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Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters

by D. W. Ings^{1,2}, R. S. Gregory³ and D. C. Schneider¹

ABSTRACT

Recruitment in marine fish is influenced by abiotic and biotic processes operating at many spatial and temporal scales. Annual recruitment to fisheries has received more attention at the scale of the population than at finer temporal scales, where spatially heterogeneous biological processes modify year-class success. We tested two hypotheses: (1) that recruitment of marine fish to the nearshore benthos at a fine temporal scale is determined by downwelling associated with onshore winds and (2) that fish arrival nearshore is related to tidal stage. During summer and autumn 1998 to 2001 and late spring to autumn 2002, we monitored recruitment of Atlantic cod (*Gadus morhua*), Greenland cod (*Gadus ogac*) and white hake (*Urophycis tenuis*) to benthic habitats at 12 sites in Newman Sound, Newfoundland every two weeks using seine nets. Seining was conducted daily at an additional site nearby for approximately two months during 2002. There were sufficient data to identify four to six annual recruitment pulses of Atlantic cod during 1999 to 2002. Greenland cod and white hake were found to recruit only once annually during 1998 to 2002. Winds were mostly offshore during the periods studied. During this same period recruitment of Atlantic cod (18 events), Greenland cod (5 events) and white hake (5 events) was found to begin on days with onshore winds or within three days following onshore wind events. Results were consistent with onshore larval transport and settlement during downwelling events. Recruitment of Atlantic cod, Greenland cod and white hake to the nearshore benthos was not associated with tidal stage. Upwelling dynamics may affect both the timing and the magnitude of recruitment of many other benthic species occupying the coastal zone.

1. Introduction

Many marine invertebrates and fish are highly fecund, producing large numbers of eggs and larvae, but few progeny survive to recruit to adult populations. Cohort size of marine fish is thought to be determined during the first year of life (Hjort, 1914), primarily during the egg and larval stages when mortality rates are high. For demersal marine fish, it is useful to define recruitment as the period of settlement to benthic habitats as mortality rates post-settlement only modify year-class strength (e.g. Fromentin *et al.*, 2001). Recruitment

1. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's Newfoundland, Canada, A1C 5S7.

2. Corresponding author. *email: ings@mun.ca*

3. Fisheries and Ocean Canada, Ecological Sciences Section, P.O. Box 5667, St. John's Newfoundland, Canada, A1C 5X1.

of fish to habitats appropriate for juvenile survival depends on biological processes acting both locally (Wroblewski *et al.*, 2005) and at a distance (Bailey, 1981). In addition to biological processes, physical processes such as retention (Isles and Sinclair, 1982; Sinclair, 1988) and dispersion (Nelson *et al.*, 1977; Bailey, 1981) are important determinants of recruitment in marine fish.

The theory guiding most of the research on 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 by 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 the larval period (up to metamorphosis) and period of prey abundance determines recruitment success. Cushing (1990) compiled evidence for increased recruitment of fish during years with overlap between peak spawning time and periods of high production. Hypothesis (2) from Hjort (1914) led to development of the “migration triangle” concept (Harden Jones, 1968); see review by Secor (2002). The central principle of the “migration triangle” is that populations are closed—spawning occurs in 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). 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 (Bailey, 1981) have been considered to be consistent with a circuit between spawning location and widespread distributions of juvenile fish.

Oceanographic processes operating over various spatial scales determine the transport of eggs and larvae of marine invertebrates and fish. Eggs and larvae of temperate marine fish can drift from continental shelf areas to coastal waters, even when prevailing winds are offshore, as in the northwest Atlantic (e.g. Pepin and Helbig, 1997). In the northeast Atlantic, results from daily sampling for juvenile fish along the coast of Norway during 1898-99 led Hjort and Dahl (1900) to postulate that wind-induced movements of coastal water masses in autumn determined Atlantic cod recruitment at the coast. This hypothesis was never tested rigorously. More recently, movements of coastal water masses and associated oceanographic fronts are known to transport invertebrate (Farrell *et al.*, 1991; Roughgarden *et al.*, 1991; McCulloch and Shanks, 2003) and fish (Boehlert and Mundy, 1987) larvae toward the coast. Tidal forcing is also known to influence the nearshore distributions of larval invertebrates and fish (Boehlert and Mundy, 1987; Pineda, 1994). Two mechanisms have been proposed. One is that larvae and juvenile fish or invertebrates are transported onshore only during the down slope progression phase when surface waters are advected onshore fortnightly (Pineda, 1994). An alternative hypothesis (Pineda, 1999) is that larvae accumulate near the surface in the tidal front or at surface slicks; then,

accumulations of larvae are transported to the coast when the tidal front and non-linear internal waves that are associated with the bore, move to the coast. These relatively weak events often occur in a series (daily) and are out of phase with the fortnightly tidal bores (Pineda, 1999). Movements of both upwelling and tidal fronts toward the coast may transport larvae and pelagic juveniles and deposit them at the coast (Farrell *et al.*, 1991; Roughgarden *et al.*, 1991; Pineda, 1994; McCulloch and Shanks, 2003).

A better understanding of recruitment processes in Atlantic cod on the northeast Newfoundland Shelf is critical now because the population has declined by more than 99% from historical levels and was declared Endangered in 2003 by the Council on the Status for Endangered Wildlife in Canada (COSEWIC, 2003). Despite the biological and socio-economic consequences of this population collapse in 1992, processes governing recruitment of Atlantic cod on the northeast Newfoundland Shelf remain poorly understood. Extended spawning by cod (Hutchings *et al.*, 1993) relative to the seasonal availability of zooplankton leaves little opportunity for recruitment variation on the northeast Newfoundland Shelf according to the match/mismatch hypothesis (Brander, 1994). Studies on transport mechanisms may be more useful, but results have been inconsistent. Simulations of particle drift in the surface layer (e.g. Helbig *et al.*, 1992) suggest that strong and prolonged onshore wind forcing would be required for larvae to be transported to coastal areas from known spawning locations on the continental shelf and slope (Hutchings *et al.*, 1993). Modeling has also suggested that only a small percentage of the larvae transported inshore would be retained there (Pepin and Helbig, 1997). However, these results stand in contrast to three observations: (1) high numbers of demersal juvenile cod are observed inshore relative to offshore (Dalley and Anderson, 1997); (2) juvenile cod recruit to coastal sites in multiple pulses annually (Methven and Bajdik, 1994; Grant and Brown, 1998); and (3) genetic analysis showed that cod recruiting to the coast originate from both offshore and nearshore sources (Beacham *et al.*, 2000). Clearly, Atlantic cod are recruiting to coastal waters from areas offshore. One simple explanation is that cod move onshore with the deeper onshore flow that necessarily replaces water moving offshore at the surface, presumably at the lower boundary of the surface layer. In light of this potential causal mechanism, we investigated recruitment to the bottom at the coast in relation to onshore and offshore shifts of this boundary in response to wind-forced upwelling.

We tested two hypotheses. The first was that demersal fish recruit to benthic habitats on the northeast coast of Newfoundland during wind-induced events (Schneider and Methven, 1988) as hypothesized by Hjort and Dahl (1900) and observed in some invertebrates (McCulloch and Shanks, 2003). For the northwest Atlantic, where the coast is leeward of the prevailing winds, we refined this to the hypothesis that demersal fish recruit to the bottom at the coast during brief periods when wind driven upwelling collapses. The patterns in recruitment of Atlantic cod, Greenland cod and white hake (hake) to the benthos were evaluated relative to downwelling events associated with cessation of upwelling-favorable winds (see Fig. 1A). The second hypothesis, developed for invertebrate larvae on

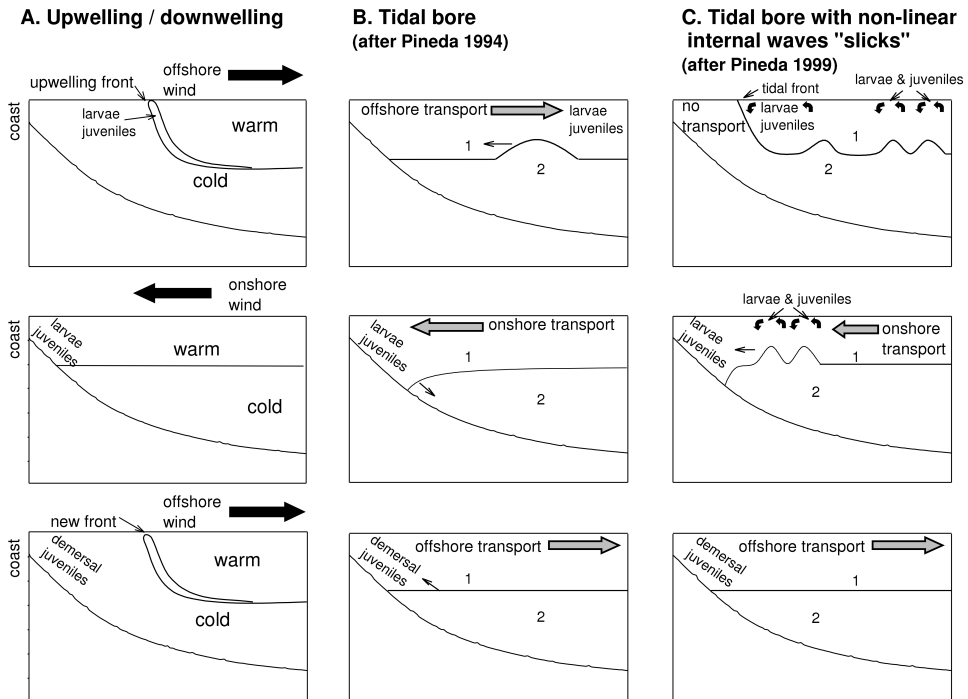


Figure 1. Diagram illustrating transport of marine larvae and pelagic juvenile fish to nearshore habitats by upwelling/downwelling (Section A), tidal bores (Section B) and nonlinear internal waves (Section C). During upwelling in confined bays along the northeast coast of Newfoundland (A, top panel) winds are offshore and an upwelling front exists a few kilometers from the coast where larval and pelagic juvenile fish accumulate. During the relaxation phase (A, 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 of section A, winds switch to offshore again and another upwelling front is established away from the coast. Larvae or pelagic juvenile fish have made the transition to the demersal juvenile stage in the bottom panels of Sections A, B and C. Two mechanisms (Sections B and C) have been proposed to explain how tidal bores advect a dense (ρ_2) water body and larvae onshore. One hypothesis is that larvae and juvenile fish or invertebrates are transported onshore only during the down slope progression phase when surface waters are advected onshore (B, middle panel). An alternative hypothesis is that larvae accumulate near the surface in the tidal front or at surface slicks (C, top panel); then, accumulations of larvae are transported to the coast when the tidal front and nonlinear internal waves that are associated with the bore, move to the coast (C, middle panel). Thick arrows indicate the overall direction of winds (black) or water transport (waves). Short arrows indicate water flow at specific locations.

the coast of southern California (Pineda, 1994; 1999, see Fig. 1B & C), was that fish recruit to benthic habitats in association with tidal forcing. To test these two hypotheses, we used fine scale temporal data to estimate recruitment dates in 1998-2002 with regard to both downwelling periods and tidal phases.

2. Material and methods

a. Study site

Off the northeast coast of Newfoundland, Atlantic cod historically ranged over most of the continental shelf from shallow coastal waters to the edge of 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 is along 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 and offshore (Helbig *et al.*, 1992, and literature cited therein). Episodic upwelling occurs along the northeast coast of Newfoundland associated with strong southwest wind events (Sleggs, 1933; Templeman, 1948). Depending on coastal configuration, either the cross shore or the longshore component of a two-day wind event has sufficient force to draw the seasonal thermocline to the surface (Schneider and Methven, 1988). However, upwelling events occur along this coast in the absence of local wind events due to propagating internal waves (de Young *et al.*, 1993). Tidal currents also influence advection on the northeast Newfoundland Shelf. Research has focused on the M2 tide which has a range of 0.14 m offshore and 0.64 m near shore (Han *et al.*, 2000); larger tidal ranges (1.2 m) occur fortnightly (Canadian Hydrographic Service).

b. Fish sampling

From 1998–2002, 12 sites in Newman Sound, Bonavista Bay (Fig. 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 seine net with 19 mm stretch mesh in the wings and belly and 9 mm stretch mesh in the codend was used to sample 880 m² (16 m along shore, 55 m offshore). The seine sampled the bottom two meters of the water column. From SCUBA observations during 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 (Grant and Brown, 1998). Fish were measured (mm SL—Standard Length) and released alive at the site of capture.

To determine arrival times of fish and size at recruitment to the benthos, beach seines were deployed daily from 11 July to 6 September of 2002 and subsequently two to four times per week until 23 October at one location (Bermuda Beach) in Newman Sound (Fig. 2). This location contained ten sampling sites with similar bottom types and depth profiles. We sampled two sites per day (e.g., 1 and 6, 2 and 7 etc.) within two hours of low tide.

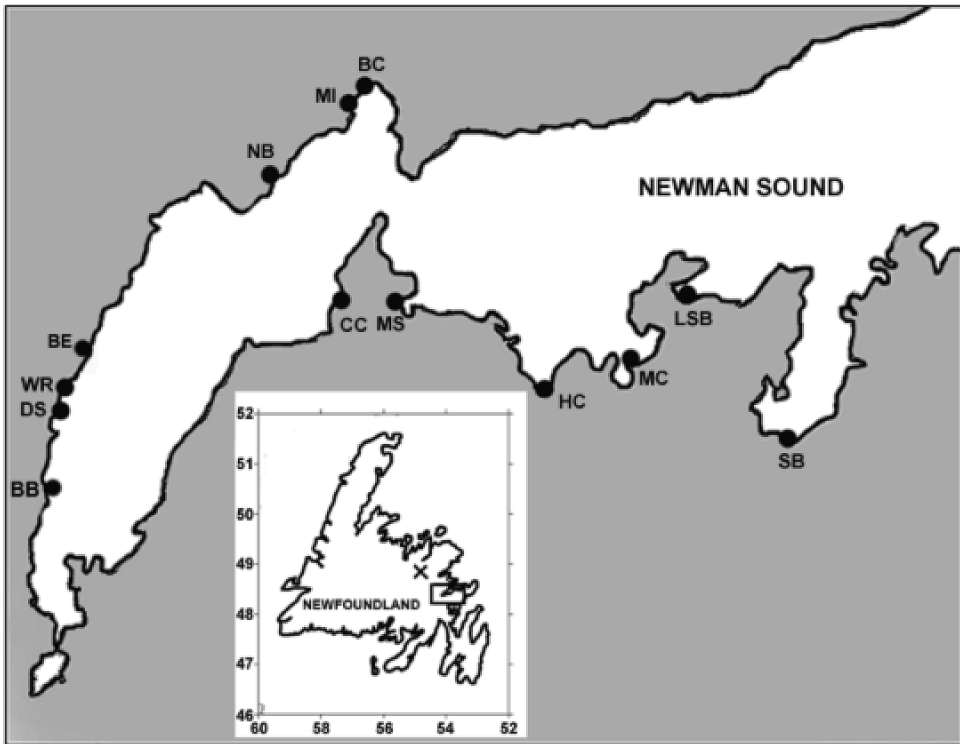


Figure 2. Map of Newfoundland showing sites in Newman Sound sampled by beach seine for *Gadus morhua*, *G. ogac* and *Urophycis tenuis* during 1998 to 2002. Sites were South Broad Cove (SB), Little South Broad Cove (LSB), Minchins Cove (MN), Hefferns Cove (HC), Mount Stanford Cove (MS), Buckleys Cove (BC), Mistaken Cove (MI), Newbridge Cove (NB), White Rock (WR), Dockside (DS) and Big Brook (BB). Daily seining was conducted at Bermuda Beach (BE). Water temperatures were monitored at Buckleys Cove (BC). Wind data were recorded at Gander Airport indicated by an X.

c. Estimation of fish size at arrival and arrival time

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. Regression analysis was used to reduce bias in estimates of fish size at arrival when few fish were collected on the first sample date post recruitment; regressions also incorporate more available data (subsequent modal lengths) than an approach using data only from the first sampling date post recruitment. 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. Daily modal lengths were averaged when bins were of equal size. 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.

Arrival times of fish (1998-2002) were also estimated from regressions of modal length of fish and Julian date. Daily plots (Atlantic cod) or biweekly plots (Greenland cod and hake) of length frequencies were constructed as above to distinguish among recruitment pulses. Recruitment events were identified in length frequency plots by the appearance of fish at the estimated size of arrival (see above) on one or two sample days. On subsequent days, a mode in each length frequency plot (when discernable) was assigned to this recruitment pulse. 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 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 into the equations obtained from regression of daily modal length of fish and Julian date.

d. Water temperature data

Water temperatures were monitored at four locations within Newman Sound (Fig. 2) by Hurgun 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 among sites; therefore, data from Buckleys Cove were analyzed as this site was monitored during all five years and was near the location seined daily.

e. Calculation of wind energy

Hourly wind speed and direction data were collected by Environment Canada during 1998-2002 at Gander Airport (Fig. 3), located 70 kilometers northwest of Newman Sound. These data were used as continuous wind speed and direction data were available from Newman Sound only during the 2000 and 2001 study periods; wind stress at Gander airport during these periods was correlated with data from Newman Sound (2000: $\chi^2 = 27.26$, $p < 0.0001$; 2001: $\chi^2 = 9.04$, $p = 0.0026$). Wind stress relative to the east coast of Newfoundland was calculated using Eq. 5b (with a drag coefficient added) in Schneider and Methven (1988):

$$W_x = cW(-W \cos(A - 50)) \quad (1)$$

where;

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

c is a constant (0.002 kg m^{-3}) representing the drag coefficient multiplied by air density

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), and

the constant, 50° , was the angle of the coast at our site.

Only the cross-shore component of wind stress was used as Newman Sound is an irrotational bay ($< 5 \text{ km}$ wide), ie. too narrow to allow longshore winds to drive upwelling.

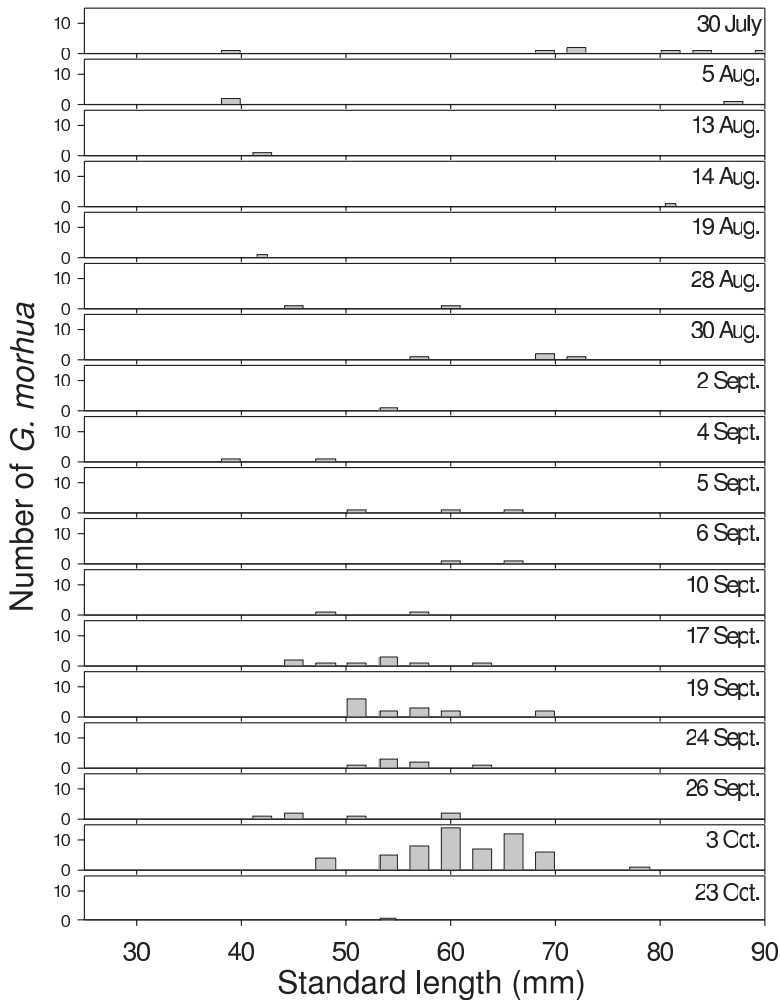


Figure 3. Daily length frequency plots for *Gadus morhua*. Data were collected by beach seine at Bermuda Beach between 11 July and 23 October 2002. Newly recruited Atlantic cod were not observed before 30 July so data between 12-29 July were not presented.

f. 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. Regression analyses were performed in SAS (1988). The odds for recruitment events versus tidal stage occurrence were tested using a generalized linear model (Proc Genmod) in SAS (1988). In all statistical testing, tolerance of type I error was set at $\alpha = 0.05$.

g. Analysis of wind influence on recruitment

We used a randomization test (Superposed Epoch analysis, Prager and Hoenig, 1989) to test for association between recruitment of Atlantic cod and onshore wind events. For this analysis, data on both recruitment and wind stress were grouped into three day periods as biweekly seining of our 12 sites was typically conducted over 2-4 days and average dates were used in analyses to determine time of fish arrival at the coast. We constructed a superposed epoch for three periods; 1-3 days prior, 1-3 days post and 4-6 days post the initiation of onshore winds or tidal stage. The test statistic was:

$$W_e = (1/N_B \sum_{i=1}^{N_E} \sum_{j=1}^{n_i} (E_i - B_{ij})) N_B^{0.5} / (1/N_B - 1 \sum_{i=1}^{N_E} \sum_{j=1}^{n_i} (E_i - B_{ij}) - (1/N_B \sum_{i=1}^{N_E} \sum_{j=1}^{n_i} (E_i - B_{ij})))^{0.5} \quad (2)$$

where;

W_e = test statistic

N_B = number of background events

N_E = number of wind events

E_i = event periods (1 or 0 for recruitment presence or absence respectively) and

B_{ij} = background periods (1 or 0 for recruitment presence or absence respectively).

Random permutations (with replacement) of the observed E_i and B_{ij} values were used to generate a set of E_i and B_{ij} values that were used subsequently to calculate a W_e value. This iteration was repeated 10,000 times to obtain a frequency distribution of the statistic. This frequency distribution was used to calculate the probability of obtaining the observed value of W_e by chance alone. Randomizations were performed in Minitab.

3. Results

a. Fish sampling

i. Daily sampling during 2002. A total of 401 Atlantic cod were collected in 127 seine hauls between 12 July and 23 October 2002 at Bermuda Beach (Fig. 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). 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. We 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.

Daily modal lengths of Atlantic cod was regressed against Julian date ($F_{[1,4]} = 5.33$, $p=0.2601$; Table 1) to estimate the length of cod at recruitment to the nearshore. The

Table 1. Length of *Gadus morhua*, *G. ogac* and *Urophycis tenuis* on the first day of recruitment at Bermuda Beach, 2002 estimated from regressions of modal length of fish and Julian date. Confidence intervals (95%) for the slope (growth rate) are provided. Data were collected daily by beach seine between 12 July and 23 October.

Fish	β	Confidence intervals		α	R^2	n	First day of recruits	Estimated length of recruits (mm)
		Lower	Upper					
<i>G. Morhua</i>	0.316	0.0481	0.584	-27.00	0.84	3	247 (4 Sept.)	43
<i>G. ogac</i>	0.788	0.762	0.814	-123.72	0.98	52	198 (17 July)	33
<i>U. tenuis</i>	0.700	0.630	0.770	-83.86	0.91	41	199 (18 July)	55

length of cod at recruitment as calculated from this equation was 43 mm. This estimate was considered unreliable because the relationship between daily modal length of Atlantic cod and Julian date was weak ($p=0.2601$; Table 1). We 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) observed previously (Grant and Brown, 1998) to begin transition from a pelagic to a benthic diet (Lomond *et al.*, 1998). Overall, the pulses we observed at Bermuda beach during 2002 were represented by a small number of fish (Fig. 3). We assumed that a relatively small number of cod collected on a particular day approximated the modal length of the population on that day.

A total of 4436 Greenland cod were collected at Bermuda Beach during 2002 (Fig. 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. 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. 4). We concluded there was one recruitment event for Greenland cod at Bermuda Beach during 2002; it began on 17 July.

To estimate the length of Greenland cod on the first day of recruitment (Julian date 198), we regressed daily modal length of fish and date for Julian date 199 onward (Table 1). Modal length of Greenland cod increased with time ($F_{[1,52]} = 3548.94$, $p < 0.0001$) according to the equation $SL = 0.7884(\text{Julian date}) - 123.72$ (Table 1). Using this equation, we backcalculated the modal length of Greenland cod on the first day of recruitment (Julian date 198) as 33 mm.

A total of 945 hake were collected at Bermuda Beach during 2002 (Fig. 5). The earliest date of hake collection during the period of study was 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

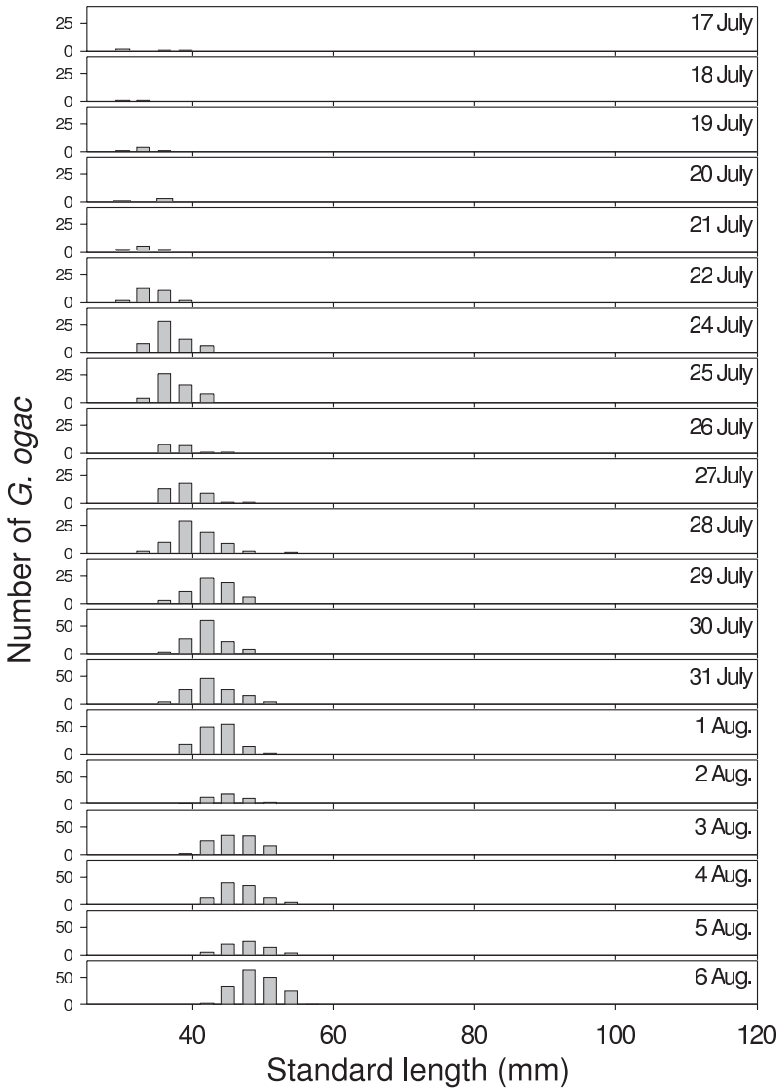


Figure 4. Daily length frequency plots for *Gadus ogac*. Data were collected at Bermuda Beach in 2002. Newly recruited *G. ogac* were not observed before 17 July so data between 12-16 July were not presented.

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. 5) than for Greenland cod (Fig. 4). However, modal length of hake increased with time (Fig. 5). We concluded there was one recruitment event for hake at Bermuda Beach during 2002. Note that three small hake were

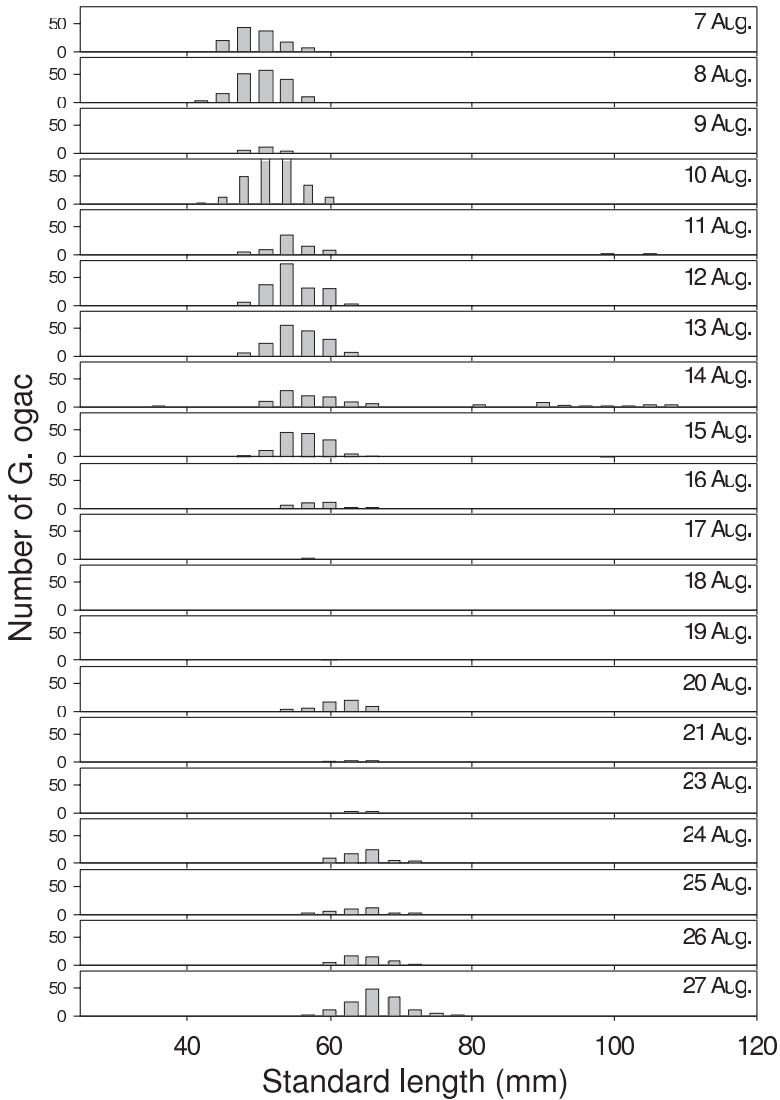


Figure 4. (Continued)

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. 8).

To determine the length of hake on the first day of recruitment at Bermuda Beach (Day 199), we regressed daily modal length of fish and date for Julian dates from 200 onward (Table 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 1). Using this equation, we

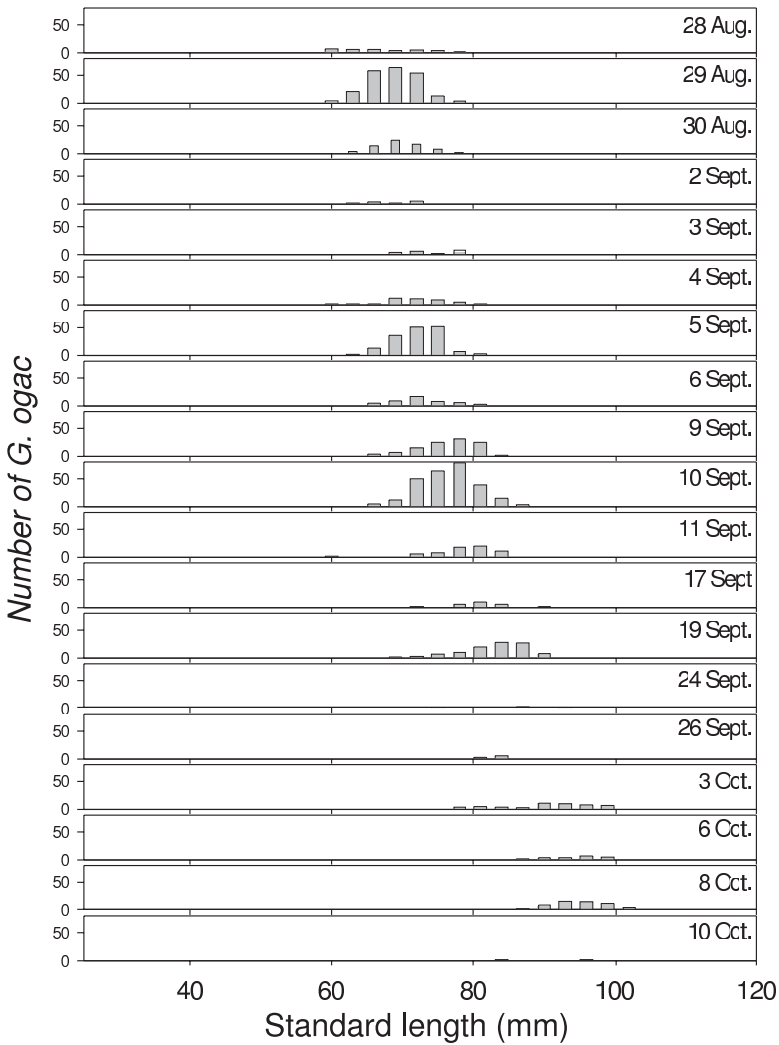


Figure 4. (Continued)

backcalculated the modal length of hake on the first day of recruitment (Day 199) as 55 mm.

ii. Biweekly sampling during 1998-2002. Average catch rates of Atlantic cod sampled during 1999 to 2002 ranged from 6.24 fish per haul in 2001 to 60.53 fish per haul in 1999 (Table 2). The average number of Greenland cod per haul ranged from 44.33 in 2001 to 76.67 in 2000 (Table 2). Data on Atlantic cod collected during 1998 were not included in analyses as only a small proportion of these fish were sub-sampled and measured. The

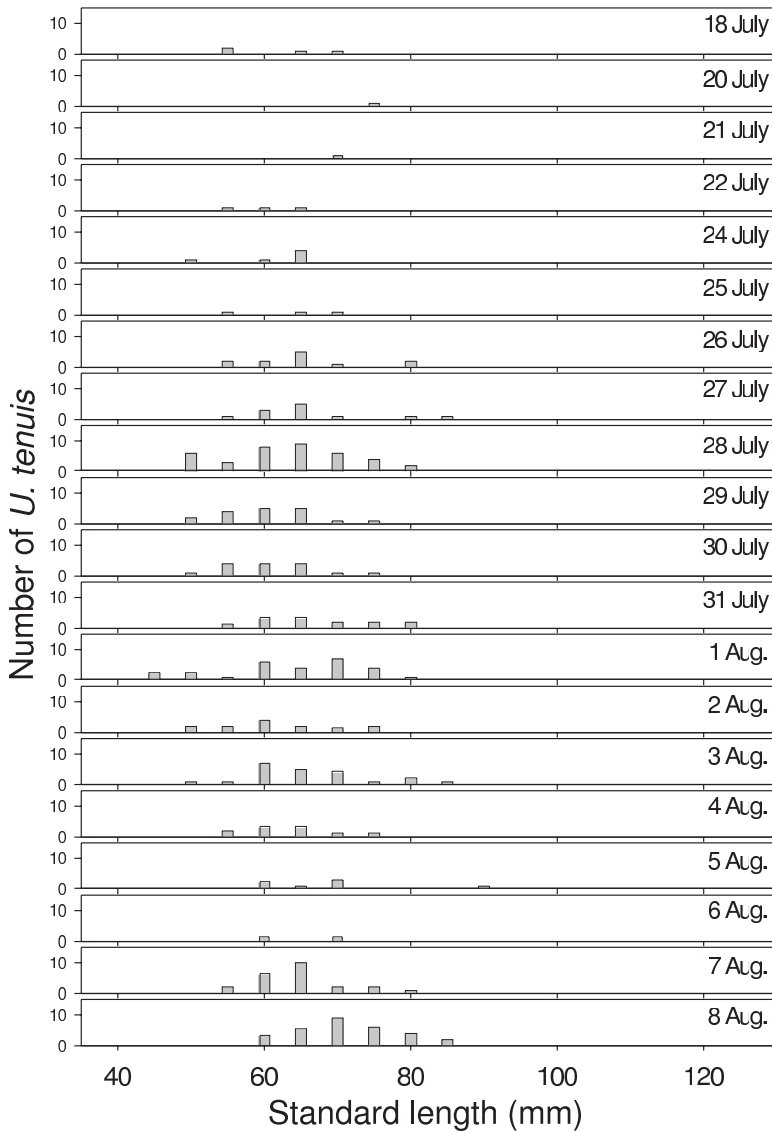


Figure 5. Daily length frequency plots for *Urophycis tenuis*. Data were collected by beach seine at Bermuda Beach between 12 July and 23 October 2002. Newly recruited *U. tenuis* were not observed before 18 July so data between 12-17 July were not presented.

average number of hake per haul between 1998 and 2002 ranged from 7.44 in 1998 to 21.56 in 2000 (Table 2).

Size frequencies of Atlantic cod sampled during 1999-2002 and Greenland cod and hake sampled during 1998-2002 were plotted (e.g. Appendix 1) to determine recruitment events.

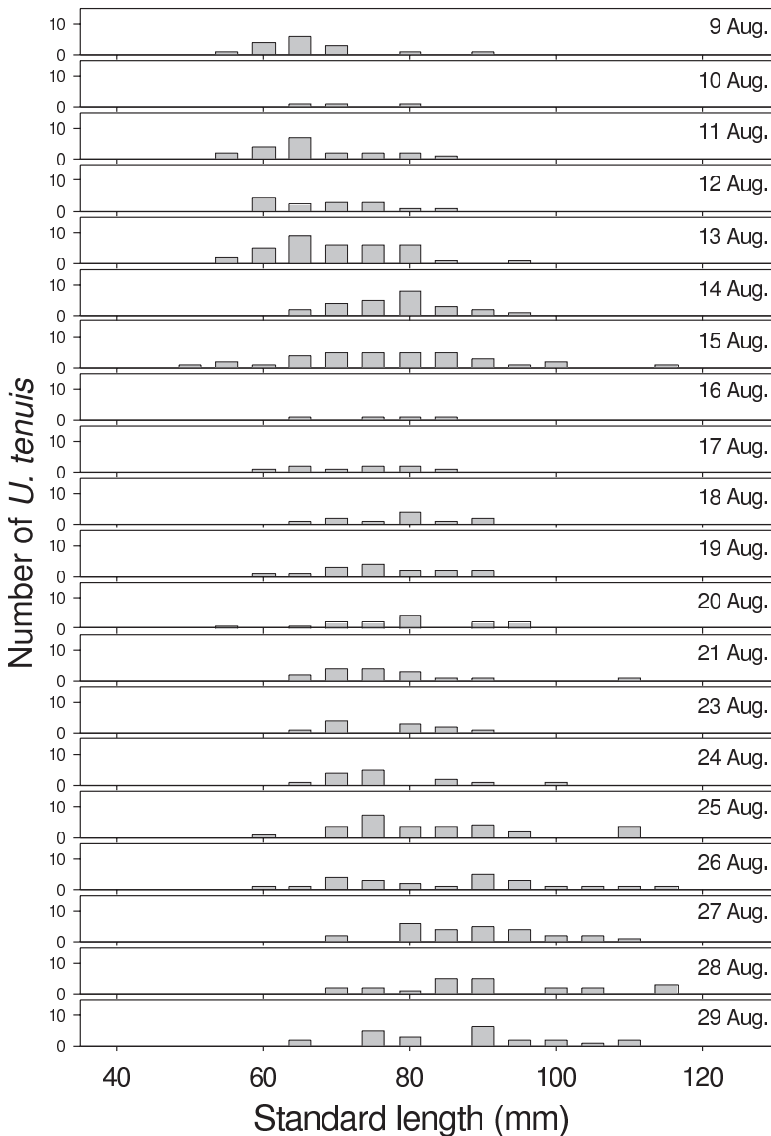


Figure 5. (Continued)

Modal lengths of fish in daily size frequency plots were determined visually and regressed against date to track pulses of recruitment through time (Table 3; e.g. 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 not significant ($F_{[1,3]} = 13.65, p = 0.0661$), possibly due to the small sample size ($n=4$). This event was removed from further analyses. Four or five recruitment events for Atlantic cod were identified each year during 1999 to 2001. During

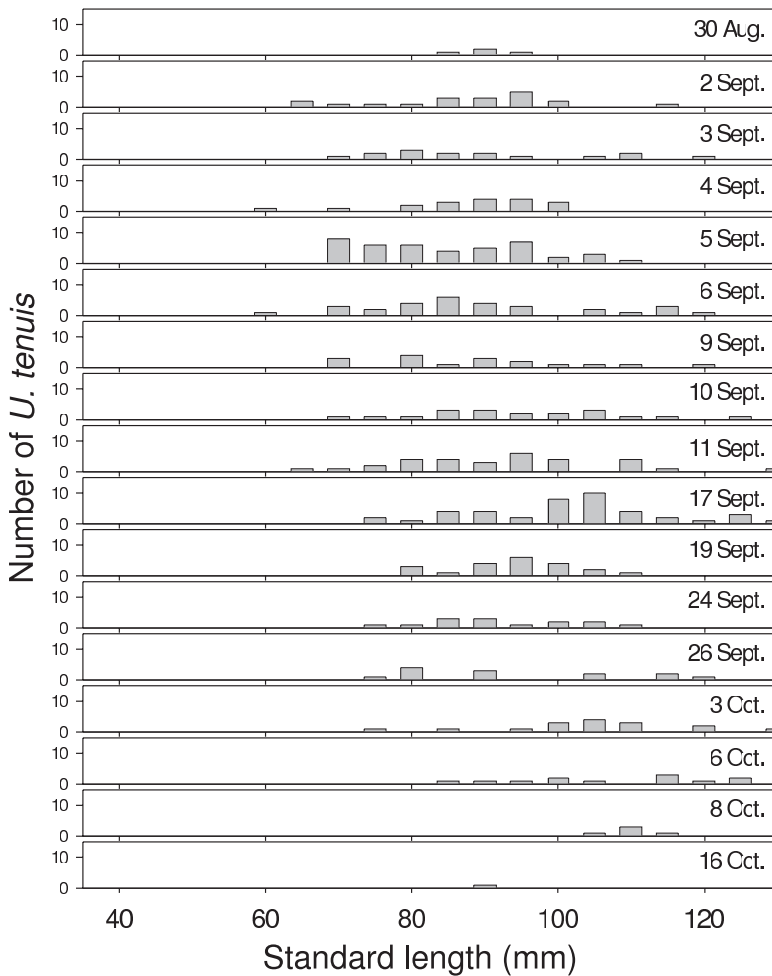


Figure 5. (Continued)

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, five recruitment pulses were identified and analyzed; the first event was estimated to begin on 21 May and the fifth on 27 September (Table 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 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

Table 2. Number of *Gadus morhua*, *G. ogac* and *Urophycis tenuis* per haul collected by beach seine at 12 sites in Newman Sound during 1998 to 2002

Year	<i>G. morhua</i> (# haul ⁻¹)	<i>G. ogac</i> (# haul ⁻¹)	<i>U. tenuis</i> (# haul ⁻¹)	Number of seine hauls
1998	28.51	54.49	7.44	112
1999	60.53	76.67	10.14	118
2000	10.99	52.09	21.56	120
2001	11.29	34.65	20.39	102
2002	12.62	28.26	9.59	159

(Day 198) in 2001 and 2002 (Table 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 5).

b. Summary of physical variables 1998-2002

Winds were mostly offshore during the periods studied (Fig. 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 4.09 Pa

Table 3. Estimated initiation dates for recruitment of *Gadus morhua* during 1999 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained from regression of daily modal length of *G. morhua* (mm SL) against Julian date. Confidence intervals (95%) for the slope (growth rate) are provided. Fish were collected by beach seine.

Year	Event	β	Confidence intervals		α	R ²	N	Estimated date of event
			Lower	Upper				
1999	1	0.703	0.581	0.825	-109.58	0.96	8	30 July
1999	2	0.670	0.574	0.766	-116.88	0.97	7	21 Aug.
1999	3	0.522	0.445	0.599	-89.87	0.97	8	4 Sept.
1999	4	0.594	0.411	0.494	-122.39	0.93	6	29 Sept.
2000	1	0.506	0.447	0.565	-66.33	0.98	9	26 July
2000	2	0.439	0.394	0.484	-58.92	0.98	9	10 Aug.
2000	3	0.257	0.175	0.339	-23.46	0.91	6	30 Aug.
2001	1	0.503	0.461	0.545	-61.53	0.99	8	19 July
2001	2	0.701	0.612	0.790	-127.57	0.98	6	28 Aug.
2001	3	0.528	0.451	0.605	-93.67	0.98	6	8 Sept.
2002	1	0.544	0.355	0.733	-37.63	0.84	8	21 May
2002	2	0.723	0.660	0.786	-79.28	0.99	5	13 June
2002	3	0.425	0.243	0.607	-50.60	0.88	5	30 July
2002	4	0.340	0.172	0.508	-43.03	0.84	5	29 Aug.
2002	5	0.645	0.423	0.867	-135.23	0.89	6	27 Sept.
2002	6	0.336	0.158	0.514	-59.34	0.87	4	20 Oct.

Table 4. Estimated initiation dates for recruitment (at 33 mm) of *Gadus ogac* during 1998 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained by regression of daily modal length (mm SL) of *G. ogac* against Julian date. Confidence intervals (95%) for the slope (growth rate) are provided. Fish were collected by beach seine.

Year	β	Confidence intervals		α	R^2	N	Estimated date of event
		Lower	Upper				
1998	0.640	0.562	0.718	-88.82	0.99	6	10 July
1999	0.685	0.563	0.807	-94.21	0.97	6	5 July
2000	0.690	0.633	0.747	-100.25	0.99	6	14 July
2001	0.651	0.617	0.686	-95.60	0.99	7	17 July
2002	0.740	0.664	0.816	113.60	0.99	7	17 July

(mean wind speed was 13.9 m s^{-1}) calculated for 15 October 1999. Onshore wind stress was never higher than 2.26 Pa (mean wind speed was 9.5 m s^{-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 $3\text{-}4^\circ\text{C}$ in May to $16\text{-}17^\circ\text{C}$ in August and then decreased to $3\text{-}4^\circ\text{C}$ by late November (Fig. 6). During 1999, the seasonal pattern of water temperature differed from other years as 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 $4\text{-}5^\circ\text{C}$ over four to eight days and a subsequent return to predecline levels.

c. Influences on arrival times

i. *Wind stress.* We analyzed data on 18 recruitment events for Atlantic cod in Newman Sound from 1999 through 2002 (Fig. 6). All 18 events occurred within three days of the

Table 5. Estimated initiation dates for recruitment (at 55 mm) of *Urophycis tenuis* during 1998 to 2002 in Newman Sound, Bonavista Bay calculated from the equation obtained by regression of daily modal length of *U. tenuis* against Julian date. Confidence intervals (95%) for the slope (growth rate) are provided. Fish were collected by beach seine.

Year	β	Confidence intervals		α	R^2	N	Estimated date of event
		Lower	Upper				
1998	0.605	0.486	0.724	-61.05	0.96	6	11 July
1999	0.607	0.541	0.673	-57.79	0.99	5	5 July
2000	0.377	0.349	0.405	-10.69	0.99	6	22 June
2001	0.454	0.410	0.498	-26.42	0.99	6	28 June
2002	0.484	0.407	0.561	-40.42	0.97	6	15 July

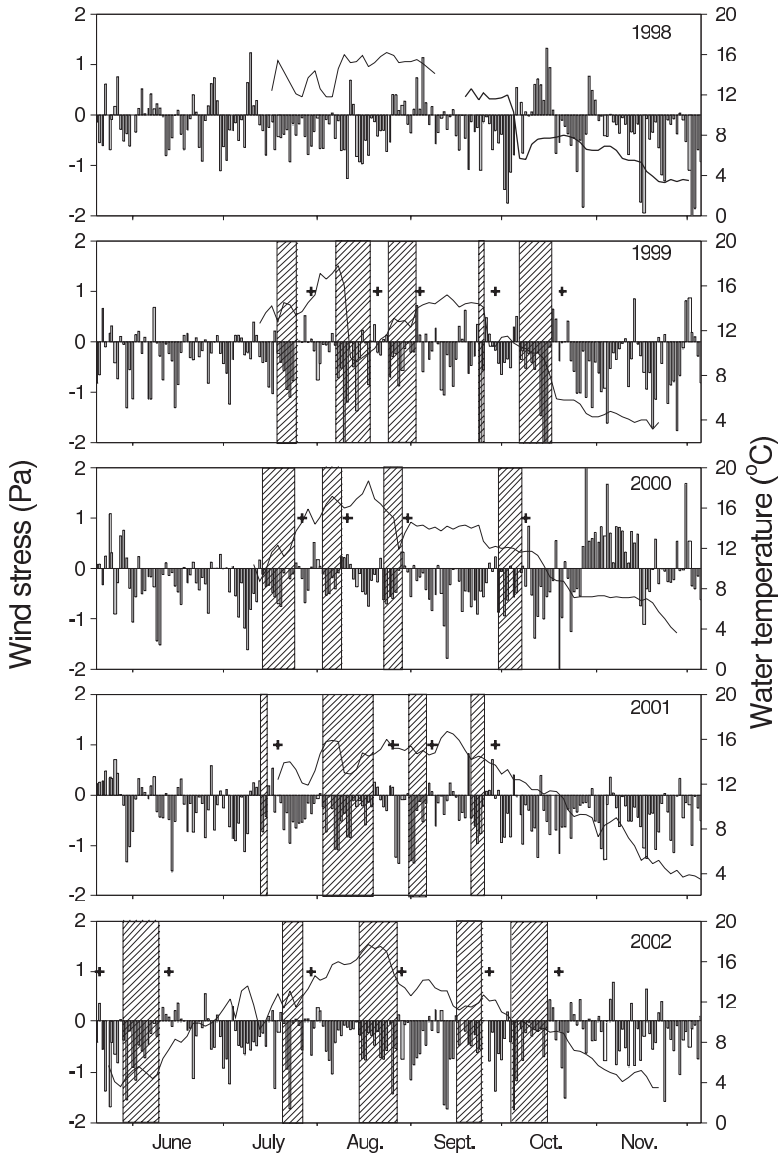


Figure 6. Estimated dates that recruitment of *Gadus morhua* began at Newman Sound during July to November, 1999 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling-favorable winds prior to arrival of Atlantic cod. + indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress. The recruitment event shown on 20 Oct. 2002 was not used in analyses as only four data values were available for regressions.

initiation of onshore winds. (Fig. 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 93 periods (3 days each) with onshore winds following offshore winds. The chance of obtaining this degree of association between recruitment of Atlantic cod and onshore wind events, based on randomization, is $p = 0.0479$. The association between recruitment of Atlantic cod and onshore wind events following upwelling exceeds that of chance alone (Fig. 6).

Similar to Atlantic cod, estimated recruitment dates of Greenland cod and hake occurred after cessation of offshore winds. During five of five years, estimated recruitment dates of Greenland cod (Fig. 7) and hake (Fig. 8) to sites in Newman Sound occurred during the three day period following initiation of onshore winds.

ii. Tidal stage. 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. 9). During the study periods, there were 42 periods with highest tides and 42 periods with lowest tides. The expected odds of recruitment on a day with highest or lowest tides was $p/1-p = (42/209)/(167/209) = 0.25:1$. Three of 18 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 18 events is $0.20:1$. The dates when recruitment was estimated to have begun were not significantly associated with highest ($\chi=0.13$, $p=0.7210$) or lowest tides ($\chi=0.130$, $p=0.7210$). On 125 periods, tides were intermediate between high and low. The expected odds of recruitment on days with intermediate tides was $p/1-p = (125/209)/(84/209) = 0.60:1$. There were 12 of 18 events estimated to have begun on days with intermediate tides. The observed odds ratio was $2.0:1$ which was not significant ($\chi=0.330$, $p=0.5644$). Greenland cod were estimated to recruit to our sites on spring tides only during 1998 and on neap tides only during 2002 (Fig. 9). Recruitment of hake to our sites on spring tides was estimated to occur only once, during 1998 (Fig. 9). Other recruitment events for Greenland cod and hake were estimated to begin between tidal extremes. We concluded that daily recruitment of Atlantic cod, Greenland cod and hake to nearshore Newfoundland waters was not related to the tidal cycle (spring and neap).

4. Discussion

Recruitment of Atlantic cod, Greenland cod and hake to benthic habitats in Newman Sound occurred an improbably high number of times during onshore winds, supporting the theory that fish recruitment near shore is associated with wind events (Hjort and Dahl, 1900), notably the cessation of upwelling in the northwest Atlantic. We propose that transport of larvae and pelagic juvenile fish to the coast is a two step process (see Fig. 1). First, larvae and juvenile fish move toward the coast in subsurface flow

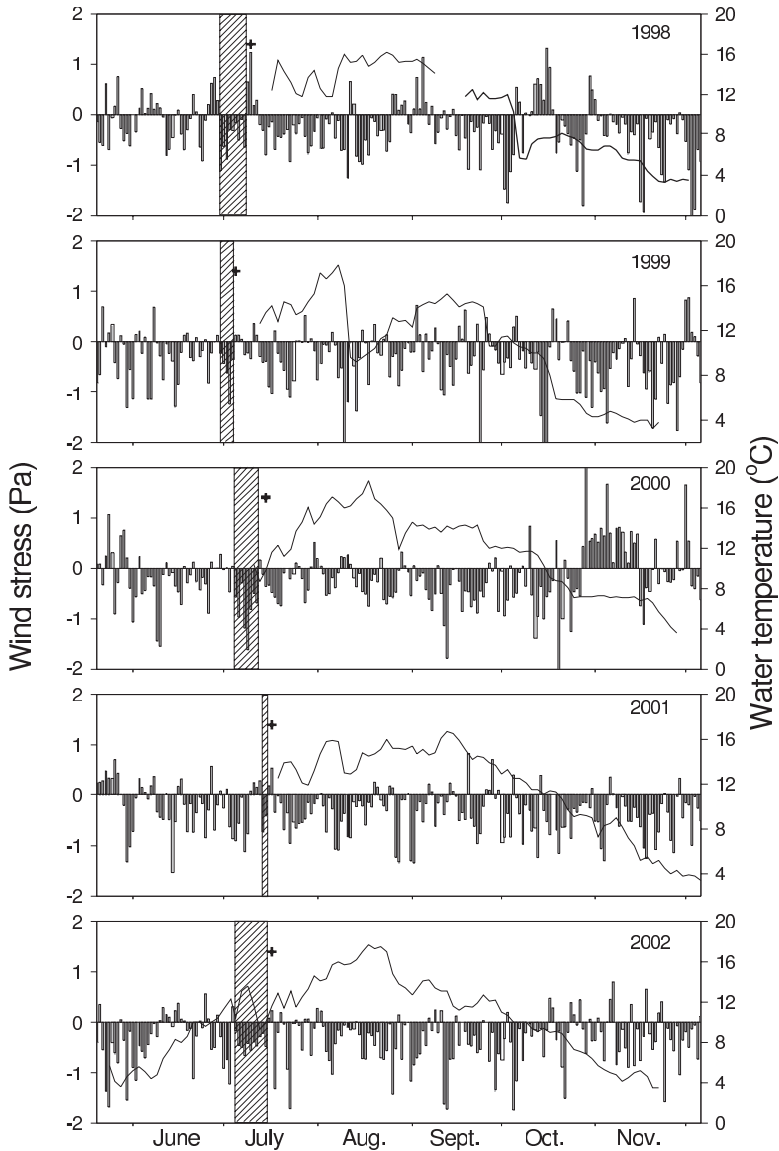


Figure 7. Estimated dates that recruitment of *Gadus ogac* began at Newman Sound during July to November, 1999 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling-favorable winds prior to arrival of *G. ogac*. + indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress.

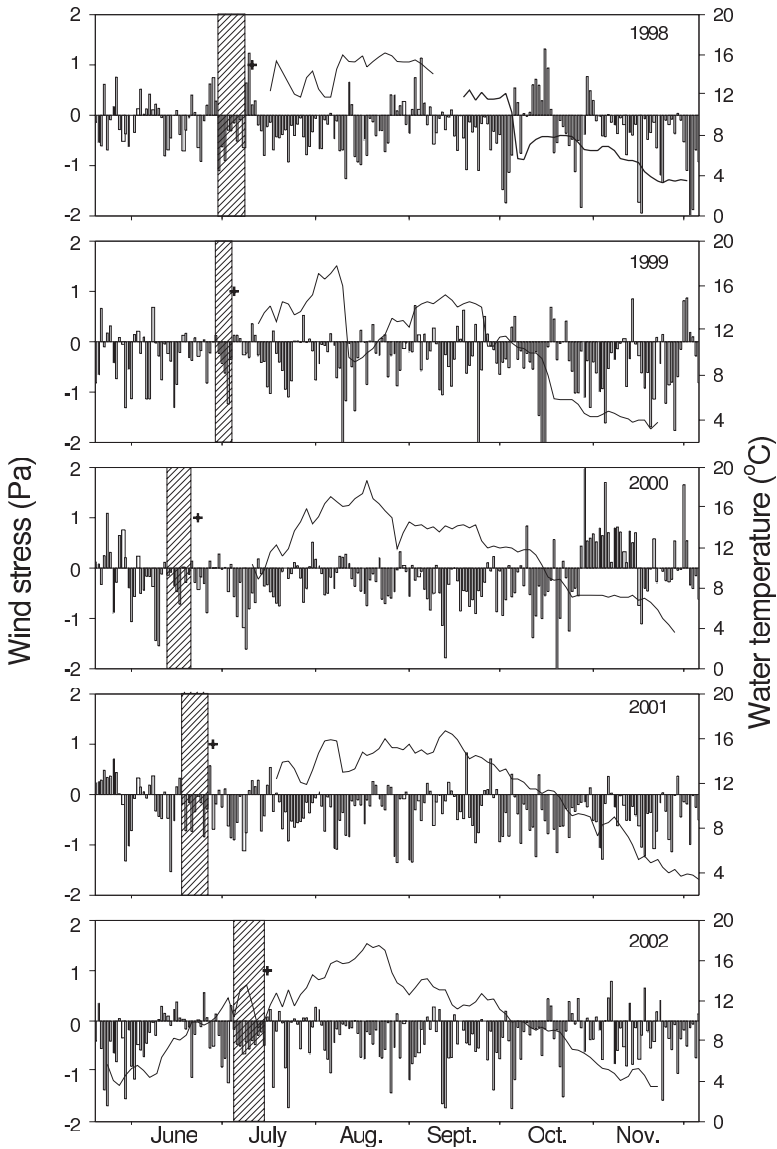


Figure 8. Estimated dates that recruitment of *Urophycis tenuis* began at Newman Sound during July to November, 1998 to 2001 and May to November 2002 plotted with daily wind stress at Gander Airport and water temperatures at Buckleys Cove. Shaded areas indicate periods of upwelling-favorable winds prior to arrival of *U. tenuis*. + indicates recruitment dates. The solid line represents water temperatures and the vertical bars represent wind stress.

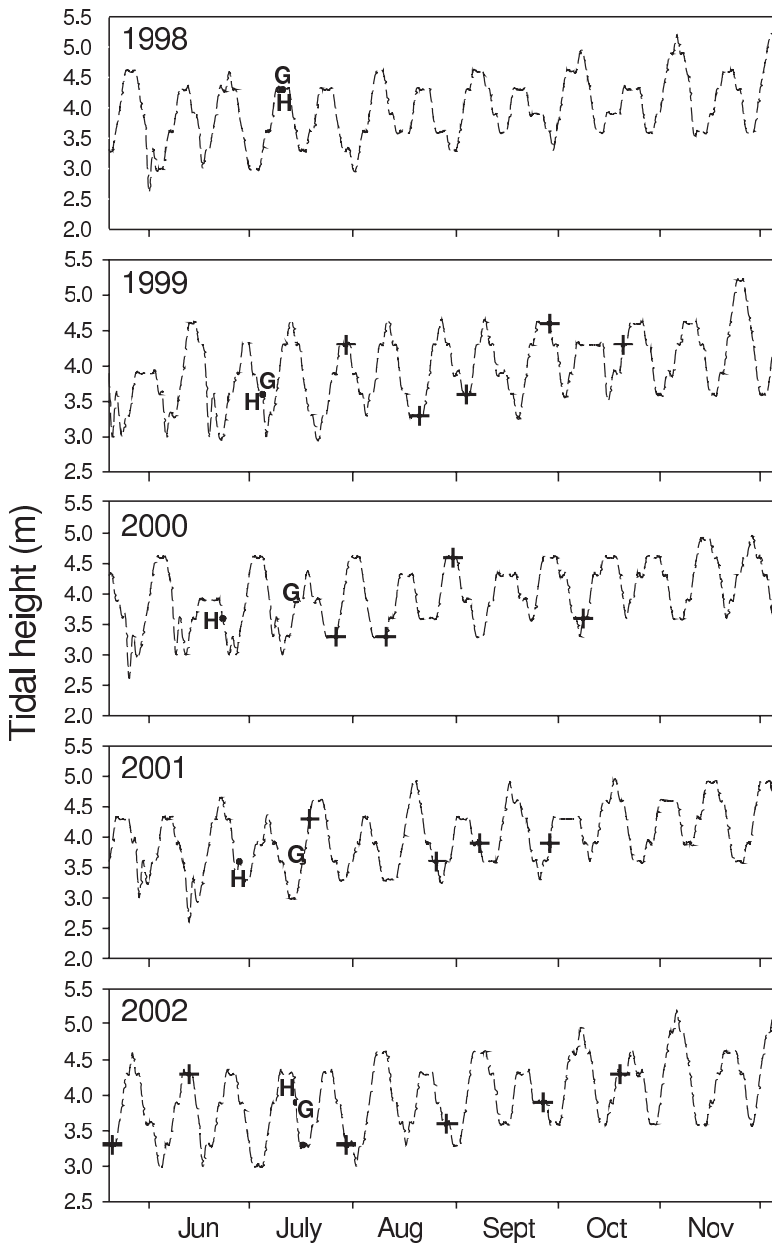


Figure 9. Estimated dates that recruitment of *Gadus morhua*, *G. ogac* and *Urophycis tenuis* began at Newman Sound during July to November, 1998 to 2001 and May to November 2002 plotted with daily tidal heights. G indicates *G. ogac* arrival, H indicates *U. tenuis* arrival and + indicates *G. morhua* arrival.

associated with the thermocline, accumulating at an upwelling front (McLaren *et al.*, 1997; Munk *et al.*, 1999). An upwelling front is known to exist off the northeast coast of Newfoundland (Schneider and Methven, 1988). Then, when upwelling winds cease, the front collapses toward the coast under geostrophic effects (episodic downwelling) and deposits larvae and pelagic juveniles consistent with deposition described by Farrell *et al.* (1991), Roughgarden *et al.* (1991) and McCulloch and Shanks (2003). If the next downwelling event occurs soon, the front moves toward the coast but contains too few larvae or juveniles to register as a recruitment event. Larvae and pelagic juvenile fish that are relatively far from the coast continue to drift shoreward beneath the surface layer but do not reach the coast (McCulloch and Shanks, 2003). These individuals resupply the next upwelling front that then deposits the next pulse of juvenile fish. There are at least three observations to support this proposed mechanism. First, recruitment of Atlantic cod to our sites was often associated with alternate periods of onshore winds, but never occurred during two consecutive onshore wind events. Second, Laprise and Pepin (1995) observed that the 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 and hence moving the surface layer toward the east side at the surface under direct forcing. But during a southerly wind event, highest abundance was on the western side, when winds push the surface layer against the western side and water temperature rises at the coast. This observation is consistent with transport of eggs and larvae in coastal water masses. Third, episodic recruitment of Atlantic cod occurs simultaneously all along the northeast coast of Newfoundland (Methven, 1997), a pattern of coherence that suggests that the large scale physical processes, at the scale of hundreds of kilometers, are responsible for recruitment pulses at the coast. It is worth noting that for all three species in this study, our results are consistent with frontal accumulation and episodic deposition during downwelling events.

Physical models of egg and larval drift on the northeast Newfoundland Shelf cannot explain observed patterns of fish recruitment at the coast. Models that incorporated storm passage (Helbig *et al.*, 1992) and later baroclinic models (Pepin and Helbig, 1997) suggest that Atlantic cod recruitment to the coast is small with retention of only 10%. Nevertheless, roughly half of the small cod Beacham *et al.* (2000) sampled from Newman Sound during August 1999 were genetically similar to adults caught offshore on Funk Island Bank; 30 percent of the fish in their October sample originated inshore. Passive drift in the surface layer cannot account for recruitment at the coast. Larvae that maintain their depth just beneath the surface layer offshore can be expected to drift onshore with compensatory return flow. Such larvae will collect at a coastal upwelling front, which is convergent at the surface (McCulloch and Shanks, 2003). Even larvae with weak swimming ability will accumulate near convergent fronts. Larvae that are weak swimmers will concentrate at depth some distance from the front while larvae

and pelagic juvenile fish with strong swimming abilities will accumulate at the front, near the surface (McCulloch and Shanks, 2003). Accumulations of Atlantic cod larvae have been found at shelf break fronts (Munk *et al.*, 1999), which are also convergent at the surface.

Larvae that accumulate at upwelling fronts near the coast are transported shoreward when upwelling-favorable winds subside and the front collapses quickly (McCulloch and Shanks, 2003). Transport of frontal waters to the coast would result in deposition of depth keeping larvae and juveniles in shallow coastal areas. This is consistent with observations of Methven and Schneider (1998) who found the distribution juvenile Atlantic cod in coastal waters was centered at depths between 4 and 7 meters.

Our results provide an explanation for the negative relation between year-class strength and offshore (upwelling favorable) winds in Norway, where year class-strength is positively related to along-shore winds (Johannessen and Tveite, 1989). Transport of both cod larvae and their prey into Norwegian fjords is inhibited by upwelling (Asplin *et al.*, 1999). Our results also provide an explanation for the negative association between salinity and annual recruitment of Atlantic cod on the northeast Newfoundland Shelf (Myers *et al.*, 1993). Because salinity on the shelf is associated with sea ice extent (Myers *et al.*, 1993) which is determined by onshore winds (Prinsenberget *et al.*, 1997) sea ice is transported farther south during years with frequent onshore winds, and a relatively high number of downwelling episodes that favor recruitment. That recruitment signals observed in juvenile cod at the coast (Ings *et al.*, 1997) carry over to the entire stock underscores the importance of coastal recruitment to overall recruitment in Atlantic cod.

Unlike Atlantic cod, Greenland cod and hake are not known to spawn offshore of our sites. Retention may thus be more important than onshore transport for these species, and for Atlantic cod eggs released at the coast. An upwelling front, together with a thermal preferendum for cold water would function to retain larvae capable of vertical migration near the front. During our five-year study, Greenland cod and hake recruited to benthic habitats near shore once annually; recruitment of both species was associated with downwelling. The timing of downwelling relative to the timing of a relatively short spawning season may determine the year-class strength of hake and Greenland cod.

Tidal forces influence the recruitment of many invertebrates and fish on the eastern margin of the Pacific in estuarine conditions (Boehlert and Mundy, 1987) and on more exposed coasts at subtropical latitudes in the California Bight (Pineda, 1999). On an exposed coast on the western margin of the north Atlantic we found no evidence of association between tide stage and recruitment from the water column. Tidally influenced recruitment of larvae from the water column may prove to be important under more sheltered conditions in the western north Atlantic.

Our analyses of association between fish recruitment and physical processes was conservative with respect to several sources of uncertainty. The temporal resolution of our

Superposed Epoch analyses (Prager and Hoenig, 1989) was limited to three days due to the logistical constraints of sampling 12 sites biweekly. Also, the temporal range used in analyses was somewhat arbitrary. We considered wind events during our fish sampling period, as we had no data on timing of fish spawning or larval presence in the water column. Lacking these data, we omitted a recruitment event for Atlantic cod that occurred late in the season. Despite the reduction in statistical power of the analysis, the observed association was statistically significant. The Superposed Epoch analysis that we used was also conservative because only the periods immediately before and after wind events were tested. This produces a conservative test relative to the use of all units (three-day periods) for testing (Prager and Hoenig, 1989).

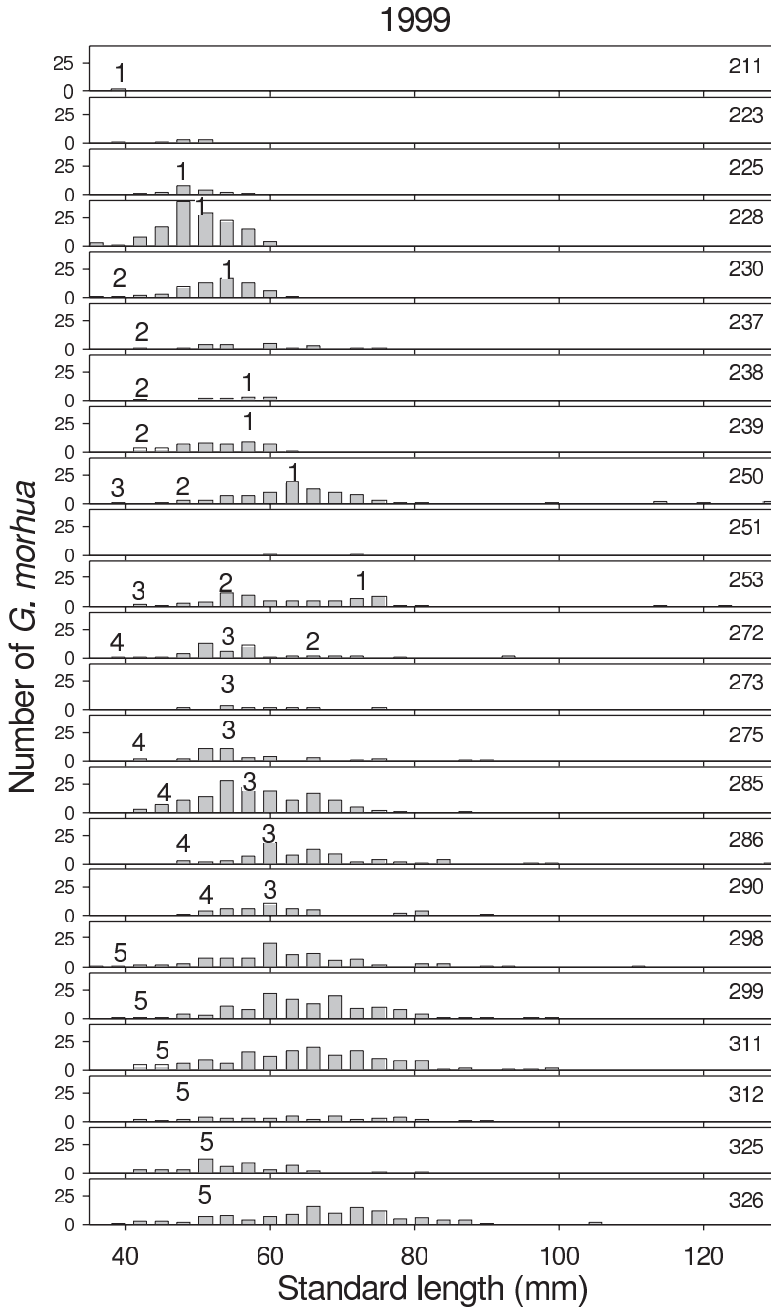
5. Conclusion

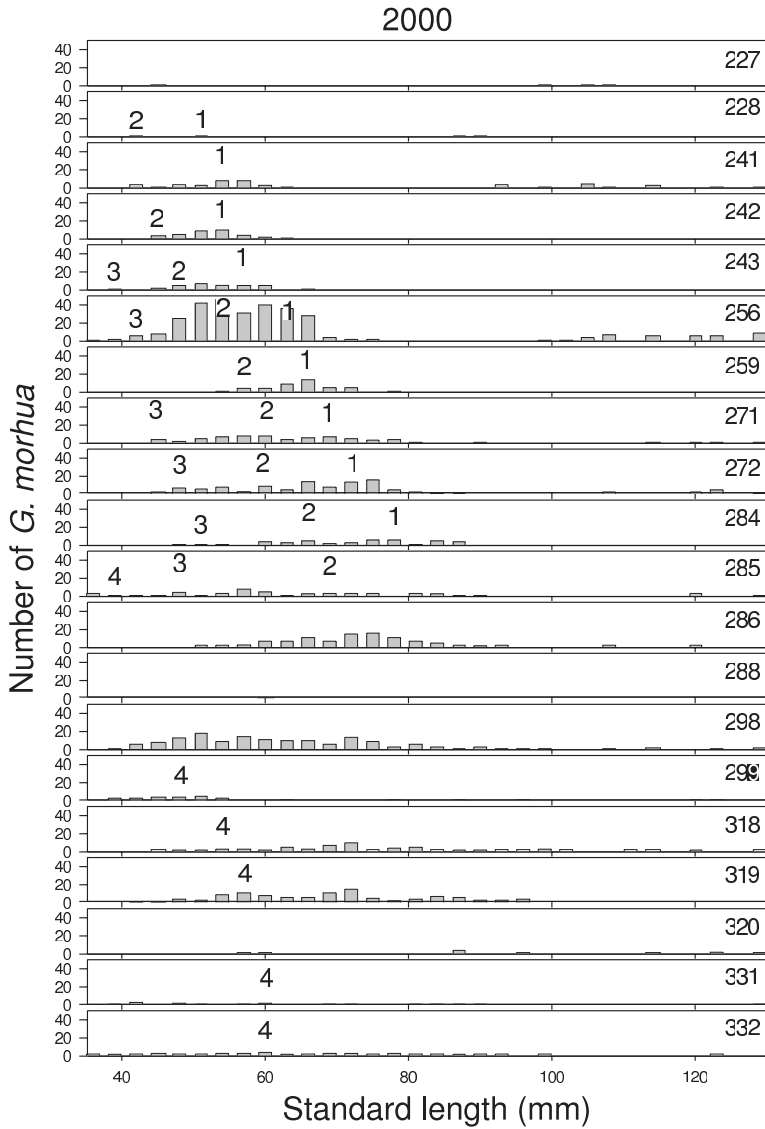
Recruitment of Atlantic cod, Greenland cod and hake to bottom habitats near shore was associated with onshore wind events following upwelling. We found no evidence that recruitment of fish at the coast was associated with tidal forcing. Atlantic cod recruited to nearshore sites during multiple (four to six) events annually during 1999 to 2002. Recruitment events occurred episodically during the summer and autumn periods studied. Hake and Greenland cod recruited to our 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, 18 of 18 estimated recruitment events for Atlantic cod during 1999 to 2002 occurred within three days following onshore winds. Results were consistent with larval transport to our sites during onshore movements of upwelling fronts that are convergent at the sea surface. Retention at an upwelling front likely depends on behavioral responses of larvae to physical gradients, a topic that was beyond the scope of this study. Our results are consistent with the hypothesis that upwelling fronts retain pelagic larvae near shore, and that episodic collapse of fronts maintained by prevailing winds results in a small number of recruitment pulses that together govern year class strength.

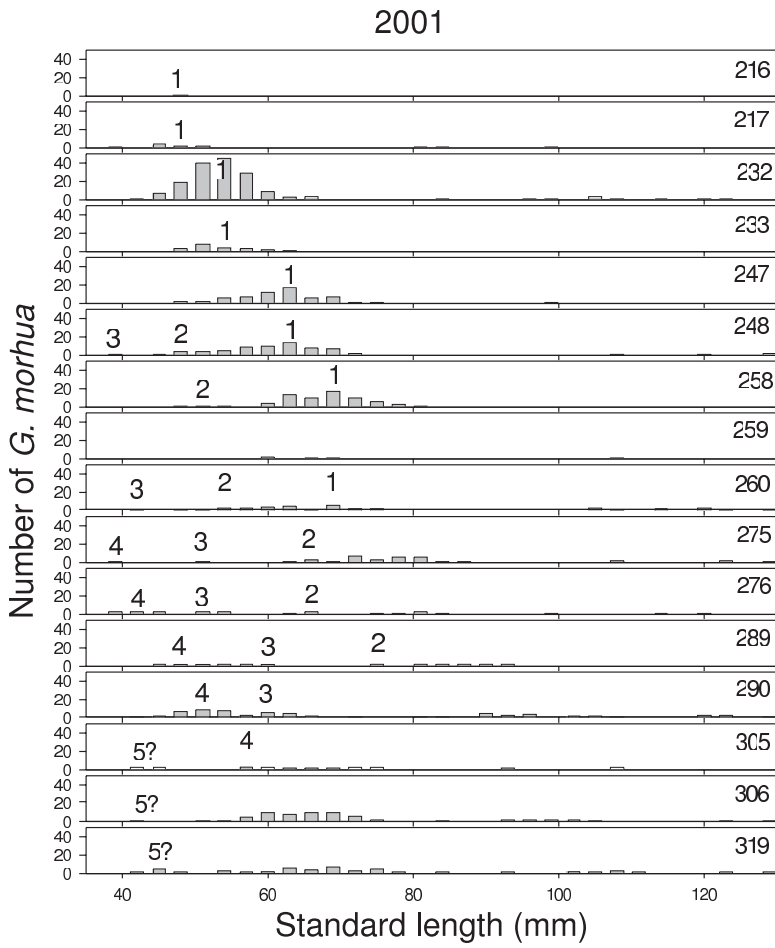
Acknowledgements. We are indebted to the many summer students, technicians, and graduate student volunteers who participated in beach seining; E. Alcock, C. Anderson, J. Anderson, L. Cole, L. Copeman, D. Cote, K. Dalley, P. Frampton, D. Gibson, A. M. Gorman, J. Hancock, B. Hammond, B. Hookey, C. Howell, R. Jamieson, T. L. Lander, B. Laurel, J. Linehan, M. Norris, M. O, A. Ogilvie, M. Pink, D. Porter, A. Powell, H. Reid, D. Remple, M. Renkawitz, P. Sargent, L. Sheppard, D. Sterling, S. Sutton, C. Vickers, N. Wells, R. Wong, and K. Young. We thank Dr. G. Sneddon for statistical advice, L. Sheppard for producing Figure 2, and several anonymous reviewers for comments that improved the manuscript. Funding was provided by NSERC and the Department of Fisheries and Oceans (Environmental Science Strategic Research Fund).

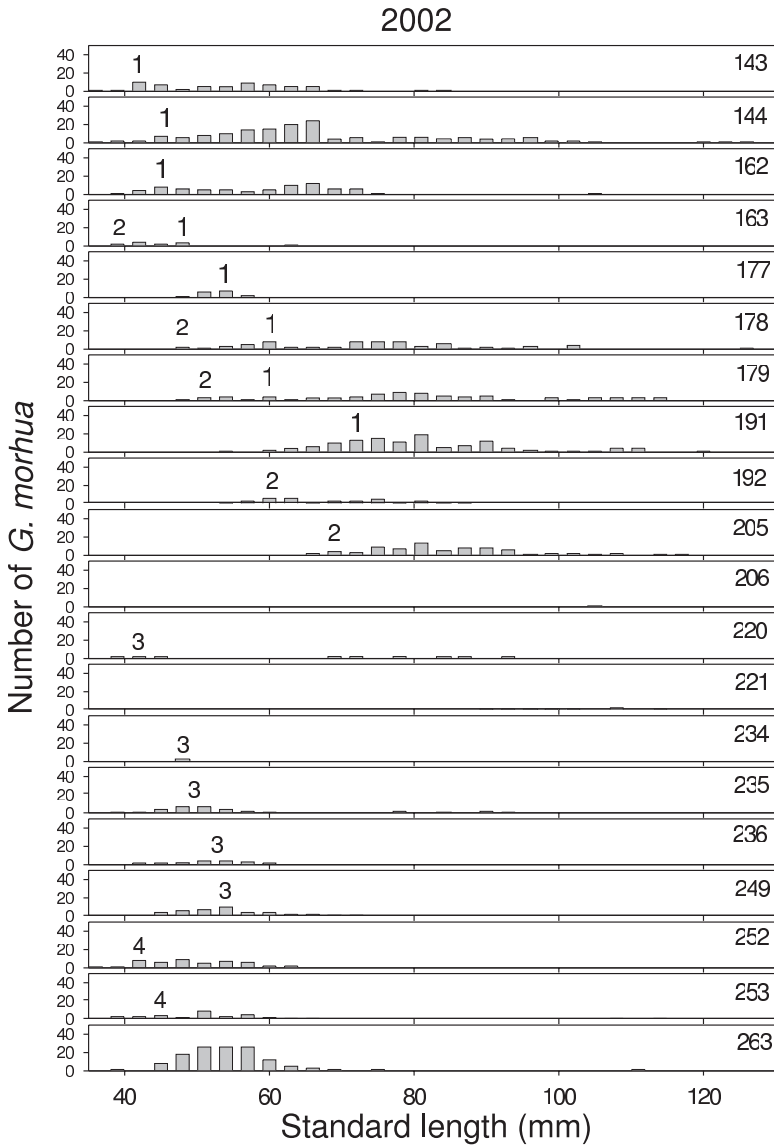
APPENDIX

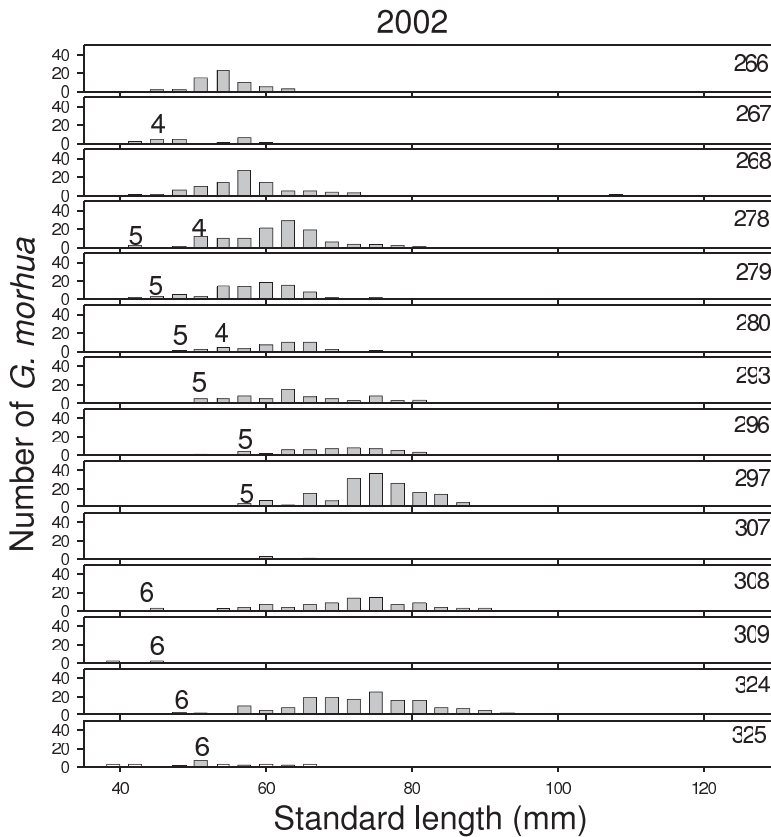
Length frequencies of *Gadus morhua* sampled at Newman Sound during 1999-2002. Numbers identify pulses of *G. morhua* observed and indicate data points used in regressions.











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