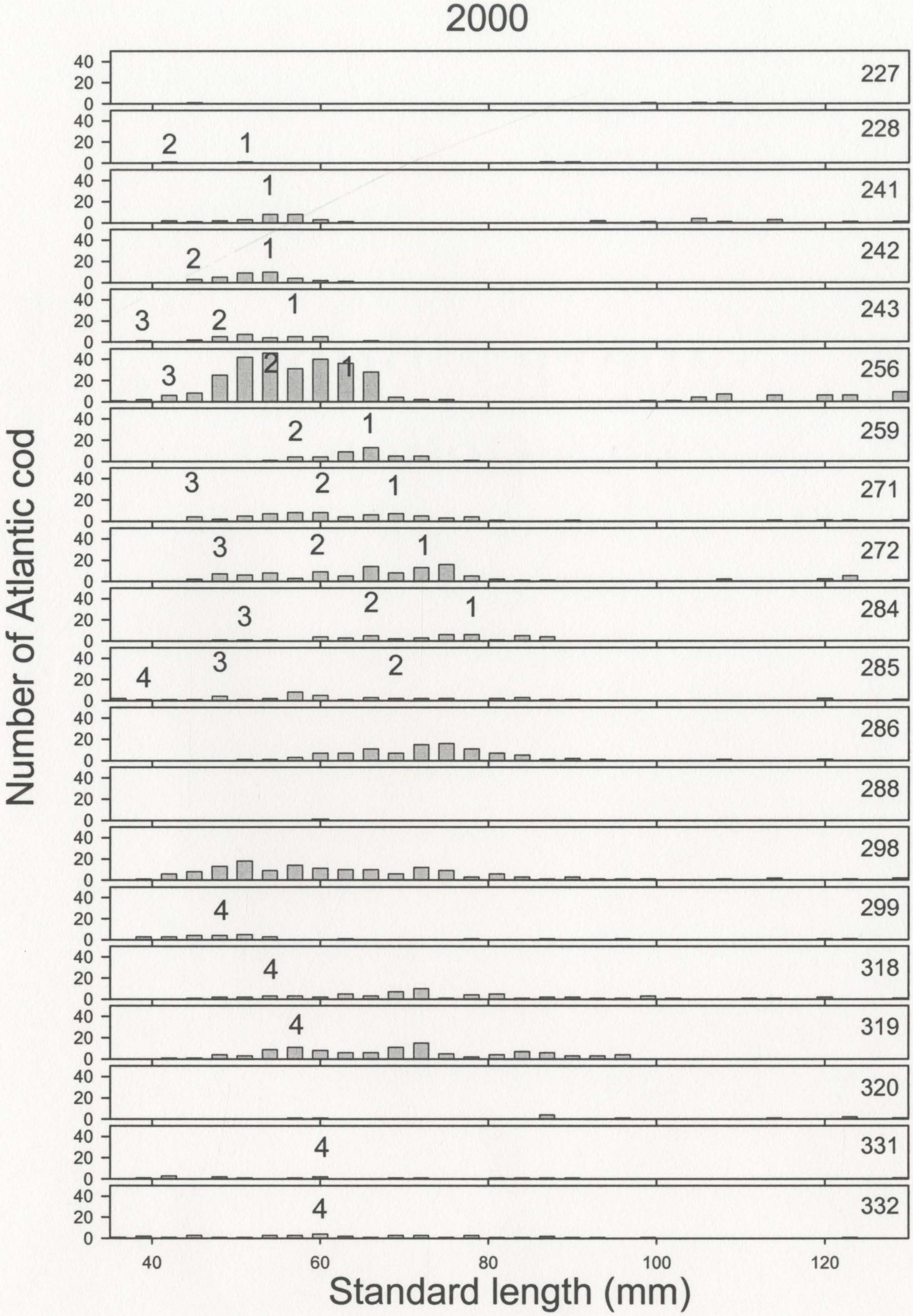
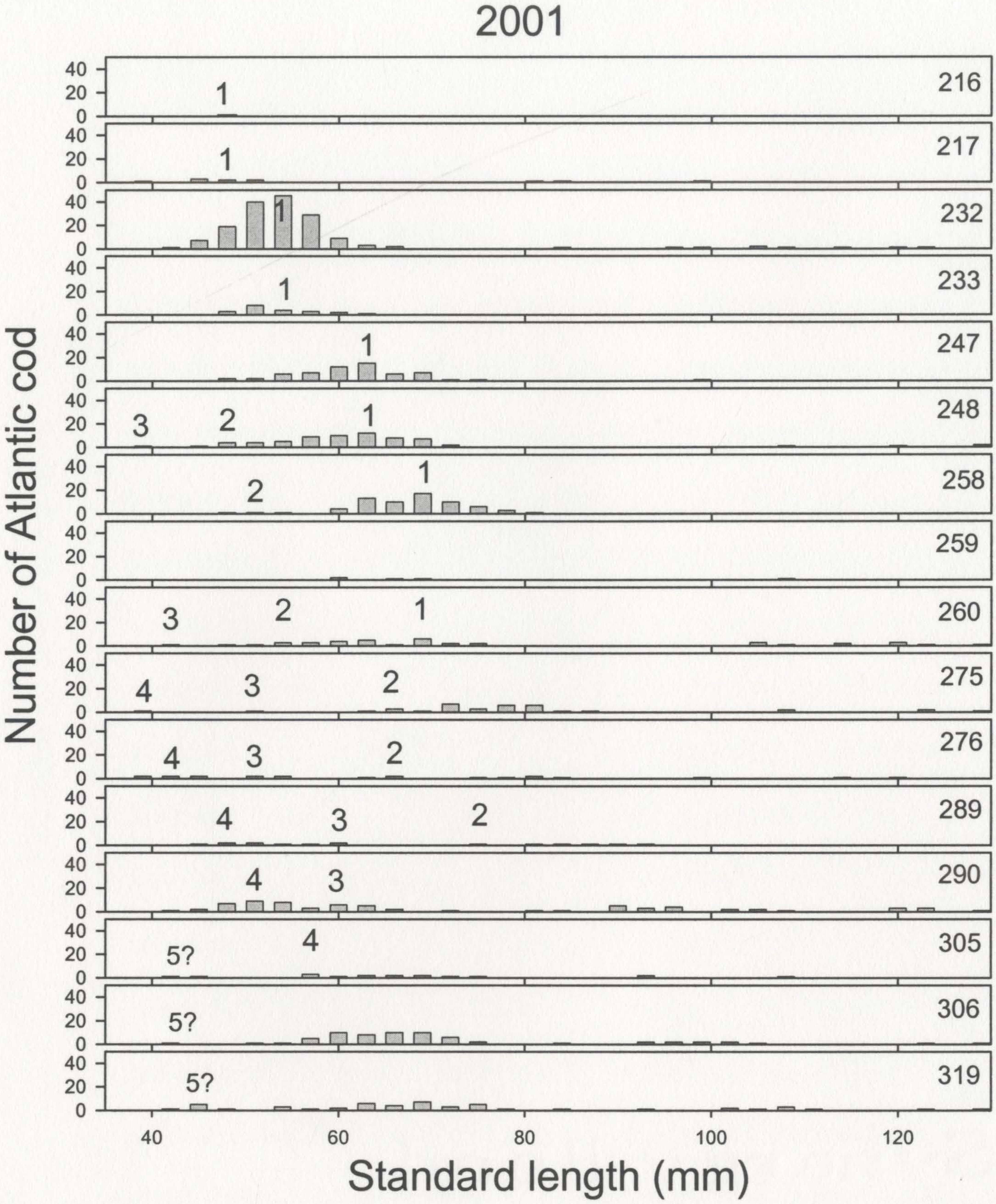


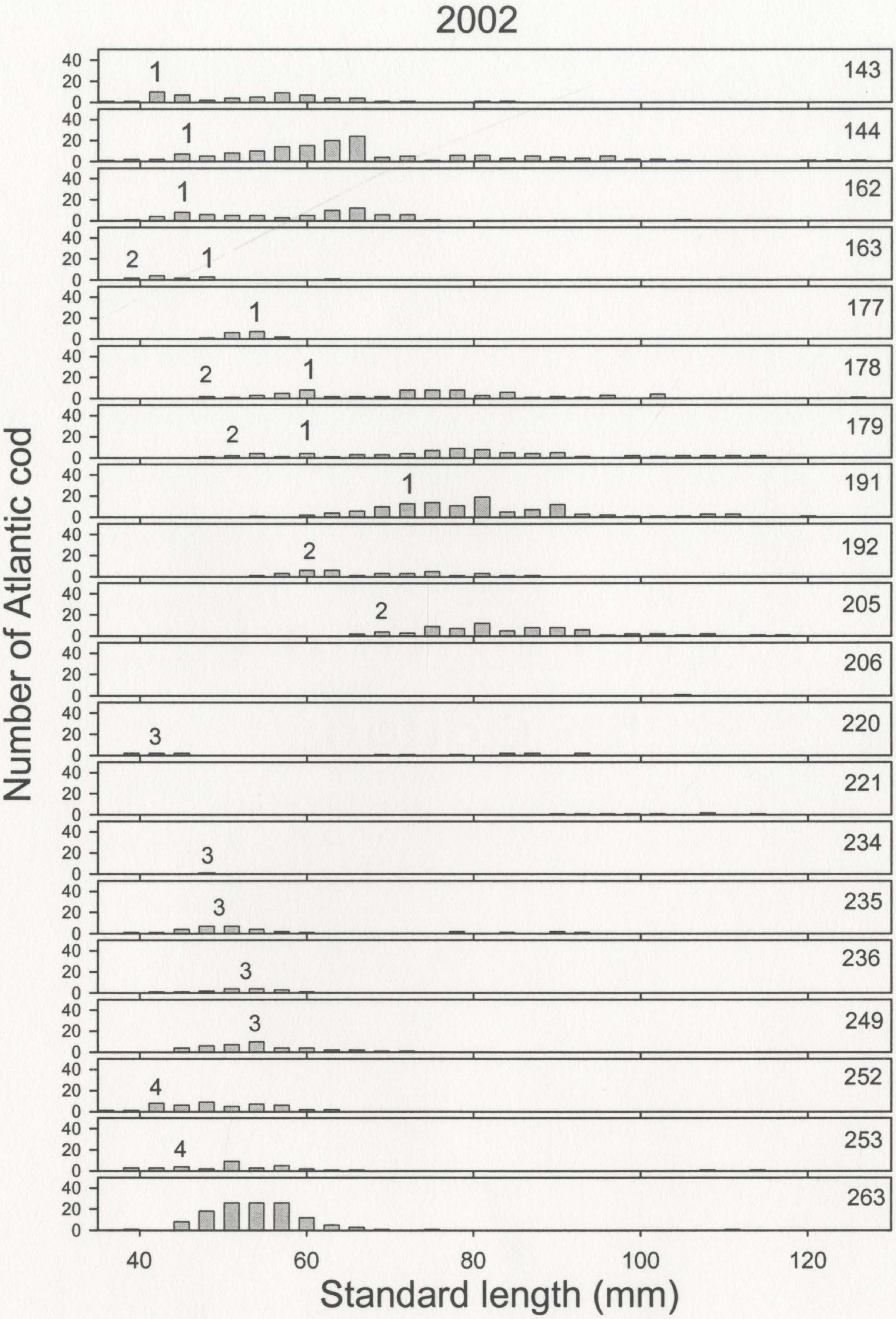
Figure 5.1.Diagram proposed by David Schneider showing the convergent mechanism at an upwelling front that aggregates marine fish larvae. On the landward side of the upwelling front depth-keeping larvae swim upward while on the seaward side of the front larvae swim downward On the landward side of the upwelling front, depth-keeping larvae swim upward while on the seaward side of the front, larvae swim downward.

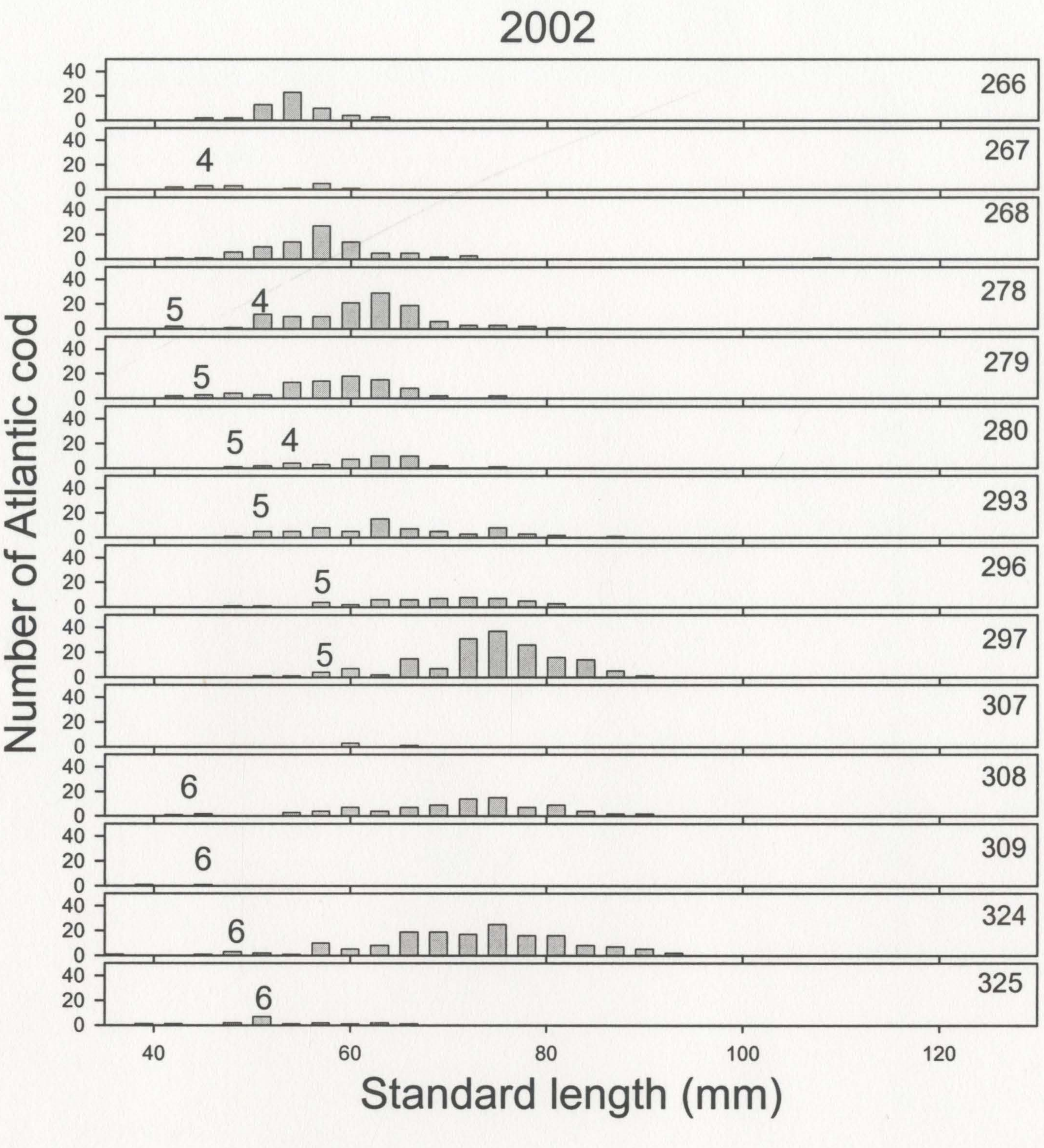
Appendix 1. Length frequencies of Atlantic cod, Greenland cod and hake sampled at Newman Sound during 1998-2002. Numbers identify pulses of Atlantic cod observed. Number (Atlantic cod) and x (Greenland cod and hake) indicate data points used in regressions. Vertical bars indicate high tides on length frequency plots for Greenland cod and hake.

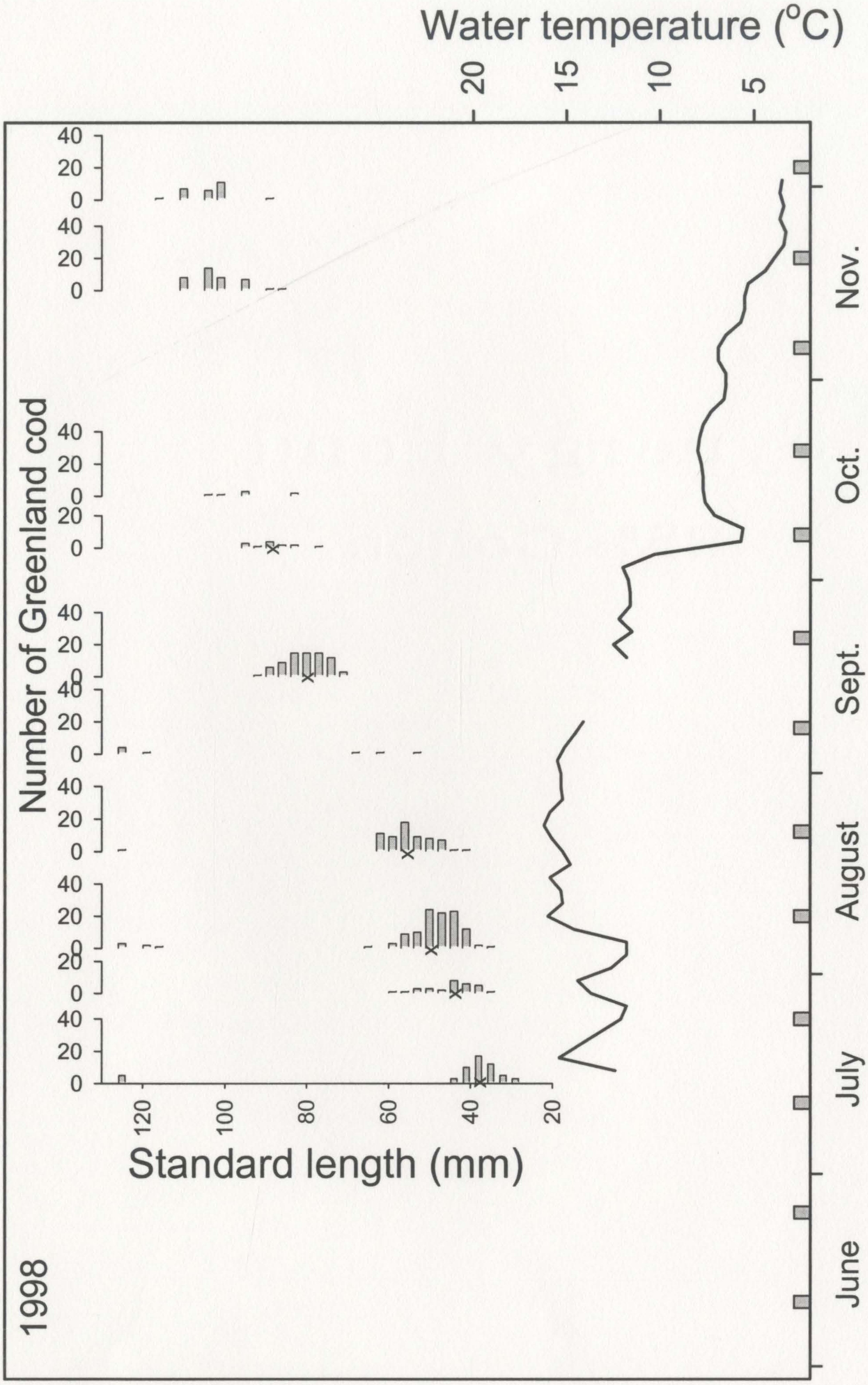


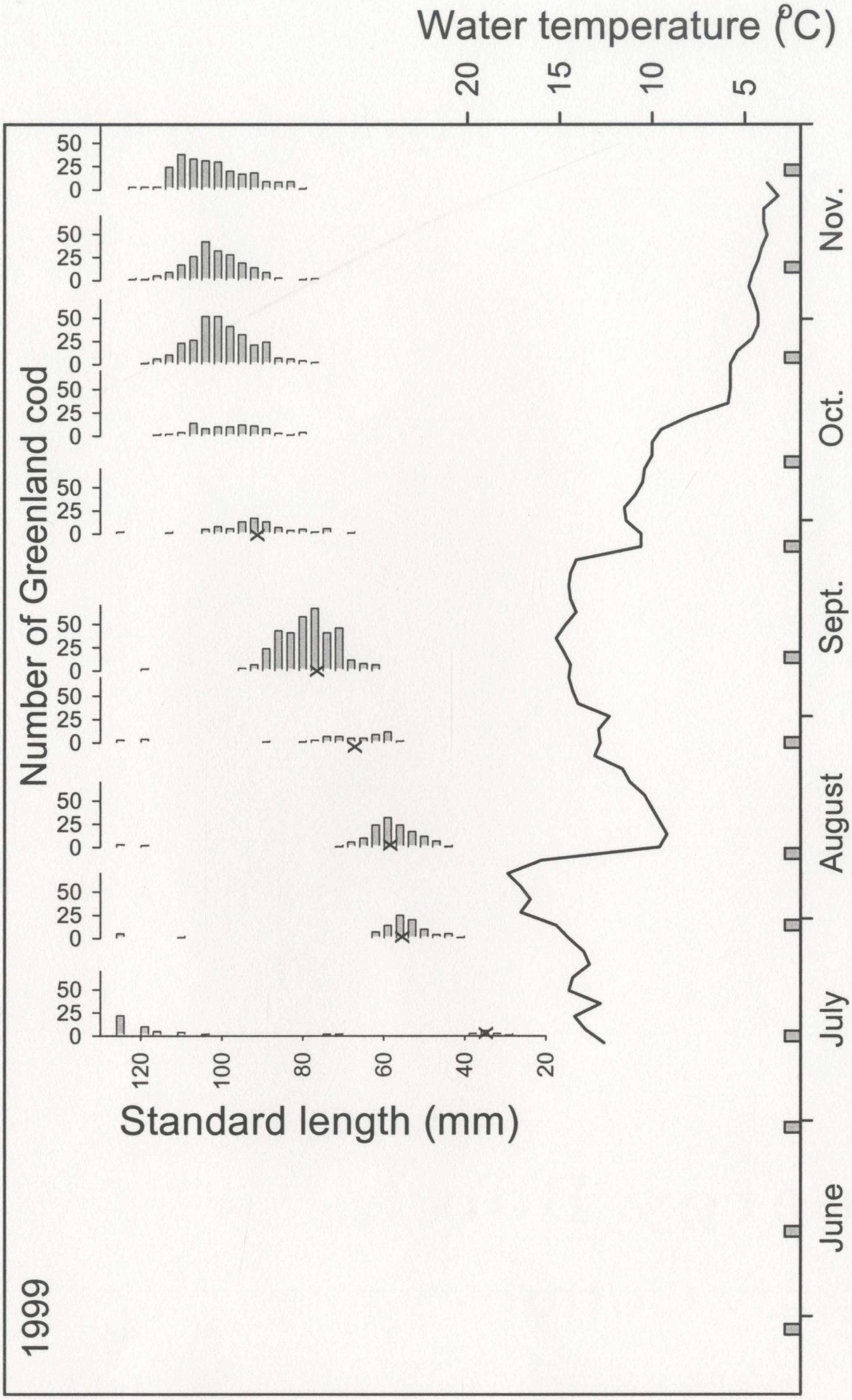

2000
227
228
241
242
243
256
259
271
272
284
285
286
288
298
299
318
319
320
331
332
1
2
3
4
40
20
0
40
60
80
100
120
Number of Atlantic cod
Standard length (mm)

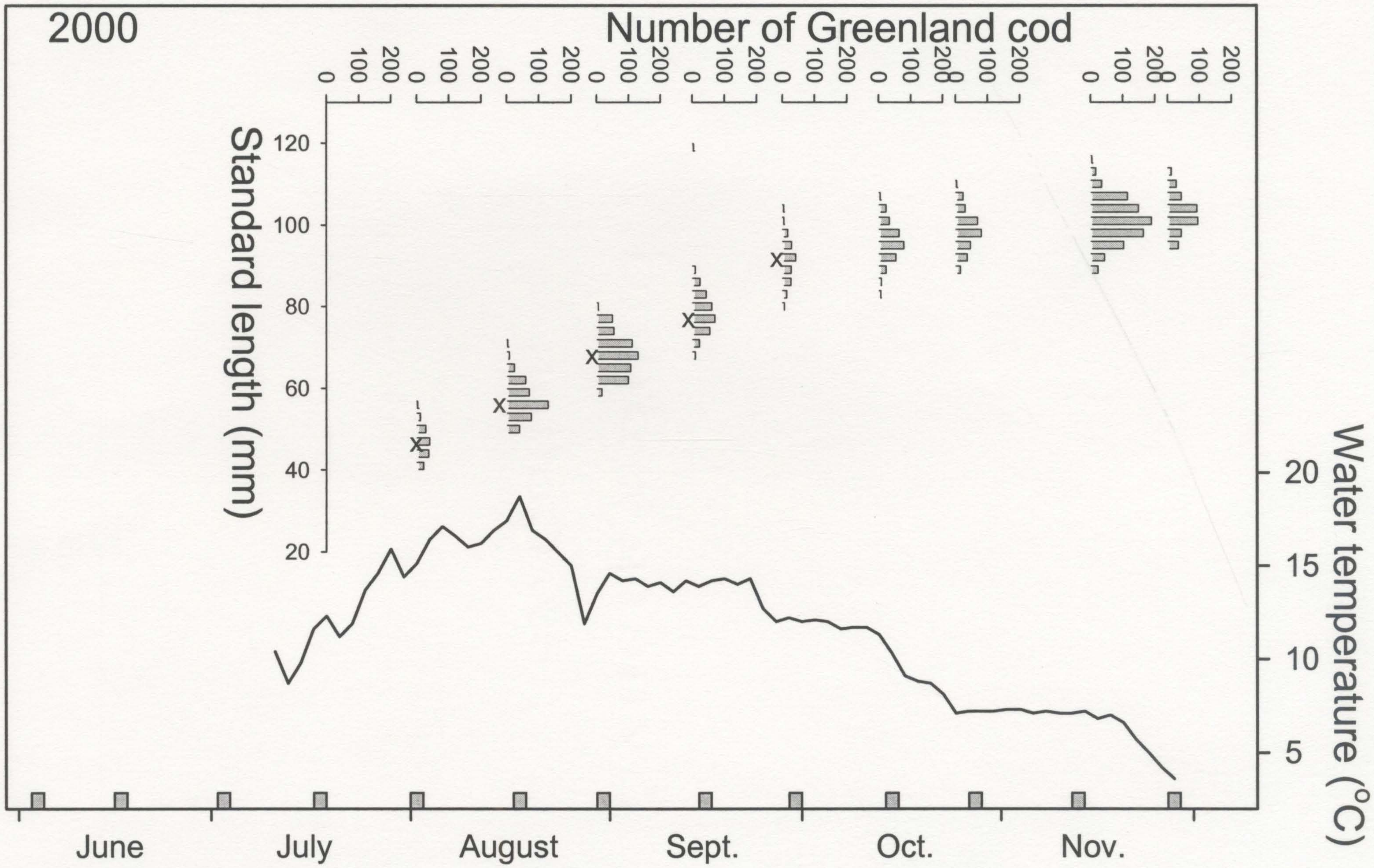

2001
216
1
217
1
232
1
233
1
247
1
248
3
2
1
258
2
1
259
260
3
2
1
275
4
3
2
276
4
3
2
289
4
3
2
290
4
3
305
5?
4
306
5?
319
5?
0
20
40
40
60
80
100
120
Number of Atlantic cod
Standard length (mm)

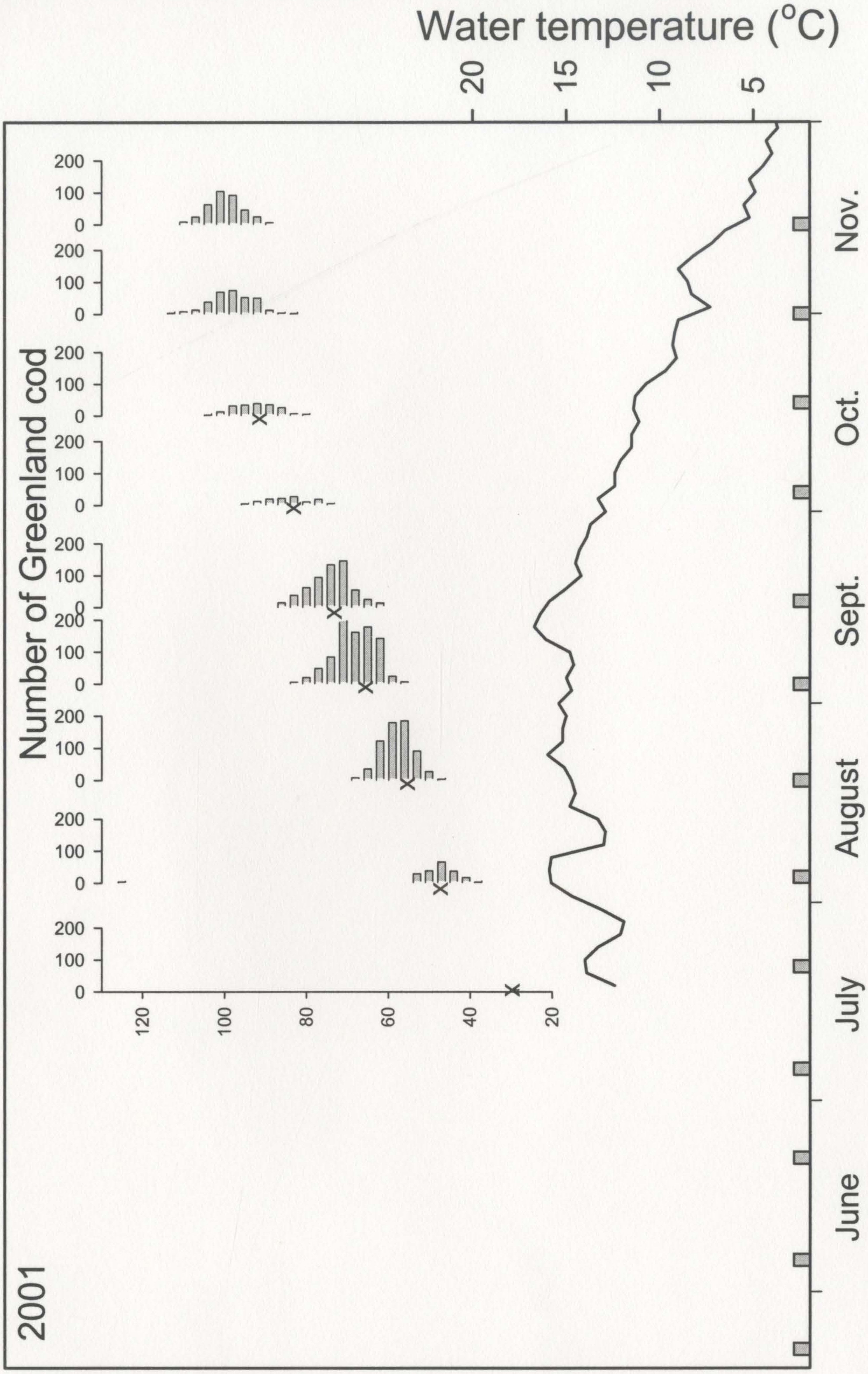

2002
143
144
162
163
177
178
179
191
192
205
206
220
221
234
235
236
249
252
253
263
1
1
1
2
1
1
2
1
2
1
1
2
2
3
3
3
3
3
4
4
0
20
40
40
60
80
100
120
Number of Atlantic cod
Standard length (mm)

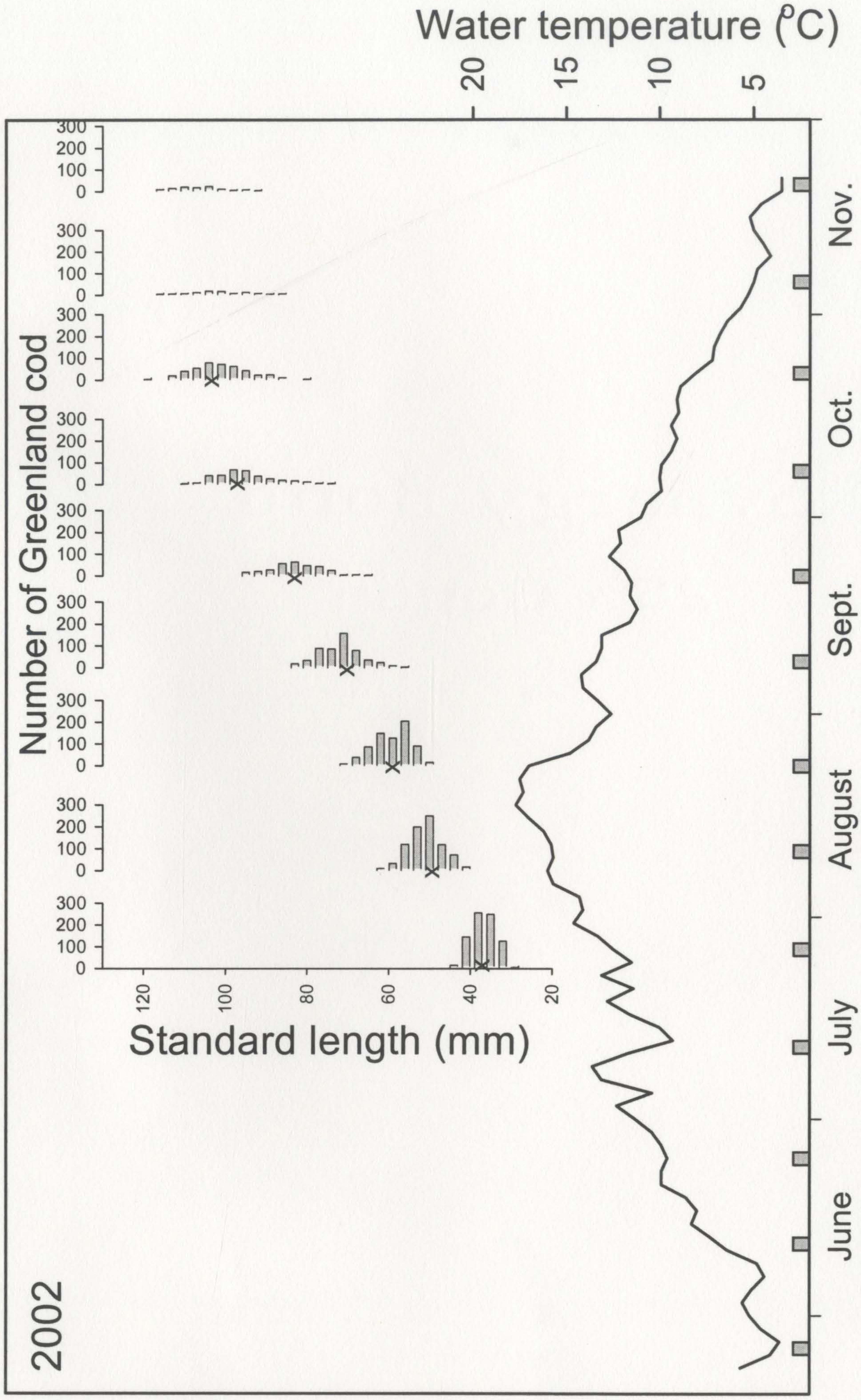

2002
Number of Atlantic cod
40
20
0
266
267
4
268
278
5
4
279
5
280
5
4
293
5
296
5
297
5
307
308
6
309
6
324
6
325
6
40
60
80
100
120
Standard length (mm)

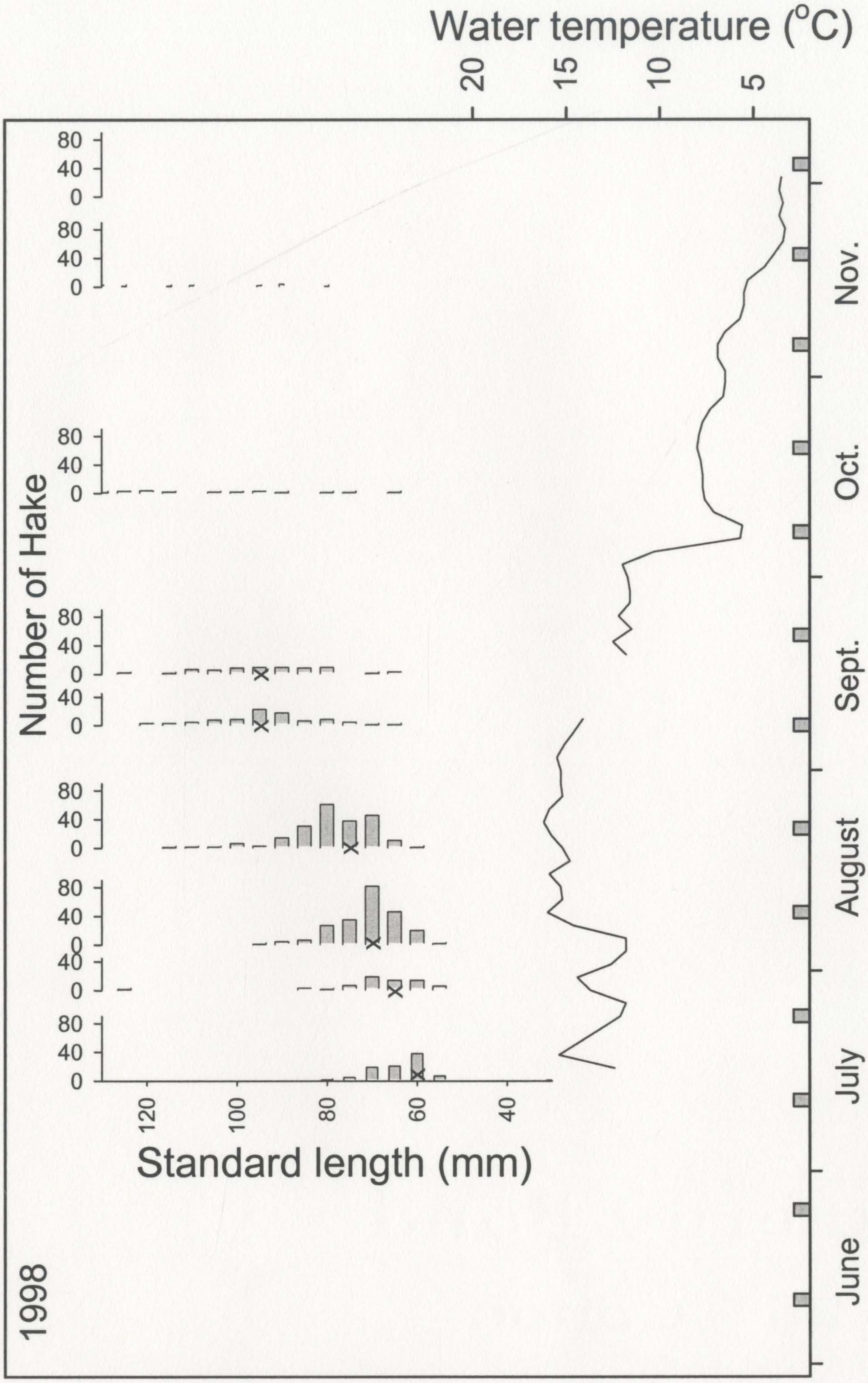

1998
Water temperature (°C)
20
15
10
5
Number of Greenland cod
0
20
40
Standard length (mm)
120
100
80
60
40
20
June
July
August
Sept.
Oct.
Nov.

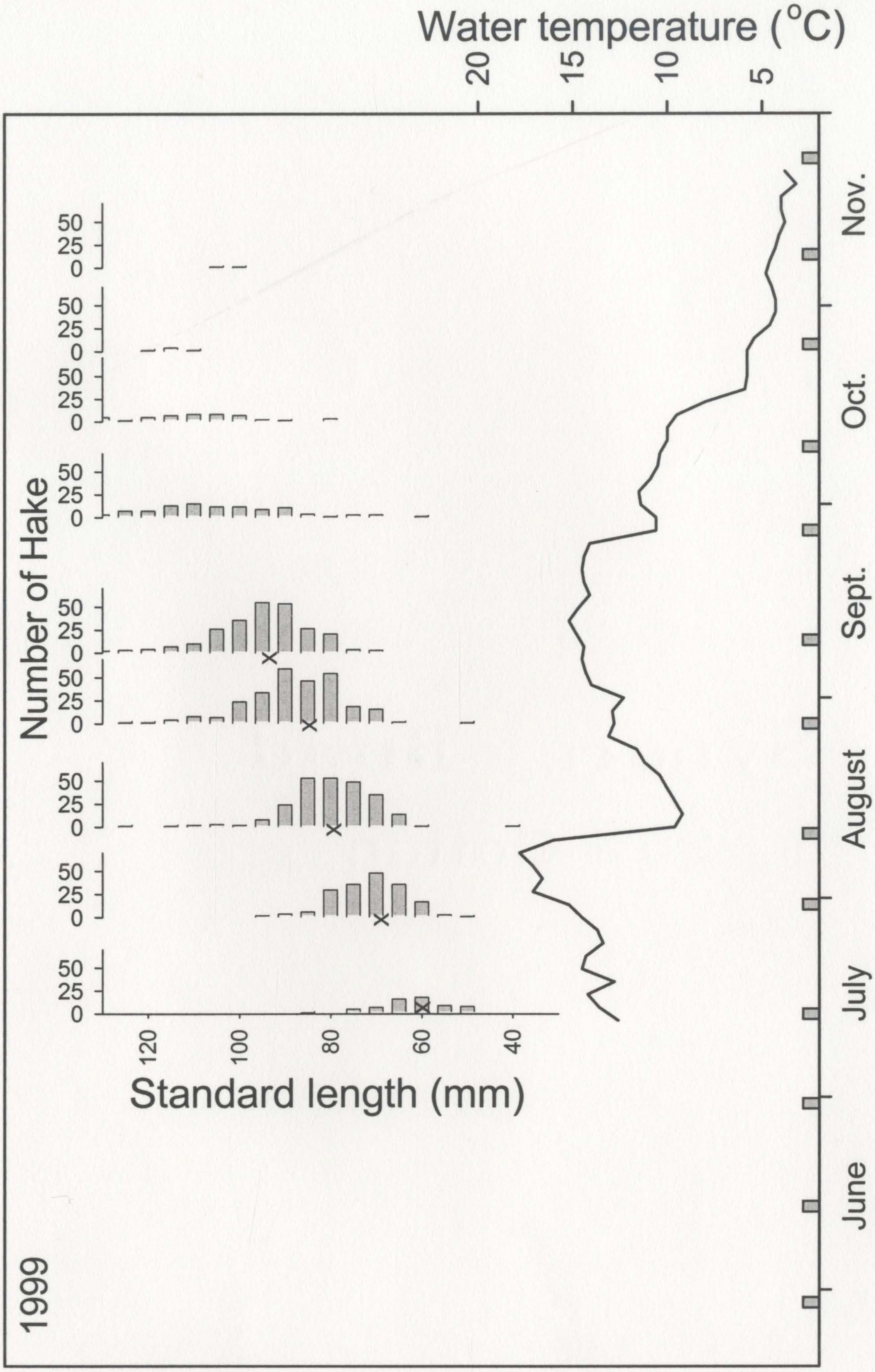

1999
Number of Greenland cod
50
25
0
Standard length (mm)
120
100
80
60
40
20
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.

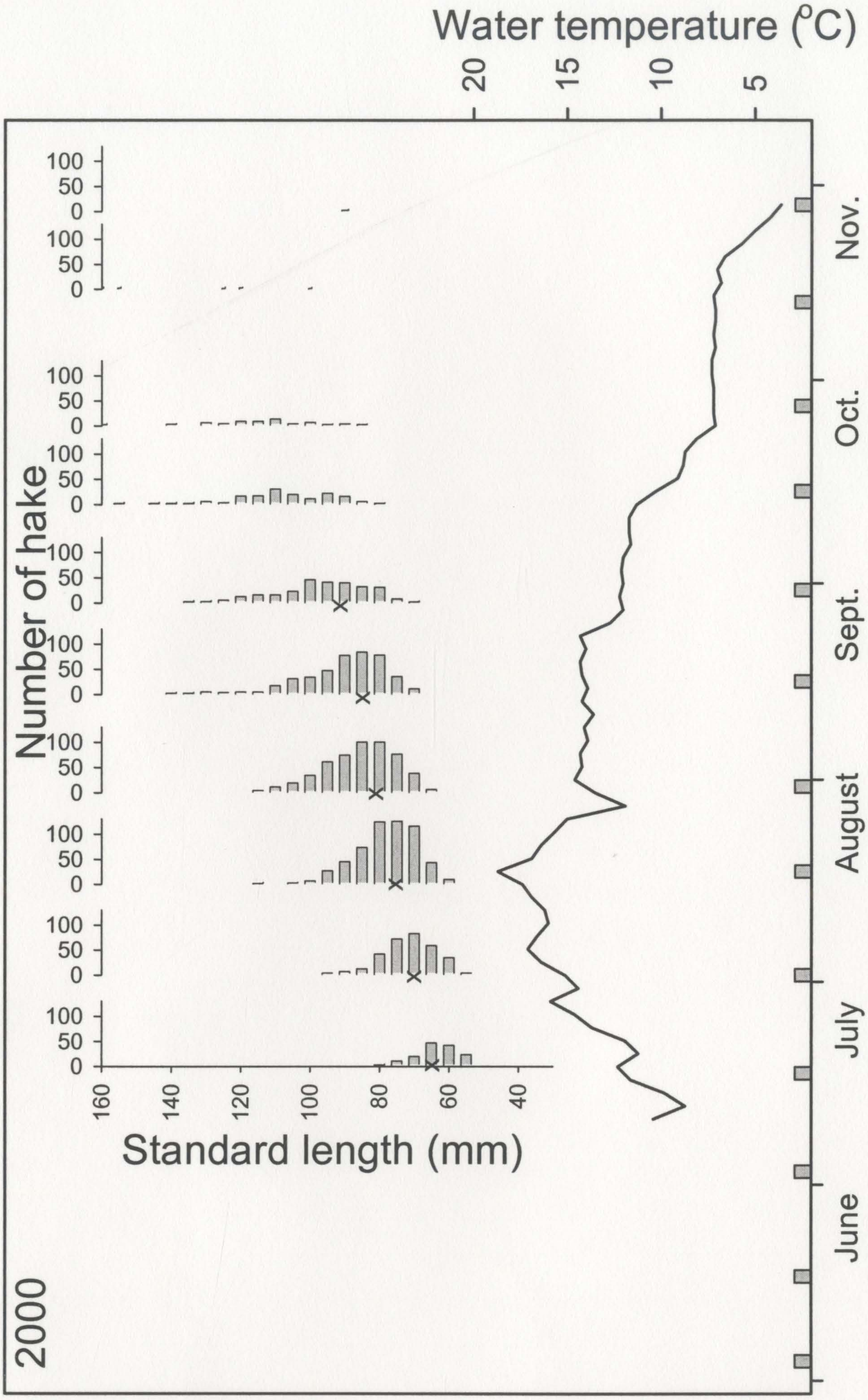

2000
Number of Greenland cod
0
100
200
Standard length (mm)
120
100
80
60
40
20
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.

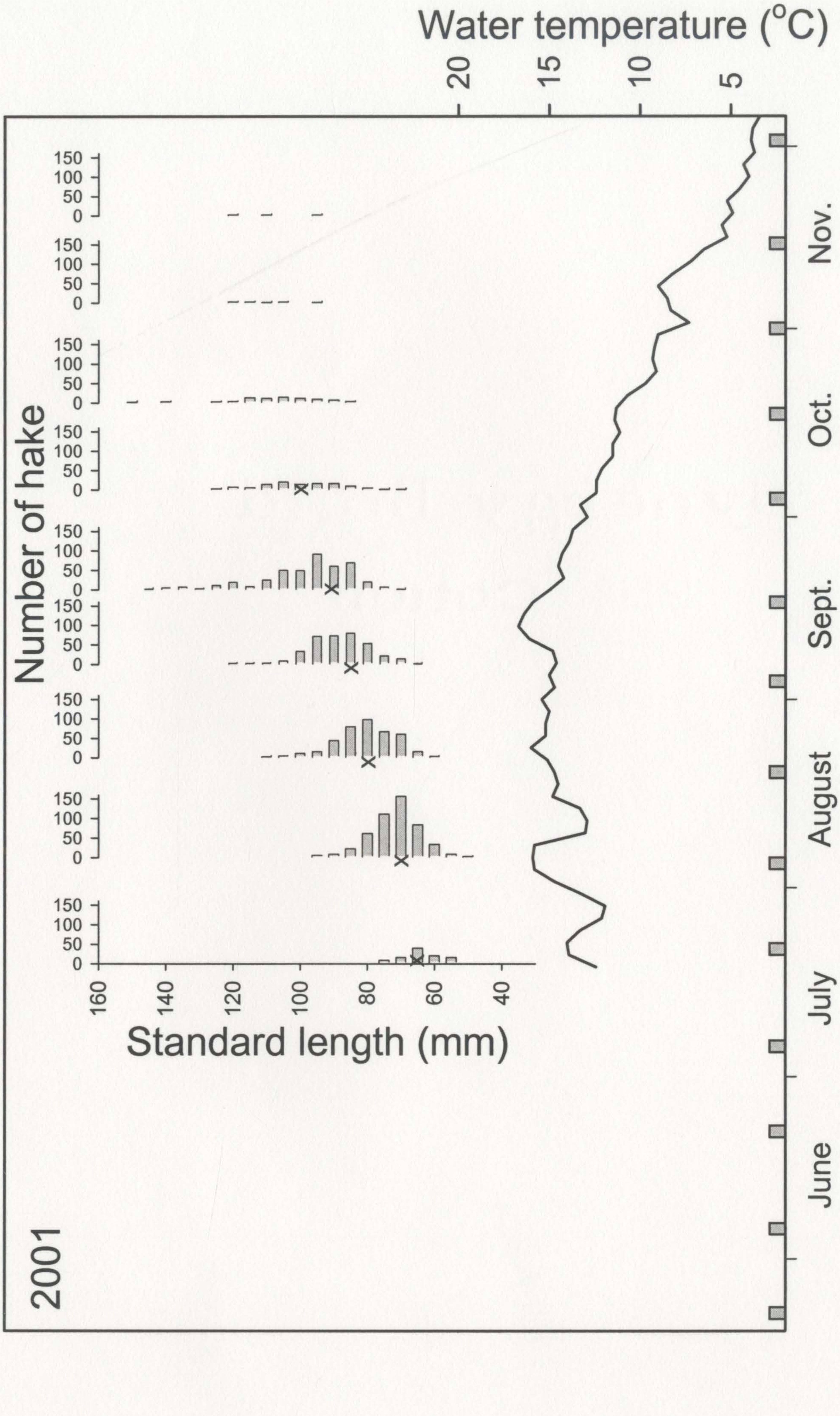

2001
Number of Greenland cod
Water temperature (°C)
20
15
10
5
0
100
200
120
100
80
60
40
20
June
July
August
Sept.
Oct.
Nov.

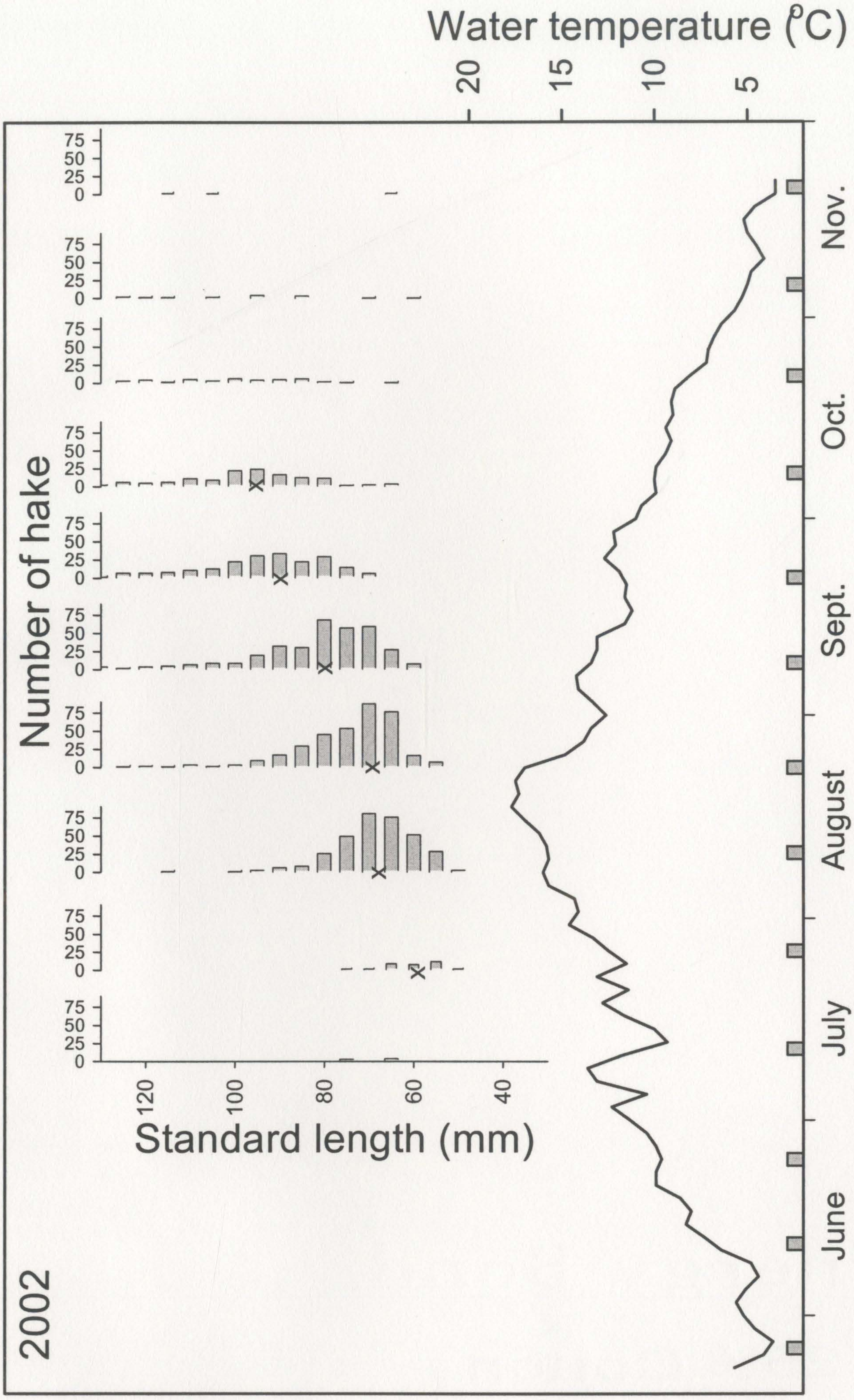

2002
Number of Greenland cod
0
100
200
300
Standard length (mm)
120
100
80
60
40
20
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.


1998
Water temperature (°C)
20
15
10
5
Number of Hake
0
40
80
Standard length (mm)
120
100
80
60
40
June
July
August
Sept.
Oct.
Nov.


1999
Water temperature (°C)
20
15
10
5
Number of Hake
50
25
0
Standard length (mm)
120
100
80
60
40
June
July
August
Sept.
Oct.
Nov.


2000
Number of hake
0
50
100
Standard length (mm)
160
140
120
100
80
60
40
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.


2001
Number of hake
0
50
100
150
Standard length (mm)
160
140
120
100
80
60
40
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.


2002
Number of hake
0
25
50
75
Standard length (mm)
120
100
80
60
40
Water temperature (°C)
20
15
10
5
June
July
August
Sept.
Oct.
Nov.

Page
Missing From
Original Text

Page
Missing From
Original Text

Appendix 2. Calculation of G statistics for the probability of recruitment of Atlantic cod to the nearshore during onshore winds after upwelling or at a particular tidal stage (low, intermediate, high).

Observed frequency (f) of recruitment events during onshore winds

	Onshore wind	Offshore wind	Totals
Recruitment	15	4	19
No recruitment	144	464	608
Totals	159	468	627

Rows x columns (p^)

	Onshore wind	Offshore wind
Recruitment	0.9430	0.001799
No recruitment	0.2145	0.7566

Expected frequencies (f^)

	Onshore wind	Offshore wind
Recruitment	59.151	1.1280
No recruitment	134.49	474.41

$G = 2 \sum f \ln f/f^\wedge = 25.10$, $p<0.001$.

Atlantic cod recruited to the nearshore an improbably high number of times during onshore winds.

Observed frequency (f) of recruitment events during high tides (same calculation for low tide)

	High tide	Other tides	Totals
Recruitment	3	16	19
No recruitment	123	485	608
Totals	126	501	627

Rows x columns (p^)

	High tide	Other tides
Recruitment	0.003760	0.02689
No recruitment	0.1980	0.7720

Expected frequencies (f^)

	High tide	Other tides
Recruitment	2.357	16.86
No recruitment	123.8	484.2

$G = 2 \sum f \ln f/\hat{f} = 0.234$, $p=0.6285$.

Recruitment of Atlantic cod to the nearshore during three high tides was not improbably high.

Observed frequency (f) of recruitment events during intermediate tides

	Intermediate tide	Other tides	Totals
Recruitment	13	6	19
No recruitment	362	246	608
Totals	375	252	627

Rows x columns (p^)

	Intermediate tide	Other tides
Recruitment	0.02372	0.007519
No recruitment	0.5748	0.3950

Expected frequencies (f^)

	Intermediate tides	Other tides
Recruitment	14.87	4.714
No recruitment	360.4	247.7

$G = 2 \sum f \ln f/f\hat{} = 0.622$, $p=0.4303$.

Recruitment of Atlantic cod to the nearshore during 13 intermediate tides was not improbably high.

Appendix 3. Analysis of the relationship between growth rate of Atlantic cod and water temperature.

Model: $G = ß_o + ß_T\, T + ß_{T2}\, T^2$

Symbols:

G = growth rate of newly-recruited Atlantic cod (%)

T=mean water temperature (°C)

Results:

Distribution: normal

link: log

Dependent variable: growth

Observations used: 14

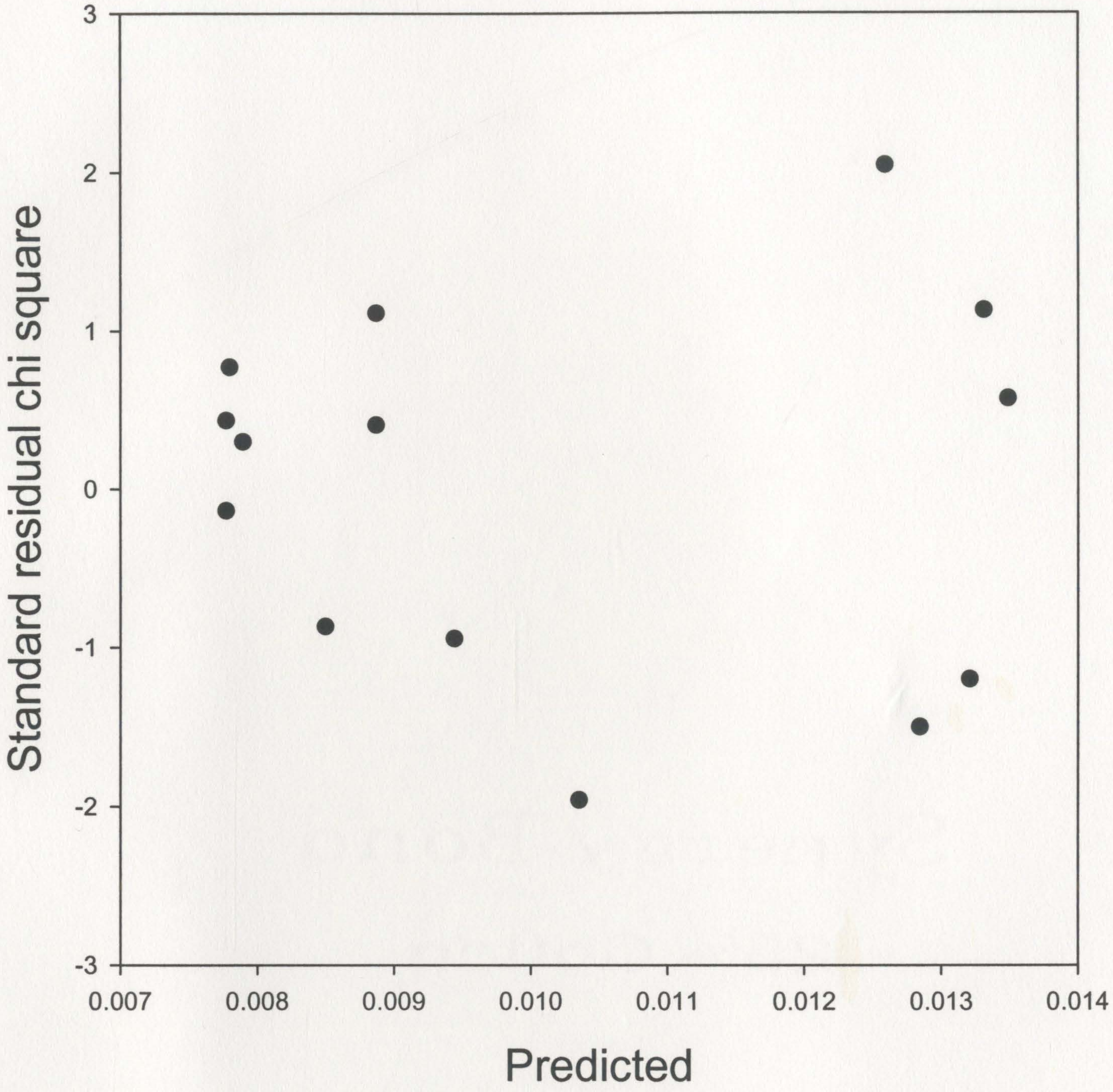
Analysis Of Parameter Estimates

			Standard	Wald 95%		Chi-	
Parameter	DF	Estimate	Error	Confidence Limits		Square	Pr > ChiSq
Intercept	1	-6.1399	0.7492	-7.6083	-4.6716	67.16	<.0001
temp	1	0.3671	0.1459	0.0812	0.6530	6.33	0.0118
temp2	1	-0.0184	0.0068	-0.0317	-0.0051	7.32	0.0068
Scale	1	0.0028	0.0005	0.0020	0.0041		

LR Statistics For Type 3 Analysis

		Chi-	
Source	DF	Square	Pr > ChiSq
T	1	5.96	0.0146
T2	1	6.39	0.0115

The regression equation is: $G=0.002155(e^{0.3671T})(e^{-0.0184T2})$


Standard residual chi square
3
2
1
0
-1
-2
-3
0.007
0.008
0.009
0.010
0.011
0.012
0.013
0.014
Predicted