ICES Journal of Marine Science, 59: 929–941. 2002
doi:10.1006/jmsc.2002.1251, available online at http://www.idealibrary.com on IDEAL®

Atmospheric forcing, larval drift, and recruitment of capelin (*Mallotus villosus*)

Edgar L. Dalley, John T. Anderson, and Brad deYoung

Dalley, E. L., Anderson, J. T., and deYoung, B. 2002. Atmospheric forcing, larval drift, and recruitment of capelin (*Mallotus villosus*). – ICES Journal of Marine Science, 59: 929–941.

Wind conditions during the period of larval drift of capelin are examined in relation to indices of larval drift and recruitment of the species over the five years 1982–1986 in Trinity Bay, Canada. Capelin larvae were abundant during all surveys except that of July 1985, when spawning was late as a result of cooler environmental conditions. Abundance of larvae was positively correlated with subsequent recruitment and inversely correlated with the time interval between northeasterly winds following spawning. Larval transport was mainly across (from northwest to southeast) and out of the bay, away from the spawning beaches. Larval transport itself was positively correlated with both the intensity of Ekman transport and a cumulative measure of wind-forcing in July, but it was negatively correlated with a measure of variability in wind speed and direction. The wind indices were related to measures of recruitment, but their slopes were opposite in sign to those observed between them and larval transport. There was no obvious relationship between larval transport and recruitment, i.e. transport of capelin larvae out of Trinity Bay was not a necessary requirement for successful recruitment. Our data are consistent with the hypothesis that wind-generated turbulence in the upper layers of the water column can modulate survival and recruitment.

Keywords: abundance, atmospheric forcing, capelin, distribution, larvae, larval drift, Newfoundland, recruitment, size, survival, transport, wind indices.

Received 25 July 2001; accepted 6 April 2002.

E. L. Dalley and J. T. Anderson: Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland, Canada A1C 5X1. B. deYoung: Department of Physics and Physical Oceanography, Memorial University of Newfoundland, St Johns, Newfoundland, Canada A1B 3X7. Correspondence to E. L. Dalley; tel: +1 709 7722002; fax: +1 709 7724188; e-mail: dalleye@dfo-mpo.gc.ca.

Introduction

Capelin, *Mallotus villosus* (Müller), occupy a prominent position in the food chain of the marine ecosystem off Newfoundland. Because they are planktivores, their predators include numerous commercial and non-commercial fish, marine mammals, and man, so creating many linkages throughout the food web. They begin a protracted early life history on beaches along the north-east coast of Newfoundland (Figure 1). Spawning is typically in late June and early July, although it was somewhat later in the 1990s (Carscadden *et al.*, 1997, 2001). Eggs incubate in beach gravel, where larvae remain for varying periods of time following hatching. The duration of this beach residence depends on environmental and meteorological conditions (Frank and Leggett, 1981). Onshore winds, which stimulate larval emergence from beach gravel, also produce a favourable predator/prey field nearshore at emergence (Frank and Leggett, 1982). At a spatial scale of small inlets and coves, post-emergent larvae are dispersed quickly away from the nearshore environment by wind-forced surface currents (Taggart and Leggett, 1987). These small coves and their associated spawning beaches are located principally along the western sides and heads of the large bays located along the northeast coast of Newfoundland (Templeman, 1948; Nakashima and Taggart, 2002). Leggett *et al.* (1984) related capelin survival to (a) the successful release of larvae from the beach sediments, facilitated by short intervals between onshore wind events following spawning (termed WIND), and (b) warm surface water temperatures

1054–3139/02/100929+13 $35.00/0

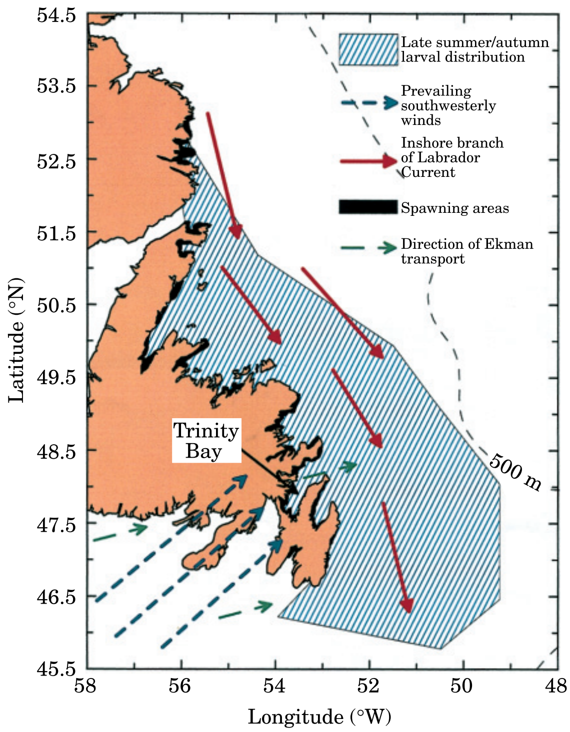

Figure 1. Large-scale map of Newfoundland and adjacent shelf showing spawning locations of capelin and their offshore distribution in the fall 1–2 months following release from beach sediments. Schematically represented is the inshore branch of the Labrador Current, prevailing southwesterly winds, and the direction of Ekman transport arising from the prevailing winds.

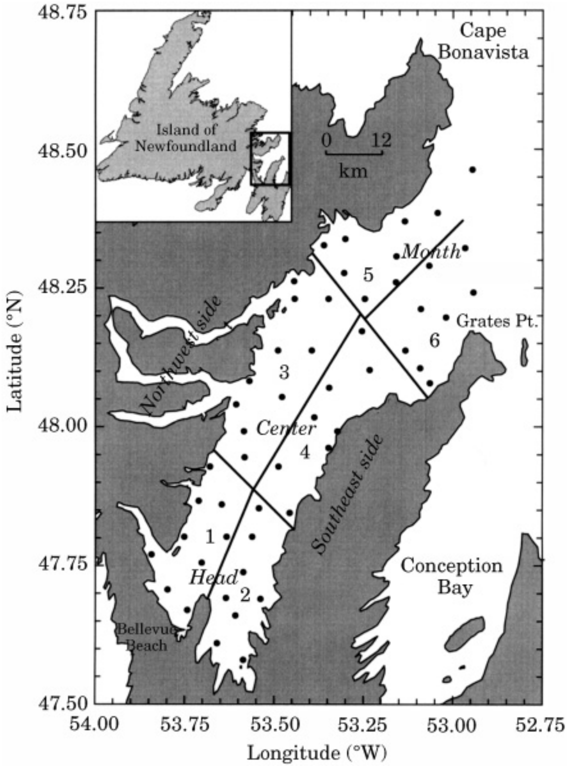

Figure 2. Map of Trinity Bay showing sampling stations within six strata aligned to test differences between opposite sides, and along the axis, from head to mouth, during larval surveys carried out in the years 1982–1986.

during the first six months following emergence (termed TEMPSUM). These two variables explained 58% of the annual variation in recruitment for the year-classes of 1966–1978. The partial correlation coefficients for WIND and TEMPSUM were -0.51 and 0.57 respectively, indicating substantial unexplained variance in recruitment. A subsequent evaluation of the model for the 1979–1990 year-classes found that WIND was significant ($R^2 = -0.50$; $p<0.04$) but TEMPSUM was not (Carscadden *et al.*, 2000).

Capelin in different areas of the Northwest Atlantic utilize different early life strategies in relation to major currents. Those in the St Lawrence Estuary disperse quickly to areas of increased productivity (Bailey *et al.*, 1977; Jacquaz *et al.*, 1977). In contrast, currents do not contribute to the transport of either capelin or flatfish larvae from the Southeast Shoal on the Grand Banks of Newfoundland after they become pelagic (Frank and Carscadden, 1989; Frank *et al.*, 1992). Along the northeast coast of Newfoundland (Figure 1), dispersal from the nearshore zone immediately following spawning is crucial to survival and is facilitated by local winds (Taggart and Leggett, 1987). Mackenzie and Leggett (1993) present evidence that wind speed is one of the most important environmental variables in studies of turbulence and plankton ecology. Dower *et al.* (1997) reviewed the effects of microscale turbulence on feeding ecology of marine fish larvae. Laboratory studies have shown positive effects of turbulence on encounter and ingestion rates, which have been hypothesized to enhance growth of fish larvae and to increase recruitment.

It is not known if retention within, or transport out of, the large bays of northeast Newfoundland is important to survival. Larger capelin larvae are found offshore on the northeast Newfoundland shelf and northern Grand Banks late in summer and early autumn, and their distribution is continuous with that of inshore larvae (Figure 1; Anderson *et al.*, 1999). Our hypothesis is that transport out of Trinity Bay is a necessary requirement for successful recruitment. We used data collected in Trinity Bay in the 1980s to assess the influence of wind conditions at the time of the surveys, and the surface transport features of Trinity Bay as dispersal mechanisms affecting capelin larvae. We then examined the effect of both fast and slow rates of dispersal on larval survival. The objectives were, first, to describe

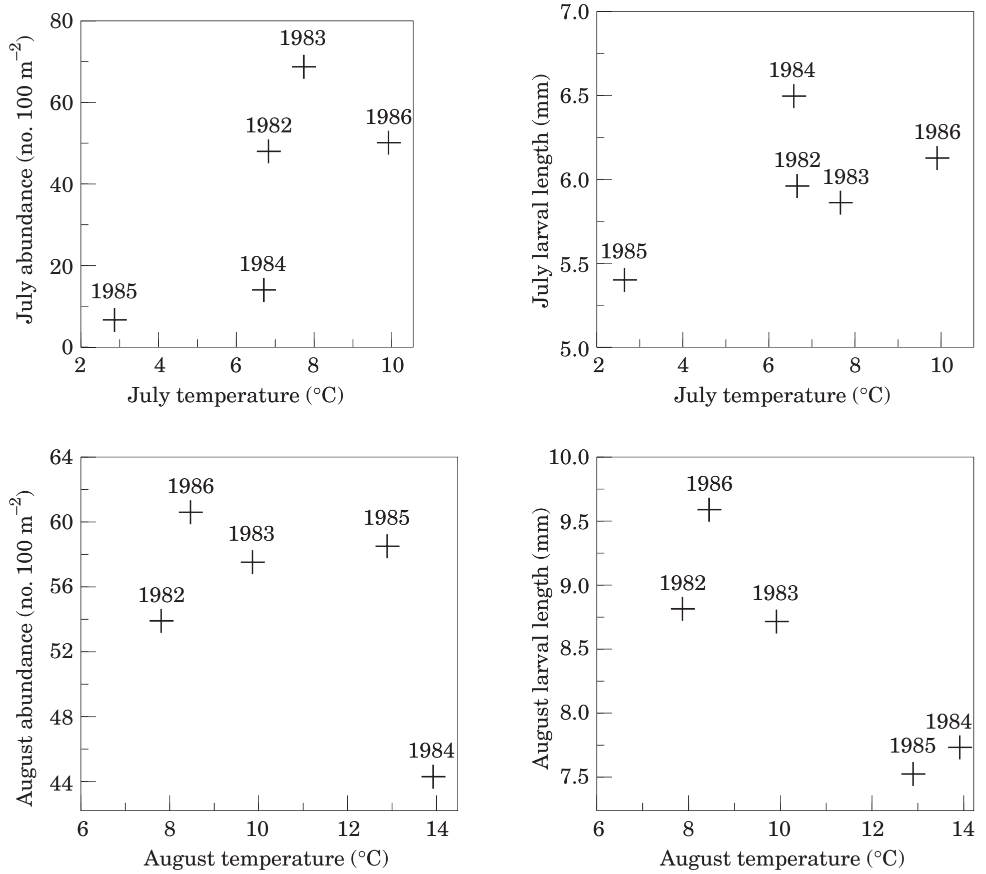

Figure 3. Relationship of mean larval abundance and mean larval length to mean temperature in July (top) and August (bottom) from larval surveys carried out in Trinity Bay, 1982–1986. Vertical scales differ between months.

inter- and intra-annual variation in abundance and size of capelin larvae in Trinity Bay on the basis of surveys conducted in July and August of the years 1982–1986, second, to develop a larval transport index and to examine the effect of wind on the direction and magnitude of larval transport, and third, to evaluate the relative importance of larval transport on survival of capelin.

Study area

Trinity Bay is one of several large embayments along the coast of northeast Newfoundland within which capelin spawn (Figure 1). Bailey (1958) used the results of a temperature and salinity survey to evaluate the current patterns in Trinity Bay. He concluded that mean currents entered the bay on the northwest side (the inshore branch of the Labrador Current) and exited it on the southeast side. His data also suggested the existence of two weak gyres within the bay. Yao (1986) confirmed the direction of these mean currents and showed that predominant southwesterly winds caused displacement

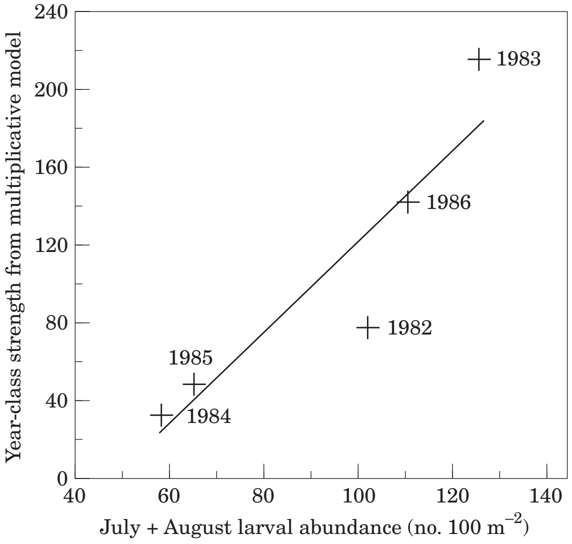

Figure 4. Total capelin abundance (larvae 100 m^{-2}) measured during July and August surveys, 1982–1986, compared with recruitment from the multiplicative model (see test; $R^2=0.84$).

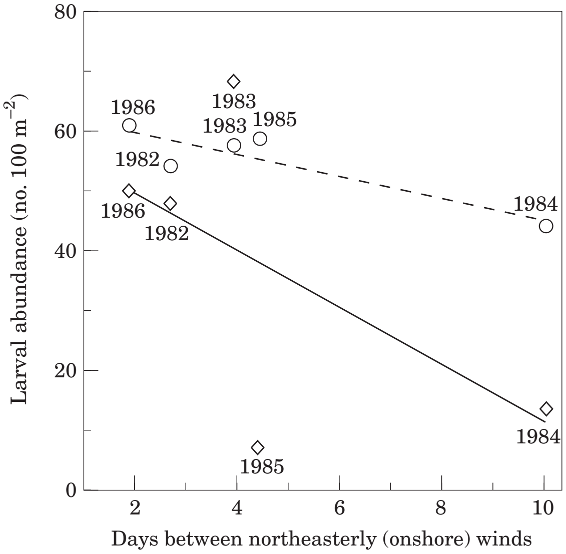

Figure 5. The relation between larval abundance during July and August surveys and the maximum interval between northeast winds immediately following the estimated mean hatching date (WIND from Leggett *et al.*, 1984). Solid line represents a linear fit for July ($R^2=0.35$) and the broken line the fit for August ($R^2=0.80$).

of the mixed surface layers, along the axis of the bay, from southwest to northeast. The numerical model of Davidson *et al.* (2001) was applied to Trinity Bay and Conception Bay (deYoung, unpublished), and residence times of 50–60 days were found near the head of Trinity Bay. Scaling relative to Conception Bay suggests that this result is consistent with the work of deYoung *et al.* (1994) in Conception Bay, because Trinity Bay is roughly twice the length of, and narrower than, Conception Bay. Both bays are orientated towards the northeast and experience much the same wind-forcing. Yao (1986) found that surface currents flowing out of the bay as a result of the predominant winds along the axis produced an upwelling of colder water along the bay's northwest side and downwelling along its southeast side.

Under average transport conditions, therefore, larvae would tend to be transported to the east and north, out of the bay. Under these conditions the only mechanism by which larvae would be transported into Trinity Bay is via incoming currents in its northwest corner. Such currents are at times stronger than outflowing surface currents, produced by the prevailing southwesterly winds, blowing out of the bay, so despite prolonged offshore wind events, a net current into the bay may prevail as a result of the Labrador Current (Yao, 1986). Capelin larvae transported south from bays farther north may therefore be transported into Trinity Bay. Winds during July and August are predominantly southwesterly, but they alternate periodically with brief-periods of northeasterly winds (Frank and Leggett, 1982). The expected effects of winds are

- infrequent NE winds release larvae from beach sediments to nearshore waters,
- SW winds transport larvae out of Trinity Bay.

Methods

Between 45 and 52 stations were occupied during each of 10 larval surveys conducted in late July and August from 1982 to 1986. During the surveys, 61-cm bongos (333 μm mesh, both sides) were towed in the standard oblique manner (Smith and Richardson, 1977) to 200 m or within 5 m of the bottom where the bottom depth was <200 m. In all, 52 stations were randomly assigned within six strata in Trinity Bay. The strata divided the bay along its axis into (a) head (strata 1 and 2), middle (strata 3 and 4), and mouth (strata 5 and 6), and (b) northwest (strata 1, 3, 5) and southeast (strata 2, 4, 6) sides (Figure 2). All samples were preserved in ~5% formalin and all analyses were performed on preserved larvae. Measurements of larva standard length were recorded to the nearest millimetre, and capelin larval density was standardized to number per square metre of sea surface. The volume of water filtered by the nets was calculated from calibrated mechanical flowmeters placed in the mouth of each side of the bongos. Mean abundance (larvae m^{-2}) from each stratum were summed to estimate mean monthly and annual abundance. Analysis of variance tests for differences in mean abundance and mean length between different strata and combinations of strata within the bay were conducted using contrast statements within the GLM (general linear models) procedure of SAS (SAS, Institute Inc., 1989). The coefficient of variation (CV) of the parameters measured was calculated as mean divided by standard deviation, expressed as a percentage.

Temperature data were collected with a portable conductivity-temperature-depth (CTD) probe attached to the towing cable immediately above the bongo frame. The instrument-sampling rate, combined with its rate of descent, allowed a temperature sample to be collected every 1–3 m, from which temperatures at 15 m were interpolated. A temperature index was derived for each survey using the mean of 12 stations positioned on three transects across the bay near its head, centre, and mouth (Figure 2). The Atmospheric Environment Service of Environment Canada collected wind data from a permanent weather station at Cape Bonavista (Figure 2). Hourly readings of direction and magnitude were used to calculate the U and V components with respect to the orientation of Trinity Bay (60 degrees east of true north) according to:

$$U = \text{wind speed} * \cos(\text{channel direction} - \text{wind direction}) \tag{1}$$

Table 1. Results of analysis of variance performed on combinations of strata to test for differences in abundance of capelin larvae along the axis and between sides of Trinity Bay. Asterisk indicates a statistically significant difference ($p<0.05$), F=F-value, p=probability level.

		1982		1983		1984		1985		1986	
Month	Zonal comparison	F	p	F	p	F	p	F	p	F	p
July	Head vs. mouth	2.2	0.144	1.6	0.206	0.0	0.851	4.5	0.039*	0.0	0.837
July	Southeast vs. northwest	4.3	0.043*	0.4	0.522	0.6	0.444	2.3	0.137	2.5	0.121
July	Head vs. centre	2.5	0.118	1.2	0.284	0.1	0.784	1.6	0.208	0.9	0.361
July	Centre vs. mouth	0.0	0.931	0.0	0.833	0.0	0.933	0.8	0.388	1.3	0.263
July	Mouth E vs. mouth W	0.4	0.516	0.0	0.942	0.6	0.450	0.8	0.371	1.4	0.244
July	Centre E vs. centre W	0.1	0.819	0.8	0.381	0.2	0.677	3.0	0.090	0.0	0.838
July	Head E vs. head W	7.21	0.010*	0.1	0.752	1.0	0.335	0.0	0.994	1.8	0.190
August	Head vs. mouth	12.9	0.001*	0.7	0.402	0.1	0.828	0.3	0.603	0.40	0.532
August	South east vs. northwest	6.1	0.017*	0.2	0.691	1.3	0.264	6.0	0.018*	0.28	0.599
August	Head vs. centre	1.0	0.327	1.3	0.260	0.1	0.711	4.6	0.038*	2.34	0.133
August	Centre vs. mouth	7.0	0.011*	0.1	0.763	0.2	0.664	2.6	0.115	0.80	0.376
August	Mouth E vs. mouth W	5.2	0.027*	0.0	0.965	1.1	0.292	2.8	0.104	0.52	0.476
August	Centre E vs. centre W	2.4	0.127	0.1	0.829	0.4	0.543	2.6	0.113	0.01	0.940
August	Head E vs. head W	0.2	0.643	0.2	0.668	0.0	0.994	1.0	0.334	0.07	0.793

Head, strata 1 and 2; centre, strata 3 and 4; mouth, strata 5 and 6; northwest, strata 1, 3, and 5; southeast, strata 2, 4, and 6; see Figure 2.

Table 2. Mean abundance of capelin larvae (number 100 m^{-2}) along the axis and on opposite sides of Trinity Bay during each survey.

	Area of Trinity Bay				
Survey	Head	Centre	Mouth	Northwest	Southeast
July 1982	81.6	31.1	34.0	71.5	21.9
July 1983	82.9	48.8	44.6	50.9	67.4
July 1984	11.0	12.4	12.2	13.7	9.7
July 1985	1.5	6.2	8.8	7.5	3.3
July 1986	60.1	22.6	68.0	72.2	23.5
August 1982	27.2	46.5	93.0	71.8	36.2
August 1983	82.9	48.8	44.6	50.9	67.4
August 1984	45.8	41.8	69.6	53.7	39.5
August 1985	70.7	33.2	61.2	38.5	73.3
August 1986	50.7	73.6	60.7	65.1	58.2

Head, strata 1 and 2; centre, strata 3 and 4; mouth, strata 5 and 6; northwest, strata 1, 3, and 5; southeast, strata 2, 4, and 6; see Figure 2.

and

$$V = \text{wind speed} * \sin(\text{channel direction} - \text{wind direction}) \quad (2)$$

The U and V estimates were smoothed using a symmetrically weighted moving average. Positive values of U indicated winds out of the bay or offshore, and negative values indicated winds into the bay or onshore. A positive value of V indicates winds towards the southeast side of the bay and a negative value indicates winds towards the northwest side. Mean U and V wind components were calculated to include winds two days prior to each survey as well as winds during actual survey days.

Three meteorological indices were developed. The first, given the importance attributed to it by Mackenzie and Leggett (1993), was total mean wind (from U, the out-of-the-bay component and V, the across-the-bay component in m s^{-3}). The second index was wind variability during each survey, measured as the sum of the coefficient of variation (CV) in both U and V velocities. The third index was Ekman transport (net transport to the right of the wind in the northern hemisphere) along and across the bay's axis.

We developed an index of larval transport based on the mean length of larvae within each of the six strata. It was assumed that differences in length among strata were a function of age and not attributable to growth differences, because studies had shown a linear

Table 3. Results of analysis of variance performed on combinations of strata to test for differences in mean length of capelin larvae along the axis and between sides of Trinity Bay. Asterisk indicates a statistically significant difference ($p<0.05$), F=F-value, p=probability level.

Month	Zonal comparison	1982		1983		1984		1985		1986	
		F	p	F	p	F	p	F	p	F	p
July	Head vs. mouth	20.5	0.000*	434.6	0.000*	565.2	0.000*	0.7	0.404	354.0	0.000*
July	Southeast vs. northwest	958.2	0.000*	16.3	0.000*	41.6	0.000*	0.9	0.349	859.0	0.000*
July	Head vs. centre	0.1	0.745	36.9	0.000*	270.1	0.000*	0.0	0.897	392.1	0.000*
July	Centre vs. mouth	21.8	0.000*	183.5	0.000*	78.2	0.000*	0.7	0.407	22.8	0.000*
July	Mouth E vs. mouth W	553.9	0.000*	4.8	0.028*	43.1	0.000*	27.2	0.000*	999.5	0.000*
July	Centre E vs. centre W	15.9	0.000*	57.2	0.000*	1.4	0.257	8.8	0.003*	70.1	0.000*
July	Head E vs. head W	574.6	0.000*	283.1	0.000*	26.9	0.000*	2.7	0.099	250.5	0.000*
August	Head vs. mouth	27.2	0.000*	45.0	0.000*	89.5	0.000*	112.1	0.000*	56.8	0.000*
August	Southeast vs. northwest	850.2	0.000*	764.1	0.000*	365.4	0.000*	47.6	0.000*	1127.4	0.000*
August	Head vs. centre	36.8	0.000*	319.0	0.000*	291.1	0.000*	404.0	0.000*	84.9	0.000*
August	Centre vs. mouth	169.6	0.000*	90.1	0.000*	5.1	0.025*	99.4	0.000*	327.0	0.000*
August	Mouth E vs. mouth W	496.9	0.000*	194.3	0.000*	102.2	0.000*	132.9	0.000*	290.9	0.000*
August	Centre E vs. centre W	141.3	0.000*	28.1	0.000*	579.9	0.000*	29.6	0.000*	853.4	0.000*
August	Head E vs. head W	367.7	0.000*	1083.2	0.000*	89.3	0.000*	70.1	0.000*	182.5	0.000*

Head, strata 1 and 2; centre, strata 3 and 4; mouth, strata 5 and 6; northwest, strata 1, 3, and 5; southeast, strata 2, 4, and 6; see Figure 2.

Table 4. Mean length (mm) of capelin larvae along the axis and on opposite sides of Trinity Bay during each survey.

Survey	Area of Trinity Bay*				
	Head	Centre	Mouth	Northwest	Southeast
July 1982	5.7	6.2	6.0	5.7	6.5
July 1983	5.5	5.7	6.4	5.6	5.9
July 1984	5.6	6.9	7.5	6.4	6.9
July 1985	5.7	5.2	5.5	5.4	5.5
July 1986	5.8	6.9	6.3	5.9	7.1
August 1982	8.6	7.9	9.1	9.6	10.4
August 1983	7.9	9.7	8.5	7.5	8.6
August 1984	7.4	8.3	7.5	7.3	8.6
August 1985	7.2	8.5	7.7	7.6	7.7
August 1986	9.6	10.3	8.9	8.7	11.0

*Head, strata 1 and 2; centre, strata 3 and 4; mouth, strata 5 and 6; northwest, strata 1, 3, and 5; southeast, strata 2, 4, and 6; see Figure 2.

relationship between the number of daily growth rings (age) in capelin and larval length (Gjøsæter and Monstad, 1985; Frank and Carscadden, 1989). Larval transport out of Trinity Bay was hypothesized to take place when differences in mean length were greatest from south to north (positive values of U indicate movement out of the bay) and from west to east (positive values of V indicate movement away from spawning beaches). The larval transport index was estimated as the sum of the U and V components, higher values indicating greater transport away from spawning areas and out of the bay, where

$$U=(L1-L3)+(L3-L5)+(L2-L4)+(L4-L6) \qquad (3)$$

$$V=(L1-L2)+(L3-L4)+(L5-L6) \qquad (4)$$

and L1, L2, L3, L4, L5, and L6 are the mean lengths of larvae within strata 1–6 respectively.

We related larval transport to relative year-class strength, which were drawn from the multiplicative model used in recent capelin assessments (Evans and Nakashima, 2001).

The variable WIND data were calculated as in Leggett *et al.* (1984). Those authors defined WIND as all winds orientated north through east (northeasterly) during the 10-day period immediately following the estimated annual median hatching date defined by themselves.

Table 5. Summary of the individual U (out of the bay) and V (across the bay from northwest to southeast) larval transport components, sums of U and V components and total larval transport index for each larval survey carried out in Trinity Bay during July and August of the years 1982–1986. L1, mean length of larvae in stratum 1; L2, mean length of larvae in stratum 2, etc.

Survey	L3–L1	L5–L3	L4–L2	L6–L4	U	L2–L1	L4–L3	L6–L5	V	Larval transport index
Jul. 1982	0.7	− 0.4	− 0.6	0.7	0.4	1.5	0.2	1.3	3.0	3.4
Jul. 1983	0.7	0.3	− 0.3	0.8	1.5	0.6	− 0.4	0.1	0.3	1.8
Jul. 1984	1.5	0.3	0.8	1.3	3.9	0.5	− 0.2	0.8	1.1	5.0
Jul. 1985	− 0.1	0.4	− 0.5	− 0.2	− 0.4	0.7	0.3	− 0.3	0.7	0.3
Jul. 1986	0.9	− 0.6	0.8	0.2	1.3	0.8	0.7	1.5	3.0	4.3
Aug. 1982	0.1	1.0	− 1.4	1.4	1.1	3.3	1.8	2.2	7.3	8.4
Aug. 1983	3.3	− 1.8	0.1	− 0.3	1.3	3.9	0.7	2.2	6.8	8.1
Aug. 1984	0.3	0.1	2.1	0.6	3.1	0.8	2.6	3.1	6.5	9.6
Aug. 1985	2.0	− 0.5	0.8	− 1.0	1.3	0.6	− 0.6	− 1.1	− 1.1	0.2
Aug. 1986	0.1	− 0.8	1.4	− 1.9	− 1.2	1.7	3.0	1.9	6.6	5.4

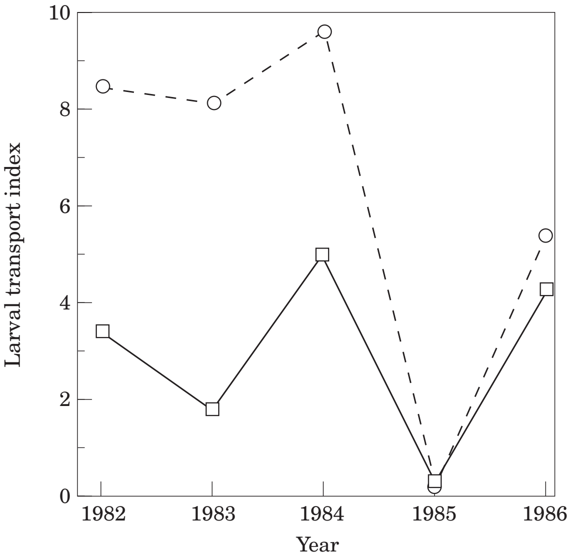

Figure 6. Transport index of Trinity Bay capelin larvae based on summed differences in mean size among the six sampling strata for July and August, 1982–1986. Solid curve, July; broken curve, August.

Results and discussion

Larval abundance

The total number of larvae caught during each survey ranged from 1506 in July 1985 to 11 985 in July 1983, and catches per stratum ranged from a minimum of 55 larvae in July 1985 to 3858 in July 1986.

Both abundance and size of larvae were positively related to mean temperature in July and inversely related to temperature in August (Figure 3). In general, when the temperature was warmer, spawning was earlier and larvae attained a given size sooner. The inverse relationship between abundance and temperature in August suggests that the optimal temperature for survival and growth of larvae was exceeded. In this case, the highest mean temperatures were 13–14°C (Figure 3).

The mean density of larvae sampled in July and August was positively related ($R^2=0.84$) to year-class strength (Figure 4). This indicates that year-class strength was determined as early as 6–8 weeks following emergence (given that spawning is typically in late June and early July) and while the fish are still in the larval phase.

Abundance of larvae in July and August was inversely related to the interval between NE winds (Figure 5), consistent with the theses of Leggett *et al.* (1984) and Carscadden *et al.* (2000) that the frequency of northeasterly winds during the hatching period contributes to the successful release of capelin larvae from beach sediments. The scarceness of larvae during July 1985 appears to be related to late spawning that year.

The overall mean abundance of capelin larvae (all strata combined) indicated that interannual variability in abundance varied by an order of magnitude during the July surveys, but by a factor of only 1.4 × during August (Figure 3). The intra-survey variability, as indicated by higher coefficients of variation in mean abundance, was relatively high during both months, but higher in July than in August.

Analysis of variance indicated significant differences ($p<0.05$) between various strata of the bay only in 1982 and 1985 (Table 1). In July 1982, larvae were more abundant overall on the northwest side (Table 2) as a consequence of recent spawning in stratum 1, allowing greatest abundance ($135.8\,\mathrm{m}^{-2}$) of relatively small larvae (5.4 mm) of any survey. During August 1982, significantly more larvae were found at the mouth than at either the centre or the head of the bay, and there was greater abundance on the northwest side of the bay. This

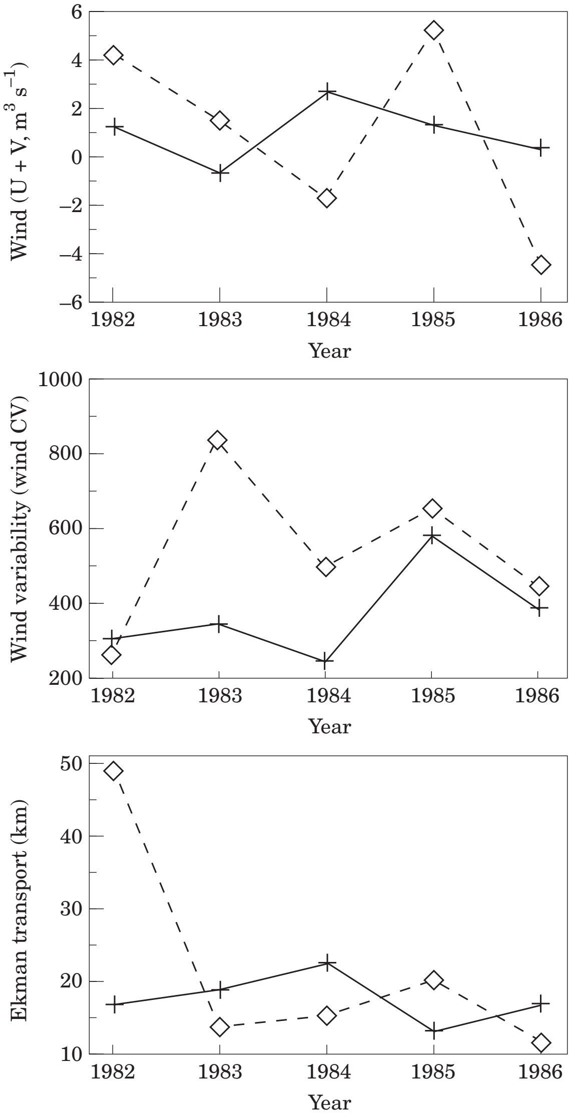

Figure 7. Summary of three wind variables, total wind (top), wind variability (middle), and Ekman transport (bottom) examined during larval surveys carried out in Trinity Bay, 1982–1986. Solid curves, July; broken curves, August.

could have resulted from the great abundance of small larvae sampled in stratum 5, in the northwest portion of the bay. This in turn might have resulted either from the larvae emerging from a late spawning in the area, or alternatively, from immigration into the northwest corner of the bay.

There were significantly more larvae at the mouth than at the head in July 1985 when, as noted earlier, spawning was late and abundance quite low. In August 1985, there were no differences in abundance between southeast and northwest in any particular strata along the axis, but in combination there were significantly more larvae on the southeast side. During August 1985, there were also significantly more larvae at the head than at the centre of the bay, the consequence of greater relative abundance of smaller larvae.

Larval length and transport

The mean length of larvae from all strata combined during July surveys ranged from 5.4 mm in 1985 to 6.5 mm in 1984 (Figure 3). In August, mean lengths ranged from 7.5 mm in 1985 to 9.6 mm in 1986. Variations in mean length, as indicated by the coefficients of variation, were consistently higher in August than July.

Mean lengths of larvae were significantly different among strata ($p<0.05$) in most instances (Table 3). In July 1985 only were the differences both along the axis of the bay and between sides not statistically significant. This finding may be related to the suggested late spawning in 1985 that resulted in low numbers suveyed and small mean sizes.

Excluding July 1985, the smallest larvae during seven of the remaining nine surveys were at the head (in comparisons along the axis). However, in six of these, the largest larvae were near the centre, rather than at the mouth of the bay (Table 4). In one case (August 1986), larvae were statistically larger at the head than at the mouth of the bay. In that case, larvae sampled at the centre were significantly larger than those at either the head or the mouth. These events support Bailey's (1958) hypothesis regarding the existence of gyres in the bay. Such gyres would tend to trap larvae, allowing them to attain greater size before being released and subjected to transport out of the bay.

The most consistent observation with respect to size of larvae was that, in comparisons between sides, larger larvae were always on the southeast side of the bay. This finding applies to all 10 surveys, and in 9 of these 10, the differences were statistically significant (Table 3).

In summary, larvae were generally larger in strata far from the spawning sites (Table 4), located mostly at the head and northwestern side of the bay. We conclude that the direction of larval transport conforms to the mean current flow within the bay, larvae being larger and older downstream in their drift than those upstream. The occurrence of the largest larvae (in comparisons along the bay's axis) towards the centre and mouth of the bay also supports the hypothesis that the direction of larval transport follows the direction of the prevailing winds (out of the bay). In addition, the fact that larger larvae were caught in the centre rather than at the mouth of the bay supports the hypothesis that gyres tend to retain larvae in the bay.

Most of the individual components of the larval transport index (Table 5) were positive in sign,

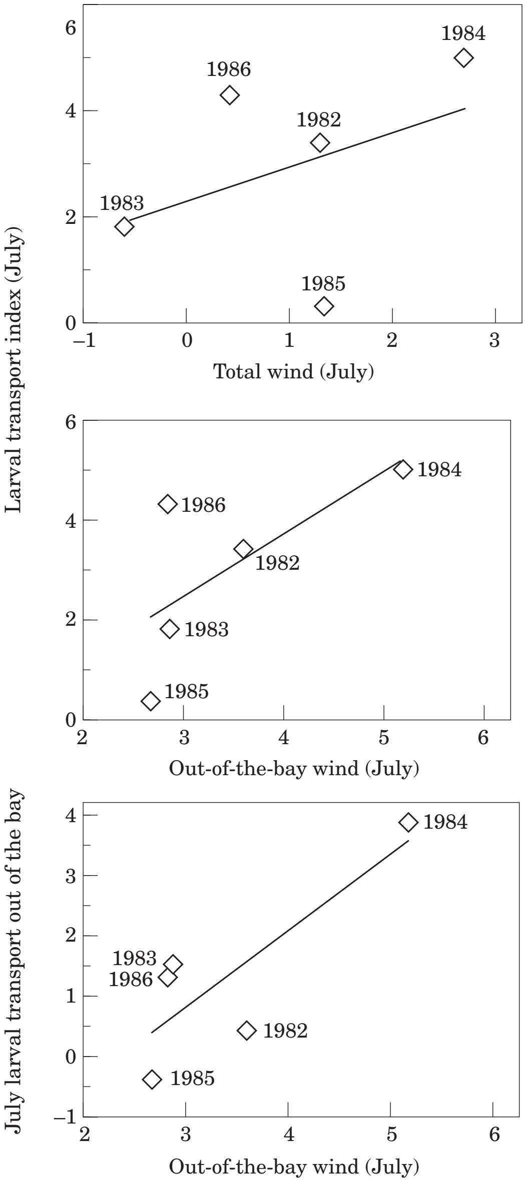

Figure 8. Relationship between wind and larval transport index: (top) total LT(U+V) and total wind (R^2=0.16); (middle) total LT and out-of-the-bay wind (R^2=0.48); and (bottom) out-of-the-bay component only of both variables (R^2=0.68).

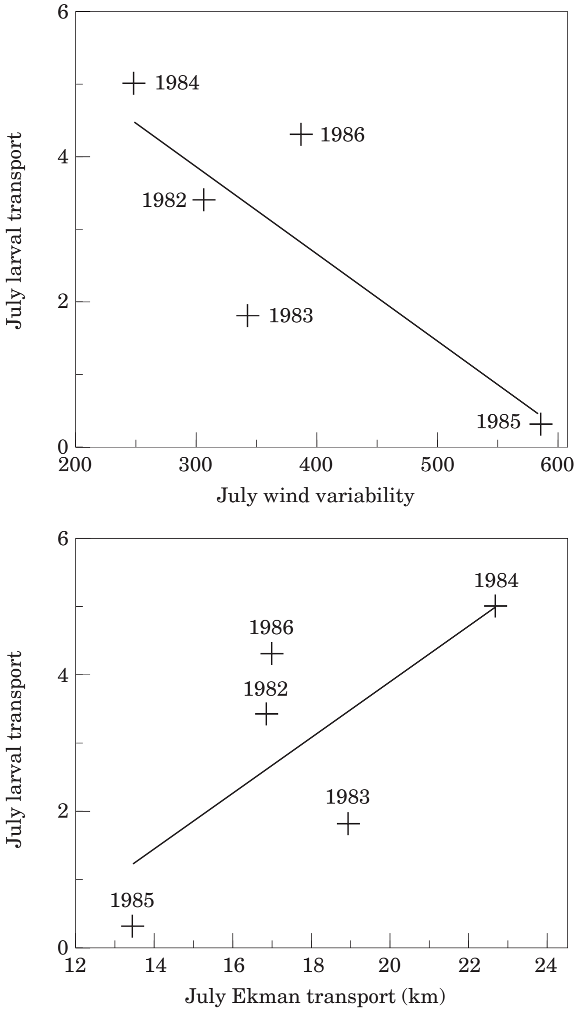

Figure 9. Relationship between larval capelin transport and wind variability in July (top; R^2= − 0.65) and Ekman transport in July (bottom; R^2=0.53), during larval surveys carried out in Trinity Bay, 1982–1986.

indicating a predominance of transport across (from northwest to southeast) and out of the bay. Larval transport covaried each month among years, being highest in 1984 and lowest in 1985 (Figure 6). The correlations between months indicate that the larval transport index is a consistent and reliable measure of transport within a particular year, but that it can vary and be less reliable among years. Slow transport during July 1985 was likely associated with the late spawning, which limited time for significant growth. Mean size of larvae was least in 1985 (both July and August surveys). In August, the overall larval transport index is low, but transport values related to the inner part of the bay are as predicted (Table 5). These were nullified by the negative values in the outer part of the bay (L5–L3, L6–L4, L4–L3, and L6–L5), which indicate that the largest fish during the August 1985 survey were in strata 3 and 5, on the outer northwest side. Larger fish in this area most likely derive from immigration of larger larvae via the Labrador Current in the northwest corner of the bay.

We examined the larval transport index in relation to the three wind indices. Total wind energy (the sum of the mean U and V components) varied among years for both July and August surveys (Figure 7, top). During

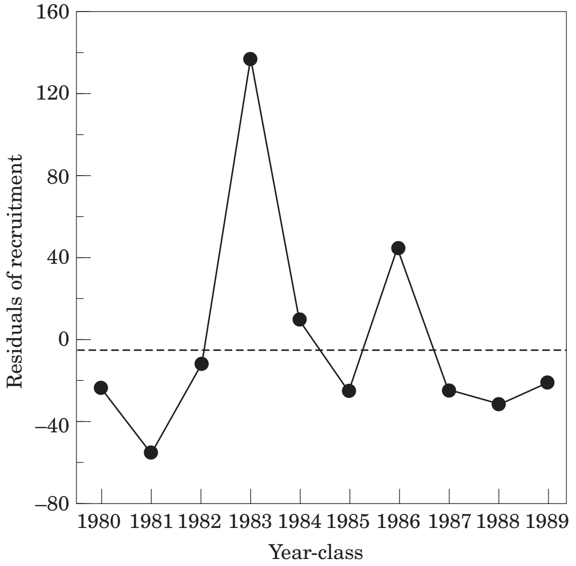

Figure 10. Recruitment in NW Atlantic capelin, standardized for the effect of successful release of capelin from beach sediments, based on the WIND variable of Leggett *et al.* (1984).

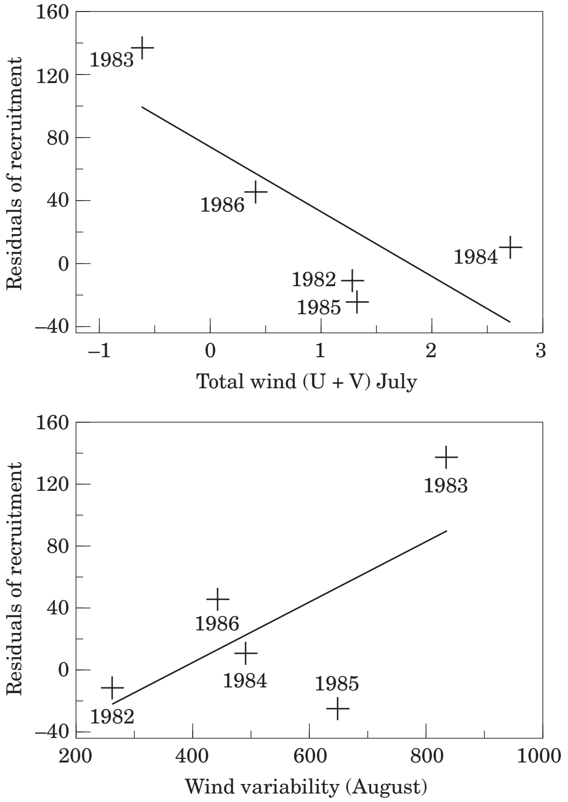

Figure 11. Relationship of the residuals of recruitment from WIND of the Leggett *et al.* (1984) model and total wind in July (top; $R^2 = -0.60$), and wind variability in August (bottom; $R^2=0.43$).

July surveys, wind energy was lowest in 1983 and highest in 1984, decreasing in each of 1985 and 1986. During August surveys, wind energy decreased from 1982 to 1984, peaked in 1985, and decreased to the lowest value of any survey in August 1986. Wind variability, as indicated by the sum of the coefficient of variation in the U and V components, also varied among years (Figure 7, middle). July values were generally lower than those of August. During August, wind variability alternated among years of low and high, the lowest being in 1982 and the highest in 1983. The third index, total Ekman transport, also varied among years, more so in August than in July (Figure 7, bottom). During July surveys, total Ekman transport increased until 1984, but was somewhat less in 1985 and 1986. August Ekman transport in 1982 was more than twice as high as in any other year.

There was only a weak relationship ($R^2=0.16$) between total larval transport and total wind in July (Figure 8, top), but a stronger relationship between the U (out of the bay) component of wind and total larval transport ($R^2=0.48$; Figure 8, middle). The strongest correlation was when only the U components of both wind and transport were compared ($R^2=0.68$; Figure 8, bottom). There was no relationship between total larval transport and wind in August ($R^2=0.13$).

Total larval transport was inversely related ($R^2= -0.65$) to wind variability in July (Figure 9, top). In August the relationship was also inverse, but insignificant ($r^2=0.06$). Larval transport in July was also positively related ($R^2=0.53$) to total Ekman transport that month (Figure 9, bottom), but it was unrelated to August Ekman transport ($R^2=0.03$). The slopes of the relationships between wind indices and larval transport were opposite in sign, i.e. larval transport was positively associated with total wind and Ekman transport and inversely related to our measure of variability in wind speed and direction.

To summarize, out-of-the-bay larval transport appears to have been facilitated by out-of-the-bay wind and Ekman transport in July. Larval transport was inversely correlated with wind variability in July, indicating that winds that were highly variable in speed and direction reduced transport. The relationships between larval transport and meteorological indices were stronger in July. We conclude, therefore, that increased size and the associated swimming ability/behaviour of larvae may moderate or alter the influence of currents on their drift. The intensity of diel vertical distribution, which could also alter transport rates, is also related to size of larvae (Jacquaz *et al.*, 1977; Frank and Carscadden, 1989).

Given the relationship between abundance of larvae and recruitment (Figure 4), we removed the effect of

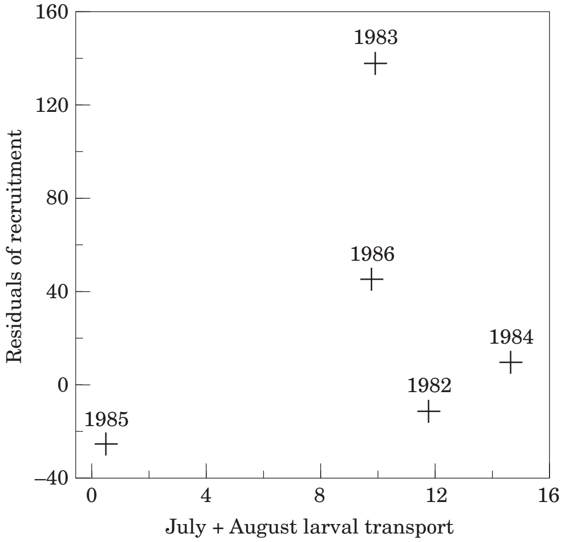

Figure 12. Recruitment of capelin standardized for successful release of larvae from beach sediments shown in relation to July plus August larval transport ($R^2=0.06$).

successful release of larvae on recruitment (WIND) prior to exploring the relationship between larval transport and recruitment. We calculated the relationship of WIND (days between northeasterly winds; Leggett *et al.*, 1984) and recruitment from the multiplicative model to be

$$\text{Year-class strength} = -9.234(\text{WIND}) + 115.013; \quad R^2=0.13 \qquad (5)$$

Of the years examined here, the residuals of recruitment from this relationship were lowest in 1982 and 1984, moderate in 1985, and highest in 1983 and 1986 (Figure 10); the last two were the largest year-classes in the series.

The relationships between July and August Ekman transport and the residuals from the standardized recruitment index were weak and of opposite sign ($R^2=0.11$ and -0.24 respectively). Total wind and wind variability were, however, associated with these residuals. Recruitment was inversely related to July total wind (sum U and V; $R^2=-0.60$; Figure 11, top), and positively related to wind variability in August ($R^2=0.43$; Figure 11, bottom). The relationship between the residuals of recruitment and August total wind was also inverse, but weaker ($R^2=-0.28$). There was no relationship between the residuals of recruitment and wind variability in July ($R^2=-0.08$).

There was no relationship between recruitment and larval transport for July ($R^2=0.00$) or August ($R^2=0.13$) separately, nor for the survey periods combined ($R^2=0.06$). In each case the low index of larval transport in 1985 appeared as an outlier. As suggested earlier, the lower index for 1985 appears to be associated with late spawning that year. If the 1985 data point is excluded as atypical or weak, there appears to be an inverse relationship between larval transport and recruitment (Figure 12).

Conclusion

Capelin larvae were abundant during all surveys except that of July 1985. They were also distributed throughout all strata of Trinity Bay during each survey. There were between-strata differences in abundance in only 1982 and 1985. Recruitment was positively correlated with bay-wide means in larval abundance, a result consistent with the general conclusion that recruitment of capelin is largely determined within a few weeks of hatching. Our results also support the Leggett *et al.* (1984) inverse relationship between frequency of onshore wind events (at hatching) and recruitment. In addition to being consistent, our results provide detailed confirmation over a larger, bay-wide geographic scale.

The larval transport index, developed from mean length of larvae in different strata, indicates that net larval transport during the surveys was (a) towards the east away from beaches (located predominantly on the northwest side and head of the bay) and (b) along the axis of the bay towards its mouth. Larval transport covaried between July and August each year, and its components were highly variable among surveys. This variability suggests the existence of oceanographic events of shorter time-scale (i.e. shorter than the period of the survey) that influence the drift of larvae in the bay, notably gyres that might retain larvae for undetermined periods of time (Frank and Carscadden, 1989; Frank *et al.*, 1992).

Larval transport was positively related to prevailing out-of-the-bay wind and the associated Ekman transport. Larval transport was inversely related to wind variability, indicating that variable wind speed and direction tended to reduce the rate of transport. Turbulent winds would tend to increase mixing within the bay and at the same time slow transport. The fact that larval transport was related to the wind indices in July but not August suggests a size-dependent relationship between wind events and transport of larvae. This relationship is possibly driven by the development of diel vertical movements of sufficient magnitude and direction to cause larvae to move between currents over a 24-h period.

The wind indices here developed, which operate during larval drift, contribute to the residual variance in recruitment from the Leggett *et al.* (1984) model. The residuals of recruitment from WIND were inversely related to total wind in July and positively related to wind turbulence in August. The slopes of these relationships are opposite to the relationships between wind indices and larval transport, so we conclude that there is no relationship between larval transport *per se* and recruitment.

Larval transport from Trinity Bay was not a necessary condition for survival. We therefore reject the hypothesis that transport of larvae out of Trinity Bay, and by extension other large bays, is a necessary requirement for successful recruitment. The results suggest that turbulent wind-mixing may be a more important mechanism affecting early survival. Winds that are highly variable in speed and direction tend to enhance production and survival of capelin larvae within the bay, a result completely consistent with the hypothesis of Mackenzie and Leggett (1997) that surface turbulence increases feeding success and recruitment. At the same time, transport from the bay would be reduced by the interruption of wind-driven currents, resulting from prevailing winds, that would tend to move larvae out. To our minds, therefore, the transport of capelin larvae to the Labrador Current is not a significant factor in their survival. Rather, the extent to which the larvae experience well-mixed (turbulent) surface waters may be more important in determining their fate.

Acknowledgements

Dr W. C. Leggett is thanked for his particularly constructive review of the diverse subject material (atmospheric, physical, and biological science) of the manuscript. Further, the support of the technical staff of the Pelagic Section of the Science, Oceans and Environment Branch in carrying out the ichthyoplankton surveys is gratefully acknowledged. In particular we thank Eugene McDonald, who co-ordinated technical aspects of the surveys. We also acknowledge the important work of the officers and crew of the research vessels "Shamook" and "Marinus".

References

Anderson, J. T., Dalley, E. L., and Davis, D. J. 1999. Year-class strength of Northwest Atlantic capelin (2J3KLNO) estimated at the larval stage and age one based on the pelagic juvenile fish surveys, 1994–1998. *In* Capelin in SA2+Div. 3KL. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat. Research Document, 99/206: 126–141.

Bailey, W. B. 1958. Trinity Bay, Newfoundland survey – September 1956. Fisheries Research Board of Canada Manuscript Report Series (Oceanographic and Limnological), 10.

Bailey, R. J. F., Able, K., and Leggett, W. C. 1977. Seasonal and vertical distribution and growth of juvenile and adult capelin (*Mallotus villosus*) in the St Lawrence Estuary and western Gulf of St Lawrence. Journal of the Fisheries Research Board of Canada, 34: 2030–2040.

Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2000. Evaluation of an environment-recruitment model for capelin (*Mallotus villosus*). ICES Journal of Marine Science, 57: 412–418.

Carscadden, J. E., Frank, K. T., and Leggett, W. C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences, 58: 73–85.

Carscadden, J. E., Nakashima, B. S., and Frank, K. T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 781–787.

Davidson, F. J. M., Greatbatch, R. J., and deYoung, B. 2001. Asymmetry in the response of a stratified coastal embayment to wind forcing. Journal of Geophysical Research, 106: 7001–7015.

Dower, K. F., Miller, T. J., and Leggett, W. C. 1997. The role of mesoscale turbulence in the feeding ecology of larval fish. Advances in Marine Biology, 31: 169–220.

deYoung, B., Anderson, J., Greatbatch, R. J., and Fardy, P. 1994. Advection-diffusion modelling of larval capelin dispersion in Conception Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 51: 1297–1307.

Evans, G. T., and Nakashima, B. S. 2001. Trends in yearclass strength of capelin (*Mallotus villosus*). *In* Capelin in SA2+3KL, pp. 186–202. Canadian Science Advisory Secretariat Research Document, 2001/161.

Frank, K. T., and Carscadden, J. E. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. Journal du Conseil International pour L'Exploration de la Mer, 45: 146–164.

Frank, K. T., and Leggett, W. C. 1981. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 38: 215–223.

Frank, K. T., and Leggett, W. C. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator prey complex associated with larval capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 39: 991–1003.

Frank, K. T., Loder, J. W., Carscadden, J. E., Leggett, W. C., and Taggart, C. T. 1992. Larval flatfish distributions and drift on the southern Grand Banks. Canadian Journal of Fisheries and Aquatic Sciences, 49: 467–483.

Gjøsæter, J., and Monstad, T. 1985. Primary growth rings in otoliths of Bering Sea capelin. FiskeriDirektoratets Skrifter Serie Havundersokelser, 17: 521–528.

Jacquaz, B., Able, K. W., and Leggett, W. C. 1977. Seasonal distribution, abundance and growth of larval capelin (*Mallotus villosus*) in the St Lawrence estuary and northwestern Gulf of St Lawrence. Journal of the Fisheries Research Board of Canada, 34: 2015–2029.

Leggett, W. C., Frank, K. T., and Carscadden, J. E. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 41: 1193–1201.

Mackenzie, B. R., and Leggett, W. C. 1993. Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons. Marine Ecology Progress Series, 94: 207–216.

Nakashima, B. S., and Taggart, C. T. 2002. Is beach-spawning success for capelin, *Mallotus villosus* (Müller), a function of the beach? ICES Journal of Marine Science, 59: 897–908.

SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6, 4th edn, Volume 2. SAS Institute Inc., Cary, North Carolina. 846 pp.

Smith, P. E., and Richardson, S. L. 1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fisheries Technical Paper, 175. 100 pp.

Taggart, C. T., and Leggett, W. C. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time series of analysis of physical-biological data. Canadian Journal of Fisheries and Aquatic Sciences, 44: 438–451.

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus* O. F. Müller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory, 17(Research): 1–151.

Yao, T. 1986. The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmospheric Ocean, 24: 235–252.