Fløde vigen rapportser., 1, 1984. ISSN 0333-2594
The Propagation of Cod *Gadus morhua* L.

THE TIMING OF COD SPAWNING ON THE SCOTIAN SHELF

J.A. Gagné and R.N. O'Boyle

Marine Fish Division, Bedford Institute of Oceanography,
P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

ABSTRACT

Gagné, J.A. and O'Boyle R.N., 1984. The Timing of Cod Spawning on the Scotian Shelf. In: E. Dahl. D.S. Danielssen, E. Moksness and P. Solemdal (Editors), The Propagation of Cod *Gadus morhua* L. Flødevigen rapportser., 1, 1984: 501-517.

We used results from the Scotian Shelf Ichtyoplankton Programme to describe the spatial and temporal distributions of cod eggs and larvae off the coast of Nova Scotia. Summer spawning is restricted to the waters along the Laurentian Channel. Eggs and/or larvae are found in the spring in all areas where spawning activities are detected. Late fall - early winter spawning takes place over several banks and along the southern coast of Nova Scotia. A match between the seasonal blooms and the time of spawning does not appear to be essential, although it might exist in the spring. Larval drift from spawning grounds to nursery grounds is apparently rare on the Scotian Shelf. These findings are discussed with reference to the match-mismatch hypothesis of Cushing.

INTRODUCTION

O'Boyle et al. (in press) recently presented an analysis of the data collected during eleven surveys conducted between 1978 and 1980 as part of the Scotian Shelf Ichthyoplankton Programme. Atlantic cod (*Gadus morhua* L.) was one of the six species included in their analysis. The data available to them suggested that cod spawning on the Scotian Shelf was restricted to the November to May period. It appeared to commence in the fall primarily around Sable Island Bank and along the Nova Scotia coast. By April, it had shifted to some of the south-western banks.

These authors saw little evidence of larval drift and indicated that for at least some of the species studied, the time of spawning did not match the seasonal blooms as proposed by Cushing (1969; 1982). They suggested that larval retention could play an important role in determining larval survival in a manner similar to that described by Iles and Sinclair (1982) for herring.

The present analysis extends the ichthyoplankton data set into early 1981 and introduces new data on the distribution of yearling cod on the Scotian Shelf. Unlike O'Boyle et al. (in press), we concentrate on cod only. We discuss the timing of cod spawning on the Scotian Shelf with respect to larval drift and the influence of the seasonal plankton blooms.

MATERIALS AND METHODS

Eggs and Larvae

The Scotian Shelf Ichthyoplankton Programme was designed in 1976 to provide basic information on the spatial and temporal distribution of fish eggs and larvae over the continental shelf off Nova Scotia, Canada. In order to survey this large area practically, a grid of 150 stations approximately 30 km apart was adopted (Fig. 1).

To achieve such an extensive coverage, only a few stations

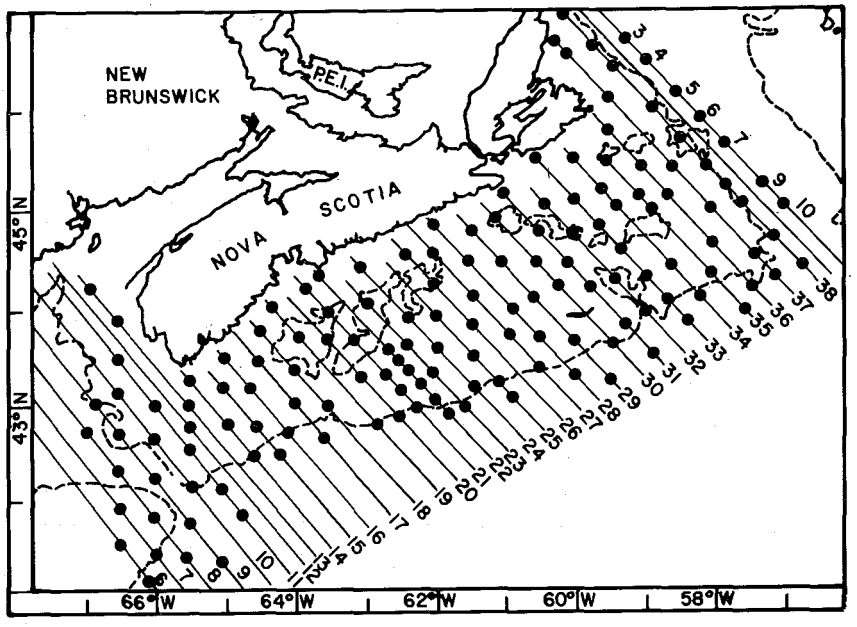

Fig. 1. Grid adopted for the Scotian Shelf Ichthyoplankton Programme. The 200 m isobath is shown.

were located near the coast or on the smaller offshore banks (Tables 1 and 2).

We refer to the areas between the coast and the 50 m isobath as coastal areas. To investigate spatial patterns, all stations within these boundaries were assigned to unit areas arbitrarly defined, although related to major geographic regions of Nova Scotia (Fig. 2).

Between 1978 and 1982, bimonthly sampling was conducted using a variety of plankton nets. The major sampling device was the 61 cm bongo frame fitted with two 0.333 mm nitex nets. Oblique tows were made from 0 to 200 m or bottom at a ship speed of 2.0 to 2.5 knots. Wire-in and -out rates were 20 and 50 $m.min^{-1}$ respectively which achieved approximately 1 m^3 of water sampled per metre of water depth. All samples used for

this paper were collected in this way and stored in 5% buffered formalin.

Our analysis examines the results of 16 of the 38 surveys completed during the programme. We cannot include the other surveys because the samples for 1976 to 1978 are currently undergoing resorting to obtain more accurate information, while the data for the 1981 and 1982 surveys have not yet been fully processed.

The greatest sampling intensity between 1978 and 1981 was achieved over the northern portion of the shelf while sampling of the southern half was limited (Tables 1 and 2).

Our current sorting protocol does not allow discrimination among the early stage eggs of cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and witch flounder (*Glyptocephalus cynoglossus* L.). Identification first becomes reliable when the length of the embryo curled around the vitellus is such that the tail reaches beyond the head. Hatching follows shortly after. Only eggs at and after this developmental stage

TABLE 1

Number of stations where an oblique bongo tow was made in each coastal area.

		J	A	S	O	N	D	J	F	M	A	M	J
Sydney Bight	79										3	6	
	79/80		3	5	1	7			4			8	7
	80/81	7	2	2	3		3			7			
Eastern Cape Breton	79										2	1	
	79/80				3	2			2			2	2
	80/81	1					2	2		1			
Eastern Shore	79										2	2	
	79/80				2	2			2			2	2
	80/81	2					2	2		2			
Halifax Area	79										3	3	
	79/80			1	2	3			3			3	3
	80/81	3					3	3		3			
South Shore	79										4	2	
	79/80				1	4			4			2	4
	80/81	2					4	5		3			
Western Shore	79										4		
	79/80		1	2	2	1			2			1	5
	80/81		1	1			4	10					

TABLE 2

Number of stations where an oblique bongo tow was made on each offshore bank. The banks below the dotted line are the southern ones.

		J	A	S	O	N	D	J	F	M	A	M	J
Misaine	79										7	4	
	79/80		10	9	8	8			8			9	10
	80/81	9	9	9	11		6	9		10			
Banquereau	79										5	9	
	79/80		13	12	5	8			1			14	11
	80/81	5	15	15	15		8	12		6			
Middle	79										3	2	
	79/80		3	3	3	3			2			3	3
	80/81	2	3	4	3		3	3		2			
Sable	79										9	5	
	79/80		10	12	10	7			6			8	8
	80/81	8	9	9	10		7	9		9			
Western	79										3	3	
	79/80		2	3	2	2						2	1
	80/81	2	2	2	3			2		2			
Emerald	79										6	3	
	79/80		6	6	6	6			5			6	6
	80/81	6	6	7	6			6		6			
La Have	79										2	1	
	79/80		2	2	2	2			1			2	2
	80/81	2	2	2			2	2		2			
Roseway	79										1	1	
	79/80		1	1	2	1			1				1
	80/81	1	1	1			1	1		1			
Baccaro	79										1	1	
	79/80		2	2		2			2				2
	80/81		3	3			1	2		2			
Browns	79										4	2	
	79/80		3	4	2	4			4			4	4
	80/81		3	4			3	4					

have been included in the present analysis.

We qualitatively summarize the abundance of cod eggs and larvae in each area as follows: absent - $0.m^{-2}$; present - specimens caught at one station only; abundant - 1 to $5.m^{-2}$ at more than one station; very abundant - greater than $5.m^{-2}$ at a few stations or 1 to $5.m^{-2}$ at most stations or specimens found at all stations.

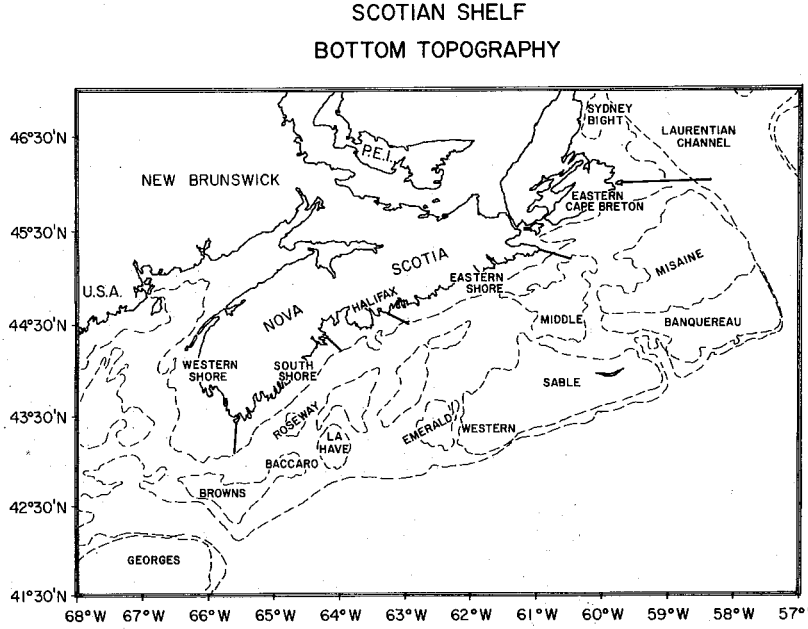

Fig. 2. Map of coastal areas and offshore banks. The 100 and 200 m isobaths are shown.

Juveniles

In order to describe the distribution of one year-old cod on the Scotian Shelf, we present data from the Canadian groundfish survey programme. These stratified random surveys have been run over the entire shelf in the summer of each year since 1970 to provide abundance estimates for the demersal finfish species of commercial interest. From 1970 to 1981, a Yankee 36 bottom trawl with a 0.6 cm liner over the codend was used. A more complete description of the survey design can be found in Halliday and Koeller (1981). We use the data for 1976 to 1981.

RESULTS

Eggs and larvae

Eggs were caught all along the coast although not necessarily at the same time (Table 3). In the Sydney Bight area, they were found mainly between May and August, a clear indication of summer spawning. Spawning in summer appears to be restricted to Sydney Bight as no eggs were found anywhere else along the coast from July to September. Spring spawning occurs in all coastal areas and there is some indication that it may start around March south of Halifax. Cod eggs were also found in late fall and/or early winter in all areas except the coast of eastern Cape Breton. Our data suggest that late autumn -

TABLE 3

Relative abundance of eggs of Atlantic Cod (*Gadus morhua* L.) along the coast of Nova Scotia. Symbols: 0 absent, • present, ● abundant, ● very abundant, - area not covered by the survey. Each category is defined in the text.

		J	A	S	O	N	D	J	F	M	A	M	J
Sydney Bight	79										0	•	
	79/80		•	0	0	0			0			0	●
	80/81	•	0	0	•		0	–		0			
Eastern Cape Breton	79										0	0	
	79/80		–	–	0	0			0			•	●
	80/81	0	–	–	–		0	0		0			
Eastern Shore	79										0	•	
	79/80		–	–	0	0			0			•	0
	80/81	0	–	–	–		•	0		0			
Halifax Area	79										0	0	
	79/80		–	0	0	●			0			●	0
	80/81	0	–	–	–		●			•			
South Shore	79										●	0	
	79/80		–	–	0	●			0			0	•
	80/81	0	–	–	–		●	0		•			
Western Shore	79										•	–	
	79/80		0	0	0	0			0			•	0
	80/81	–	0	0	–		•	0		–			

early winter spawning could be more important than spring spawning in at least two areas, Halifax and the South Shore. Finally, no eggs were found along the coast in September or October (Sydney Bight excepted) and in January or February.

Cod larvae show a distribution similar to that of the eggs in the coastal areas (Table 4). Larvae were caught in summer only in the Sydney Bight area while they were found in late spring and early summer in all areas south of eastern Cape Breton. Larvae were quite abundant off Halifax and the South Shore in November and December and also present in Sydney Bight and along the Eastern Shore. No larvae were caught anywhere in early fall or in January. Not a single cod larva was caught in the eastern Cape Breton area.

Table 5 presents the relative abundance of cod eggs over the offshore banks. Between June and August, cod eggs were found over Misaine and Banquereau Banks at the northeastern egde of

TABLE 4

Relative abundance of cod larvae along the coast of Nova Scotia. Symbols as for Table 3.

		J	A	S	O	N	D	J	F	M	A	M	J
Sydney Bight	79										0	0	
	79/80		0	0	0	•			0			0	0
	80/81	●	0	0	0		0	–		0			
Eastern Cape Breton	79										0	0	
	79/80		–	–	0	0			0			0	0
	80/81	0	–	–	–		0	0		0			
Eastern Shore	79										0	0	
	79/80		–	–	0	0			0			•	•
	80/81	0	–	–	–		•	0		0			
Halifax Area	79										•	●	
	79/80		–	0	0	●			0			●	•
	80/81	0	0	–	–		●	0		•			
South Shore	79										●	0	
	79/80		–	–	0	●			•			•	0
	80/81	0	–	–	–		•	0		0			
Western Shore	79										●	–	
	79/80		0	0	0	0			0			•	•
	80/81	–	0	0	–		0	0		–			

TABLE 5

Relative abundance of cod eggs over the offshore banks. The banks below the dotted line are the southern ones. Symbols as for Table 3.

		J	A	S	O	N	D	J	F	M	A	M	J
Misaine	79										0	•	
	79/80		•	0	0	0			0			•	0
	80/81	0	0	0	0		0	0		0			
Banquereau	79										0	•	
	79/80		0	0	0	●			0			●	•
	80/81	0	0	0	•		●	0		•			
Middle	79										0	0	
	79/80		0	0	0	●			0			●	0
	80/81	0	0	0	0		•	0		0			
Sable	79										●	0	
	79/80		0	0	0	●			0			●	0
	80/81	0	0	0	●		●	•		●			
Western	79										●	0	
	79/80		0	0	0	0			–			0	0
	80/81	0	0	0	0		–	0		●			
Emerald	79										●	0	
	79/80		0	0	0	0			0			0	0
	80/81	0	0	0	0		–	0		●			
LaHave	79										0	0	
	79/80		0	0	0	0			0			0	0
	80/81	0	0	0	–		0	0		•			
Roseway	79										0	0	
	79/80		0	0	0	0			0			–	0
	80/81	0	0	0	–		0	0		0			
Baccaro	79										0	0	
	79/80		0	0	–	0			0			–	0
	80/81	–	0	0	–		0	0		•			
Browns	79										•	0	
	79/80		0	0	0	•			0			0	0
	80/81	–	0	0	–		0	0		–			

the shelf. The station by station data show that the eggs caught over Banquereau came from the northeastern half of that bank.

Spring spawning activity was detected on most offshore banks, being especially intense on Sable and Western Banks. While spawning appears to start at the same time on all the banks, i.e. around March, it seems to last longer on Banquereau, Middle and Sable Banks where eggs were caught until May. On the other banks spawning could be over around the end of April.

Our egg data suggest that fall and early winter spawning occurs mainly on the northeastern banks: Banquereau, Middle and Sable. On Middle and Sable Banks the intensity of spawning during that period is comparable to that observed in the spring. No evidence of autumn spawning could be seen on any of the banks south of Sable Bank, with the exception of Browns Bank where eggs were found once in November. As observed for the coastal areas, no spawning activity seems to take place on the offshore banks for two or three months in late summer and early fall (Misaine excepted) and in mid-winter.

The distribution of larvae offshore (Table 6) generally agrees with the scheme suggested by the egg data. Indeed, Misaine and Banquereau are the only banks where larvae were caught in August and September, obviously as a result of summer spawning. Interestingly, the larvae caught on Banquereau all come from the stations near the northeastern edge of the shelf. Therefore both the egg and the larval data indicate that summer spawning is restricted to the waters bordering the Laurentian Channel. On La Have and Browns Banks, larvae were present only in the spring while on Western and Emerald Banks larvae were caught from January to May or June. Finally, larvae could be found on Banquereau, Middle and Sable Banks at any time between October and June.

When both the egg and the larval data are considered together for the offshore banks, the following picture emerges. Summer spawning is restricted to the waters along the Laurentian Channel. Spring spawning most certainly occurs on all the banks with the possible exception of Roseway Bank where

no spawning activity was detected. Spawning takes place in late autumn and early winter on Banquereau, Middle and Sable Banks. Winter spawning of limited intensity is also suggested for Western and Emerald banks by the larval distribution and for Browns Bank by the egg distribution. Based on the month during

TABLE 6

Relative abundance of cod larvae over the offshore banks. The banks below the dotted line are the southern ones. Symbols as for Table 3.

		J	A	S	O	N	D	J	F	M	A	M	J
Misaine	79										0	0	
	79/80		●	●	0	•			0			0	•
	80/81	•	0	0	0		0	0		0			
Banquereau	79										0	0	
	79/80		●	•	0	●			0			●	•
	80/81	0	0	0	•		•	0		0			
Middle	79										•	•	
	79/80		0	0	0	●			0			●	•
	80/81	0	0	0	0		0	0		0			
Sable	79										●	●	
	79/80		0	0	0	●			•			●	●
	80/81	0	0	0	●		●	●		●			
Western	79										●	●	
	79/80		0	0	0	0			—			•	0
	80/81	0	0	0	0		—	•		●			
Emerald	79										●	●	
	79/80		0	0	0	0			0			●	●
	80/81	0	0	0	0		—	●		●			
LaHave	79										0	0	
	79/80		0	0	0	0			0			•	•
	80/81	0	0	0	—		0	0		0			
Roseway	79										0	0	
	79/80		0	0	0	0			0			—	0
	80/81	0	0	0	—		0	0		0			
Baccaro	79										0	0	
	79/80		0	0	—	0			0			—	0
	80/81	—	0	0	—		0	0		0			
Browns	79										●	0	
	79/80		0	0	0	0			0			●	0
	80/81	—	0	0	—		0	0		—			

which eggs were found and on the approximate time required for larvae to hatch (Wise, 1961), there appears to be no cod spawning on the offshore banks in summer (Misaine and Banquereau Banks excepted) and in mid-winter (Sable Bank excepted).

In all areas of the Scotian Shelf where we find evidence of cod spawning both in autumn and in spring, it appears to follow a bimodal pattern with no or very reduced activities in mid-winter. This important pattern was not observed by O'Boyle et al. (in press). Its possible ecological significance is discussed in the last section.

Juveniles

Table 7 shows the distribution of one-year old cod on the Scotian Shelf. It indicates that on the average between 1976 and 1981, they were in higher concentrations over Sable, Middle and Banquereau Banks than anywhere else on the shelf. The distribution of the two-year old cod (not shown here) follows the same pattern with about 60% of the young fish residing over these three banks.

TABLE 7

Relative abundance of 1-year old Atlantic cod (*Gadus morhua* L.) over the main banks and basins of the Scotian Shelf. (% of the estimate for the entire shelf; data from Canadian groundfish surveys.)

BANKS:	1976	1977	1978	1979	1980	1981	MEAN
Misaine	0	<1	0	11	0	0	2
Banquereau	7	39	2	8	16	5	13
Sable	61	11	26	14	14	64	32
Middle	12	7	2	2	26	3	9
Western	3	<1	1	6	6	1	3
Emerald	0	2	0	0	1	0	<1
LaHave	<1	0	0	<1	0	1	<1
Baccaro	<1	0	0	1	0	<1	<1
Roseway	0	1	0	1	0	<1	<1
Browns	1	8	1	<1	0	0	2
BASINS:							
Emerald	0	0	2	0	0	0	<1
LaHave	0	0	0	0	0	0	<1

DISCUSSION AND CONCLUSION

Timing of Spawning

The productivity cycle over the Scotian Shelf appears to be typical of boreal waters with a major bloom in April and probably a minor one in October (O'Boyle et al., in press). In all areas where there was evidence of spawning by cod, major spawning activities always occurred between March and May. This situation is very similar to those described by Cushing (1969; 1982) in support of his match-mismatch hypothesis. However, late autumn - early winter spawning is a common occurrence on the Scotian Shelf and its intensity is comparable to spring spawning in some areas. It is much more difficult to suggest a relationship between the bloom and the spawning activities in the fall since the major concentrations of larvae are found in November and December, well after the bloom. This suggests that seasonal blooms are not essential for the achievement of intense spawning by cod. This is further exemplified by the situation along the Laurentian Channel where cod seem to spawn extensively in summer, right between the two seasonal blooms.

Water temperature could be the reason why cod spawning does not start before November in most areas. In September and October, the temperature of the surface waters where the eggs would be found is often in the vicinity of 16°C on the Scotian Shelf. Evidence from the literature (Brawn, 1961; Wise, 1961; Laurence and Rogers, 1976) indicates that cod does not spawn in water warmer than 12°C, possibly because it is too warm for the embryos to develop properly. Temperature may also explain the reduction or the absence of spawning in mid-winter and therefore be responsible for the bimodal pattern observed in several areas; the surface waters would then be too cold for cod eggs to be released and/or to develop.

Larval Drift

The sampling design adopted for the Scotian Shelf Ichthyoplankton Programme does not permit a detailed analysis of the

drift patterns followed by planktonic organisms. However, if cod eggs and larvae drift on the Scotian Shelf in the way suggested by Jones (1968), i.e. away from discrete spawning areas, we should find many stations where only eggs or larvae were caught. Combining all the stations visited during the 16 cruises included in this analysis, we find a total of 73 stations where cod eggs and/or larvae were caught at least twice. Of these 73 stations, four produced only eggs and eight only larvae.

Moreover, our analysis of the distribution of one and two year old cod shows that they are concentrated over the banks identified as major spawning areas, i.e. Banquereau, Middle and Sable Banks. This strongly suggests that the spawning and the nursery grounds are often within the same geographical area. From this evidence, we conclude that over most areas of the Scotian Shelf, cod larvae do not drift from spawning grounds to nursery grounds; instead, they are generally retained within large areas where both types of grounds are located, as suggested by O'Boyle et al. (in press). These authors proposed that gyres may provide the required retention mechanism, at least over some of the banks.

A Hypothesis

It is generally accepted that concentrations of suitable prey organisms sufficient to permit the survival of fish larvae are available only at certain times and in certain areas of the ocean. Based on this and on the results of the present analysis, we now put forward a hypothesis to explain the timing of cod spawning on the Scotian Shelf as outlined by our data.

We propose that the spawning of Atlantic cod on the Scotian Shelf is restricted to those time periods when the temperature of the surface layer of the ocean is between approximately $0^{\circ}C$ and $12^{\circ}C$. We suggest that within these time periods, spawning occurs only in areas where prey organisms of the right size are likely to be sufficiently concentrated for the larvae to survive. In some areas, these conditions would be met only at the time of the spring bloom and spawning there would take

place only in the spring. In other areas, sufficient food concentrations could become available in early summer before the temperature gets too high, or in mid-autumn and early winter before the temperature becomes too low; summer and/or autumn and early winter spawning could then be observed.

O'Boyle et al. (in press) found that cod eggs and larvae were mostly concentrated over the banks of the Scotian Shelf, only a few being caught over the deeper basins. We observed the same situation for all the cruises included in our analysis. O'Boyle et al. also indicated that higher concentrations of zooplankton were apparently associated with the offshore banks where smaller, probably more productive species dominated. It is therefore possible that cod spawning is concentrated over the banks and the coastal areas where the availability of prey organisms is better.

Iles and Sinclair (1982) proposed that the presence of retention areas and their size determine the identity and the size of herring stocks. O'Boyle et al. (in press) suggested that the same relationship could explain the association between cod spawning and the offshore banks, the presence of gyres associated with the banks providing the required retention mechanism. Although we agree with this interpretation in general, we believe that the evidence currently available suggests that the existence of retention mechanisms is a means, not a cause, behind the observed features of cod spawning; larval retention would be another mechanism whereby the larvae would remain in contact with suitable prey organisms. On the Scotian Shelf, it appears that retaining the larvae within the area where adequate food is available is the major mechanism towards achieving the survival of cod larvae. In other areas from which evidence is available, as for instance the Norwegian coast, larval drift appears to be prevalent (Cushing, 1982). The relative importance of these mechanisms seems to be determined by the hydrography of each area. Depending on the local conditions cod larvae, in order to find the required food concentrations, may have to either drift with or towards prey aggregations or be retained with them. As suggested earlier,

sufficient food concentrations may, but do not have to, depend on the seasonal plankton blooms.

We realise that our hypothesis is highly speculative. Unfortunately we did not have the time to carry out our analysis any further before the June meeting. We are now studying the temporal and spatial variations in water temperature and zooplankton concentrations to see if they support our hypothesis. We also want to compare the survival rate of the larvae produced at different times of the year.

ACKNOWLEDGEMENTS

We want to express our gratitude towards Carson Ludsley, Mark Fowler, Carla Dale, and in particular Linda Currie for their dedicated work at providing us with the necessary raw data. We also acknowledge the special talents and especially the diligence of our draftsman, Christopher Cody and our typist Valerie Myra. Very special thanks go to Peter Hurley for his enduring help at all stages of this work. We also thank Steve Campana and Robin Mahon for their thorough review of an earlier manuscript.

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