

# Temporal variation in fish egg and larval production by pelagic and bottom spawners in a large Newfoundland coastal embayment

Paul V.R. Snelgrove, Ian R. Bradbury, Brad deYoung, and Sandra Fraser

**Abstract:** In highly seasonal environments such as coastal Newfoundland, local production, advection, and life history may influence ichthyoplankton community structure. The spring bloom occurs in cold water that slows development of eggs from pelagic spawners and may transport propagules from optimal nearshore areas before hatch. For bottom spawners that affix eggs to the bottom, the problem is reduced because only actively swimming larval stages are pelagic. We hypothesize that larvae of pelagic spawners are limited to warmer, summer waters, whereas larvae of bottom spawners are less constrained temporally and less subject to flushing from the nearshore environment. Ichthyoplankton taxa sampled in Placentia Bay, Newfoundland, during spring–summer in 1997–1999 showed consistent seasonal peaks in egg and larval abundance. Although pelagic egg production spanned spring and summer, larval abundance peaked late in summer or early fall in the most productive areas of the bay. Larval abundance of bottom spawners peaked in spring for most taxa. Thus, pelagic eggs hatch quickly in summer, and larvae can utilize the late peak in nearshore copepod abundance. Bottom spawners can utilize spring zooplankton because temperature-dependent development does not influence egg advection. Coastal advection and temperature influence how different life history groups exploit spatial and temporal peaks in production.

**Résumé :** Dans les environnements fortement saisonniers, tels que la côte de Terre-Neuve, la production locale, l'advection et le cycle biologique peuvent influencer la structure de la communauté de l'ichtyoplancton. Le foisonnement des algues au printemps se produit en eau froide qui ralentit le développement des oeufs des reproducteurs pélagiques et peut éloigner les propagules des sites optimaux près des côtes avant l'éclosion. Chez les reproducteurs benthiques qui fixent leurs oeufs au fond, le problème est moins important seulement parce que les seuls stades à nage active sont pélagiques. Notre hypothèse veut que les larves des reproducteurs pélagiques soient restreintes aux eaux estivales plus chaudes et que les larves des reproducteurs benthiques soient moins limitées dans le temps et moins sujettes à être entraînées loin de l'environnement côtier. Les taxons de l'ichtyoplancton échantillonnés dans la baie de Placentia, Terre-Neuve, au printemps et à l'été 1997–1999 accusent des maximums cohérents d'abondance d'oeufs et de larves. Bien que la production pélagique des oeufs s'étende sur tout le printemps et l'été, l'abondance des larves atteint un sommet en fin de l'été ou au début de l'automne dans les régions les plus productives de la baie. L'abondance larvaire de la plupart des espèces à reproduction benthique est maximale au printemps. Ainsi, les oeufs pélagiques éclosent rapidement en été et les larves peuvent utiliser le pic tardif d'abondance des copépodes côtiers. Les reproducteurs benthiques peuvent profiter du zooplancton printanier, car le développement dépendant de la température n'affecte pas l'advection des oeufs. La température et l'advection sur la côte influencent comment les groupes à cycles biologiques différents exploitent les maximums spatiaux et temporels de production.

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## Introduction

Early life history stages have long been thought to be critical for recruitment success (e.g., Hjort 1914; Horwood et al. 2000) and the establishment of spatial pattern of marine fish

assemblages (e.g., Sherman et al. 1984; Hare et al. 1999). For most marine species, mortality during this period is extremely high, and there has been considerable discussion on the importance of matching larval hatching with availability of food (Hjort 1914; Cushing 1990), low predator abundance

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(Frank and Leggett 1982, 1983), and appropriate habitats (Frank and Leggett 1982; deYoung and Rose 1993). Recent emphasis has been placed on circulation patterns and their importance to local retention near suitable habitat (e.g., Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000). Availability of food and appropriate habitat are heavily dependent on how circulation patterns regulate distribution of eggs and early larval stages (e.g., deYoung and Rose 1993; Davidson and deYoung 1995; Bradbury et al. 2000), and in strongly seasonal environments, these relationships are further complicated by temperature-dependent development rates that may prolong hatching time and obfuscate any link between specific spawning location and hatching site (Bradbury et al. 2000). For species that produce pelagic eggs (hereafter pelagic spawners), the role of circulation and spawning location are even more pronounced than for species that spawn on the bottom and affix their eggs to the substrate so they do not disperse (hereafter bottom spawners). Hatched larvae have a relatively greater capacity than pelagic eggs to influence their own transport and spatial pattern, suggesting that passive dispersal in pelagic spawners is likely to be more pronounced than in bottom spawners. Work on reef fishes (e.g., Kingsford and Choat 1989; Hickford and Schiel 2003) suggests that there is no simple relationship between dispersal and developmental mode, but temporal persistence of patterns in larvae from bottom spawners relative to pelagic spawners led Suthers and Frank (1991) to suggest that pelagic spawner larvae may disperse further.

Coastal environments may be advantageous as a larval habitat for several reasons. Food may be more abundant than in shelf environments (Frank and Leggett 1982; Taggart and Leggett 1987; Bailey et al. 1995), predators may be less abundant (Frank and Leggett 1982), and critical habitat for bottom spawners and nursery habitat for juveniles may be more readily available (Ellertsen et al. 1981; Gotceitas et al. 1997). Coastal waters are often warmer than offshore areas, potentially resulting in reduced egg development times (Pepin 1991; Bradbury et al. 2000) and increased larval growth rates (Bailey et al. 1995). Faster growth may also reduce mortality resulting from predation on eggs and small, vulnerable larvae (Houde 1996). Thus, regardless of the taxonomic affiliation or adult habitat and ecological niche occupied by a given species, there may be considerable survival advantage in placing hatching larvae in a food-rich, coastal environment, particularly in temperature conditions that favour rapid egg development and (or) larval growth.

The goal of our study was to examine temporal variation in ichthyoplankton patterns in pelagic and bottom-spawning species through the spring and summer reproductive season in a large coastal embayment where physical variables exhibit strong variability in space and time. Placentia Bay is a large embayment on the south coast of Newfoundland that is characterized by strong cyclonic flow. Unlike the smaller embayments in the region for which ichthyoplankton has been studied (e.g., Frank and Leggett 1982; Laprise and Pepin 1995; Pepin et al. 1995), flow conditions are generally temporally consistent, at least along the sides of the bay, and are not as strongly coupled to changes in wind forcing (Bradbury et al. 2000; Schillinger et al. 2000). Moreover, the strength and consistency in predominant flow creates an additional problem for the retention of propagules within the

coastal environment, in that spawning in some areas of the bay may lead to immediate and predictable flushing into the offshore environment.

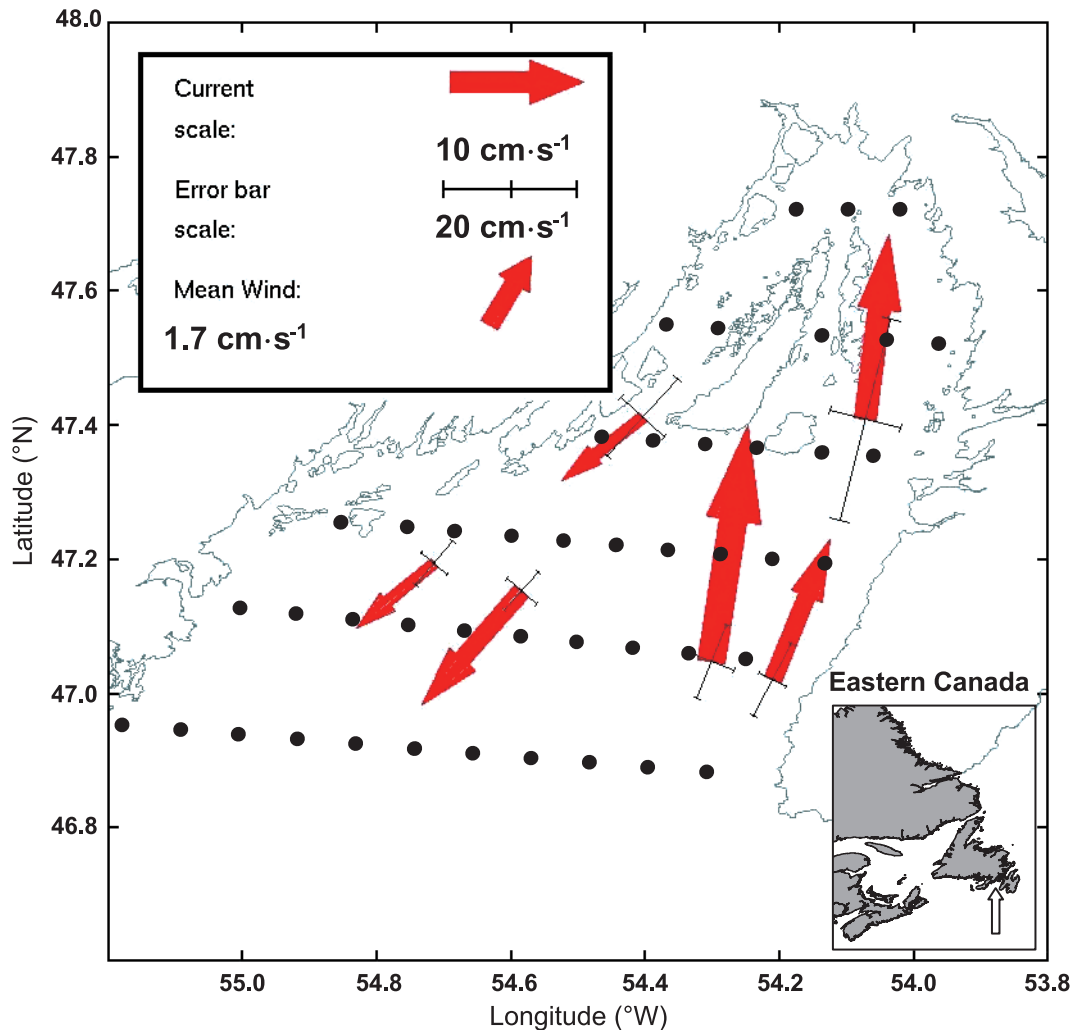
We hypothesized that timing of larval peaks would coincide with peak food availability (Cushing 1990) and (or) periods when development times would be minimized, but that this pattern would depend on spawning strategy. For pelagic spawners, we predicted that spawning would occur in mid- to late summer, at locations and in temperature conditions where eggs would develop quickly in warm summer waters and larvae would hatch in the nearshore environment before being flushed from the bay. For bottom spawners, we predicted that protracted spawning would predominate because advective loss of their planktonic larvae, which have some swimming capacity, was expected to be less than that for pelagic eggs (e.g., Suthers and Frank 1991), particularly during the spring bloom. Egg development for bottom spawners could occur slowly in the bottom environment during late winter without advective loss from nearshore areas. Finally, we asked whether eggs of pelagic spawners are released "upstream" of areas of higher secondary production (e.g., Munk et al. 1995), thereby placing larvae in a favourable environment, and whether this pattern is similar to that observed in larvae of bottom spawners. These questions are addressed in the spatially and temporally dynamic context of Placentia Bay circulation and flushing, with the goal of understanding how spawning strategies link to coastal dynamics in seasonal environments.

## Materials and methods

The Placentia Bay study area is a large embayment (~130 km long by ~100 km wide at its southern mouth) on the southeast coast of Newfoundland (Fig. 1). Bottom depths are several hundred metres in the deepest channels that pass between scattered banks, and elongated islands divide the northern portion of the bay into three channels. Currents flow into the bay along the eastern side towards the north and in a southerly direction out of the bay along the western side; currents near the head of the bay and near the center of the bay are weaker and more variable (Bradbury et al. 2000; Schillinger et al. 2000).

Ichthyoplankton samples were collected on a grid of 45 stations along six parallel transects (see Fig. 1) that were 8 nautical miles (1 n.mi. = 1.853 km) apart and ran perpendicular to the long axis of the bay. Stations were 4 n.mi. apart along each transect, except where landmasses or bottom topography required that they be shifted slightly. The mouth of a Tucker trawl (2 m × 2 m) with decreasing mesh sizes of 1000, 570, and 333  $\mu\text{m}$  was equipped with two General Oceanic flowmeters to allow estimates of flow volumes. Oblique tows at a towing speed of two knots (1 knot = 1.853  $\text{km}\cdot\text{h}^{-1}$ ) were collected for 15 min to a maximum depth of 40 m. Previous studies in coastal Newfoundland have found that >95% of the ichthyoplankton occurs in the upper 40 m (Frank and Leggett 1982; Laprise and Pepin 1995). The Tucker trawl is a more effective sampler than bongo nets because it results in higher estimates of species diversity and lower variability, although the Tucker trawl may slightly underestimate larvae <5 mm (Pepin and Shears 1997). Cruises took place in April, June, and August of

**Fig. 1.** Chart showing Placentia Bay ichthyoplankton sampling stations. Solid arrows denote mean circulation at a depth of 20 m for days 108–178, 1999. The results of covariance analysis are indicated in the figures by the solid axes. These axes show the standard deviation of the current along the direction of maximum variance and perpendicular to it. The scales for the current velocity and the variance are included in the left-hand corner. The mean wind velocity is included with the scales. Lower inset shows Atlantic Canada and Newfoundland; open arrow indicates location of Placentia Bay.



1997, 1998, and 1999; additional cruises took place in May 1997 and September 1998. Not all stations in the outer bay were sampled in the April and September trips because of weather and time constraints, and a few stations were missed during other cruises for similar reasons. These stations were therefore excluded for those time periods when they were not sampled.

Ichthyoplankton samples were preserved in 4% buffered formalin in seawater. In the laboratory, egg or larval taxa represented by >300 individuals were subsampled with a Motoda splitter (except April and June 1998, which were processed by the Atlantic Reference Center and subsampled as per Van Guelpen et al. 1982). All eggs and larvae were identified to the lowest taxonomic level possible. Eggs were grouped into four developmental stages using the scheme of Markle and Frost (1985). Although eggs of the *Gadus morhua* – *Melanogrammus aeglefinus* – *Glyptocephalus cynoglossus* (Atlantic cod – haddock – witch flounder) complex are difficult to differentiate during the first three developmental stages, we assumed from large differences in the relative

abundances of larvae that the vast majority of eggs were Atlantic cod. A similar line of logic was used in assuming *Enchelyopus cimbrius* (fourbeard rockling) eggs were the major constituent of the *E. cimbrius* – hakes complex. The absence of hake larvae precluded resolution to species for this taxon. A similar assumption could not be made with the *Tautogalabrus adspersus* – *Limanda ferruginea* (cunner – yellowtail flounder) egg complex because larvae of both species were relatively common. Mean larval sizes (nearest 0.5 mm) were determined within each cruise for every taxon represented by more than five individuals within a given cruise.

Zooplankton in Tucker trawls were enumerated by subsampling with a Motoda splitter so that at least 300 individuals were counted per sample. The full sample was also examined to enumerate large taxa that were relatively low in abundance and therefore poorly estimated in subsamples. At each of the stations where ichthyoplankton–zooplankton samples were taken, vertical CTD (conductivity–temperature–depth sensor) casts were collected using either a Seabird 19

**Table 1.** Average egg and larval concentrations (individuals:(1000 m<sup>3</sup>)<sup>-1</sup>) for pelagic spawners in Placentia Bay, 1997–1999.

Pelagic spawners	April			May			June			August			September	
	1997	1998	1999	1997	1998	1999	1997	1998	1999	1997	1998	1999	1998	1999
<b>Gadidae</b>														
<i>Enchelyopus cimbrius</i> – hakes	0.00	0.00	0.00	0.00	0.00	0.00	0.05	4.42	5.47	1.47	1.01	1.84	2.77	
<i>Enchelyopus cimbrius</i>	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	2.62	1.12	0.50	1.71	
<i>Gadus morhua</i> – <i>Glyptocephalus cynoglossus</i>	663.59	122.60	119.33	171.83	181.75	181.97	194.19	181.75	181.97	23.01	86.15	81.36	20.30	
<i>Gadus morhua</i>	0.00	0.00	0.26	0.03	0.06	0.20	0.04	0.06	0.20	0.29	7.71	0.88	2.72	
<i>Pollachius virens</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	
	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.06	
<b>Labridae–Pleuronectidae</b>														
<i>Glyptocephalus cynoglossus</i>	0.00	0.00	0.02	0.00	0.00	0.47	0.00	0.00	0.47	0.45	0.53	0.48	0.39	
<i>Hippoglossiodes platessoides</i>	25.17	10.57	57.81	82.05	77.95	130.51	8.83	77.95	130.51	2.27	5.00	2.14	0.70	
	0.00	0.00	0.01	0.00	0.32	0.53	0.00	0.32	0.53	0.08	0.62	0.16	0.11	
<i>Limanda ferruginea</i>	0.00	0.00	0.00	0.00	0.00	0.44	0.00	0.00	0.44	0.10	0.26	0.16	0.01	
<i>Tautogalabrus adspersus</i> – <i>Limanda ferruginea</i>	0.01	0.00	0.00	0.00	23.35	77.95	18.53	23.35	77.95	1475.92	900.41	841.25	3.41	
<i>Tautogalabrus adspersus</i>	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	609.01	359.87	407.21	58.84	
<b>Scophthalmidae</b>														
<i>Scophthalmus aquosus</i>	0.00	0.00	0.00	0.00	0.02	0.07	0.00	0.02	0.07	0.00	0.00	0.00	0.00	
Other eggs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	
<b>Pelagic taxa</b>														
Eggs	688.78	133.17	177.13	253.88	287.47	395.90	221.60	287.47	395.90	1502.68	992.57	926.59	27.19	
Larvae	0.04	0.00	0.29	0.03	0.49	1.72	0.04	0.49	1.72	612.54	370.11	409.39	63.84	
<b>Total</b>	688.82	133.17	177.43	253.91	287.96	397.62	221.68	287.96	397.62	2115.22	1362.69	1335.98	91.07	

**Table 2.** Larval concentrations (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) for bottom spawners in Placentia Bay, 1997–1999.

Bottom spawners	April		May		June		August		September	
	1997	1998	1999	1997	1998	1999	1997	1998	1999	1998
Agonidae										
<i>Agonus decagonus</i>	Larvae	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Aspidophoroides</i> sp.	Larvae	0.25	0.00	0.20	0.08	0.03	0.02	0.00	0.00	0.00
Ammodytidae										
<i>Ammodytes</i> sp.	Larvae	64.05	8.79	18.66	47.37	4.20	0.01	0.00	0.02	0.01
Anarichadidae										
<i>Anarhichas lupus</i>	Larvae	0.07	0.13	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Clupeidae										
<i>Clupea harengus</i>	Larvae	0.00	0.02	0.08	0.00	0.00	0.00	0.00	0.00	0.52
Cottidae										
<i>Gymnocanthus tricuspis</i>	Larvae	0.00	0.28	0.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Icelus bicornis</i>	Larvae	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Myoxocephalus aeneus</i>	Larvae	0.04	0.01	0.38	0.00	0.22	0.00	0.00	0.01	0.00
<i>Myoxocephalus octodecemspinosus</i>	Larvae	1.48	0.67	0.08	0.14	0.00	0.00	0.00	0.00	0.00
<i>Myoxocephalus scorpius</i>	Larvae	2.72	1.41	1.53	0.26	0.03	0.00	0.00	0.00	0.00
<i>Triglops</i> sp.	Larvae	0.01	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Cyclopteridae										
<i>Cyclopterus lumpus</i>	Larvae	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.06	0.02
<i>Liparis</i> spp.	Larvae	0.01	0.87	0.95	1.12	0.10	0.33	0.37	0.45	0.08
Gadidae										
<i>Gadus ogac</i>	Larvae	0.02	0.14	0.90	0.00	0.00	0.00	0.00	0.00	0.00
Hemirhamphidae										
<i>Hemirhamphus americanus</i>	Larvae	0.03	0.01	0.35	0.00	0.00	0.00	0.00	0.00	0.00
Labridae–Pleuronectidae										
<i>Pleuronectes americanus</i>	Larvae	0.00	0.00	0.00	0.00	0.03	0.12	0.01	0.06	0.04
Osmeridae										
<i>Mallotus villosus</i>	Larvae	0.11	0.50	0.01	0.00	0.02	700.23	467.54	101.72	486.09
Pholidae										
<i>Pholis gunnellus</i>	Larvae	0.01	0.37	1.03	0.02	0.00	0.00	0.00	0.00	0.00
Scombridae										
<i>Scomber scombrus</i>	Larvae	0.00	0.00	0.00	0.00	0.00	0.94	0.77	0.05	0.01
Scorpaenidae										
<i>Sebastes</i> sp.	Larvae	0.18	0.01	0.00	0.00	0.03	3.91	1.12	1.98	0.45
Stichaeidae										
<i>Lumpenus</i> sp.	Larvae	0.20	0.20	0.17	0.02	0.20	0.01	0.00	0.00	0.00
<i>Stichaeus punctatus</i>	Larvae	0.32	0.09	0.25	9.46	0.07	0.00	0.00	0.00	0.00
<i>Ulvaria subaffurcata</i>	Larvae	0.21	0.00	0.16	0.00	0.23	3.40	0.39	1.21	0.08
Unidentified	Larvae			0.00		0.05			0.70	
Bottom spawner totals	Larvae	69.73	13.73	24.95	58.49	5.16	708.96	470.28	106.25	487.30
Bottom spawner totals minus <i>Mallotus villosus</i>	Larvae	69.62	13.23	24.94	58.49	5.14	8.73	2.74	4.53	1.21

(May and June 1997) or Seabird 25 (all other cruises). These casts made it possible to contrast mixed-layer temperatures by averaging the upper 40 m from each profile.

### Data analysis

Ichthyoplankton abundances were divided by the volume filtered and expressed as the number of individuals·(1000 m<sup>3</sup>)<sup>-1</sup>. Temporal trends in total concentration of individuals were examined by plotting average concentrations for the total bay with standard errors. Bar charts provided a means of comparing egg stage composition over time, where each value represented the mean of all stations sampled in a given cruise. Temporal trends in dominant larval taxa were compared by plotting all observations versus the sampling date. These temporal scattergram plots permit an intuitive view of presence or absence as well as concentrations, which are confounded by very high spatial variability within a cruise.

To provide a summary representation of spatial patterns in total egg and larval concentrations and interpolate the discrete station data, spatial distribution of total eggs and larvae were contoured using linear kriging in Surfer 7.0 (Golden Software, Golden, Colorado). This contouring allowed interpolation between stations, smoothed variability inherent in ichthyoplankton sampling, and provided a comprehensive and easily interpretable plot of spatial variability.

## Results

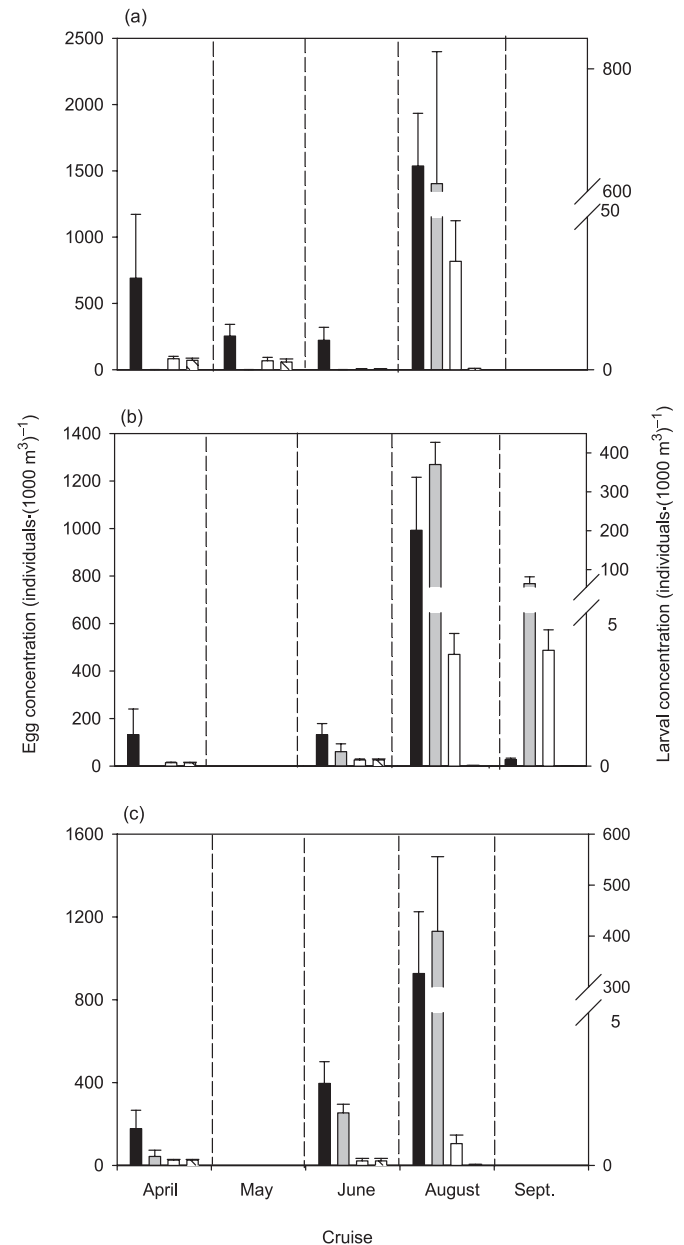
### Ichthyoplankton

Temporal peaks in eggs and larvae varied considerably among taxa (Tables 1, 2), but total concentrations of eggs and larvae were highest in August during the 3 years sampled (Fig. 2). Although high numbers of eggs were observed in the spring and summer, larval numbers were low except during August and September. We also observed differences in the timing of egg production among species. Early stage Atlantic cod egg abundance was high in April and June of all years and began to decline by August (Fig. 3; Bradbury et al. 2000). A similar pattern was observed in American plaice, *Hippoglossoides platessoides*, but for both of these taxa late-stage eggs were much more abundant in the August and September sampling periods (Fig. 3). Early stage eggs of cunner – yellowtail flounder were abundant in June but peaked in August; late stages were again abundant in August and September. Early stages of fourbeard rockling were abundant in June and September, whereas late stages were most abundant in August and September.

Temporal patterns in larval concentrations of pelagic spawners were consistent with patterns in late-stage eggs (Fig. 4). Atlantic cod, American plaice, cunner, yellowtail flounder, witch flounder, and fourbeard rockling were all most abundant in the August and September sampling periods and were uncommon in April through June, despite the fact that egg production in some of these taxa peaked during those time periods.

Temporal patterns in the dominant taxa of bottom spawners were markedly different than those of pelagic spawners. With the exception of capelin, *Mallotus villosus*, where larval concentrations peaked in August and September, larval production in all the dominant taxa of bottom spawners peaked before or during June (Fig. 5). Larvae of bottom

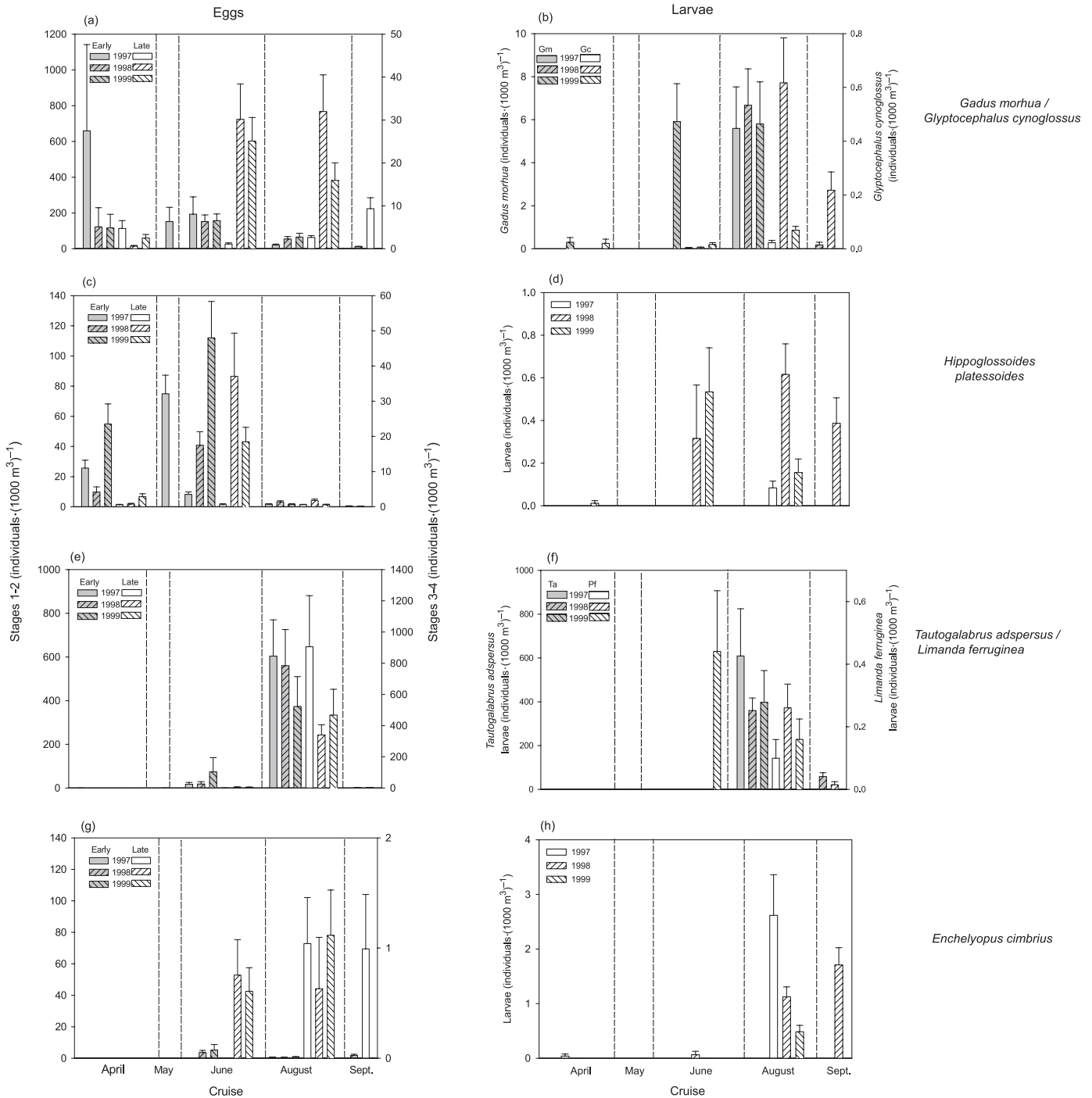
**Fig. 2.** Concentrations of eggs and larvae averaged for each sampling trip over the entire sampling area for (a) 1997, (b) 1998, and (c) 1999. Solid bars denote pelagic-spawner eggs, light shaded bars denote pelagic-spawner larvae, open bars denote bottom-spawner larvae, and hatched bars denote bottom-spawner larvae excluding capelin (*Mallotus villosus*). Error bars denote 1 standard error.



spawners were also present over a wider sampling period than those of pelagic spawners; the latter were rarely observed before August, whereas the former were abundant from April through June. Larval sizes also varied over time; mean larval size was larger for most taxa during the earlier sampling periods than during later surveys and coincided with a change in species composition from larvae predominantly of bottom spawners to those of pelagic spawners (Fig. 6).

Distributions of stage I eggs of pelagic spawners, which provide an indication of spawning location, suggest that

**Fig. 3.** Mean concentrations of early and late egg stages and larvae for pelagic spawners during each sampling trip in each year of sampling for (a) Atlantic cod (*Gadus morhua*) – haddock (*Melanogrammus aeglefinus*) – witch flounder (*Glyptocephalus cynoglossus*) eggs, (b) Atlantic cod – witch flounder larvae, (c) American plaice (*Hippoglossoides platessoides*) eggs, (d) American plaice larvae, (e) cunner (*Tautogalabrus adspersus*) – yellowtail flounder (*Limanda ferruginea*) eggs, (f) cunner – yellowtail flounder larvae, (g) fourbeard rockling (*Enchelyopus cimbrius*) – hakes eggs, (h) fourbeard rockling larvae.

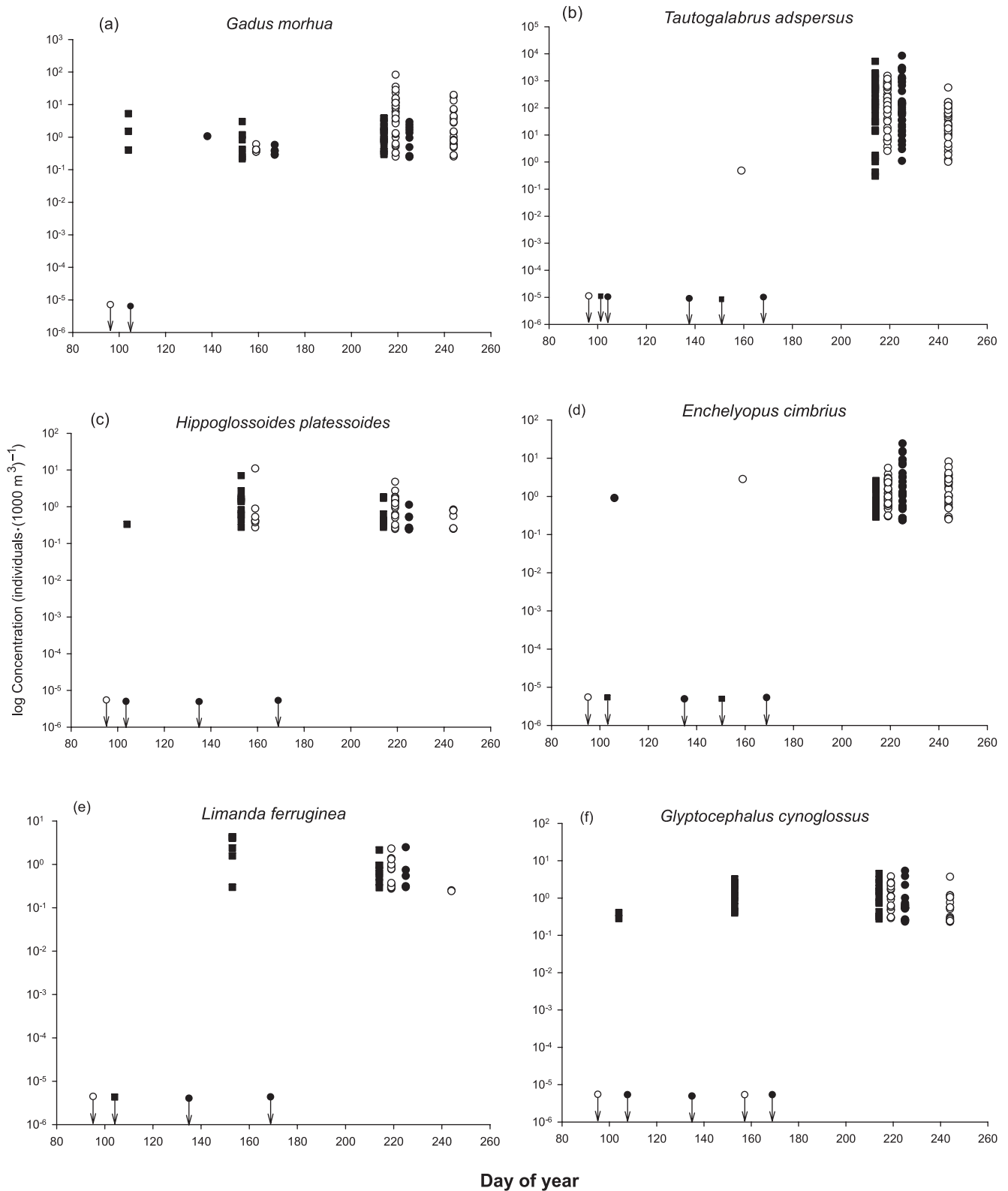


some taxa utilize the same areas of the bay repeatedly over time. Concentrations of early stage Atlantic cod (Fig. 7) and fourbeard rockling (Fig. 8) were typically highest near the head of the bay, although fourbeard rockling eggs were also abundant along the eastern side. Early-stage American plaice (Fig. 9) and cunner – yellowtail flounder eggs (Fig. 10) were typically most abundant along the western side of the bay,

though both were abundant along the eastern side as well. For all these taxa, peak abundance was at the head or on the western side of the bay.

Larval concentrations for these pelagic spawning taxa were negligible until August, when the vast majority of larvae occurred at the head or along the western side of the bay (Figs. 7–10). The spatial coherence among larvae of pelagic

**Fig. 4.** Concentrations of larvae of dominant species of pelagic spawners at all stations sampled for 1997 (solid circles), 1998 (open circles), and 1999 (solid squares). Arrows above horizontal axes indicate sampling times where no individuals were collected at any stations.

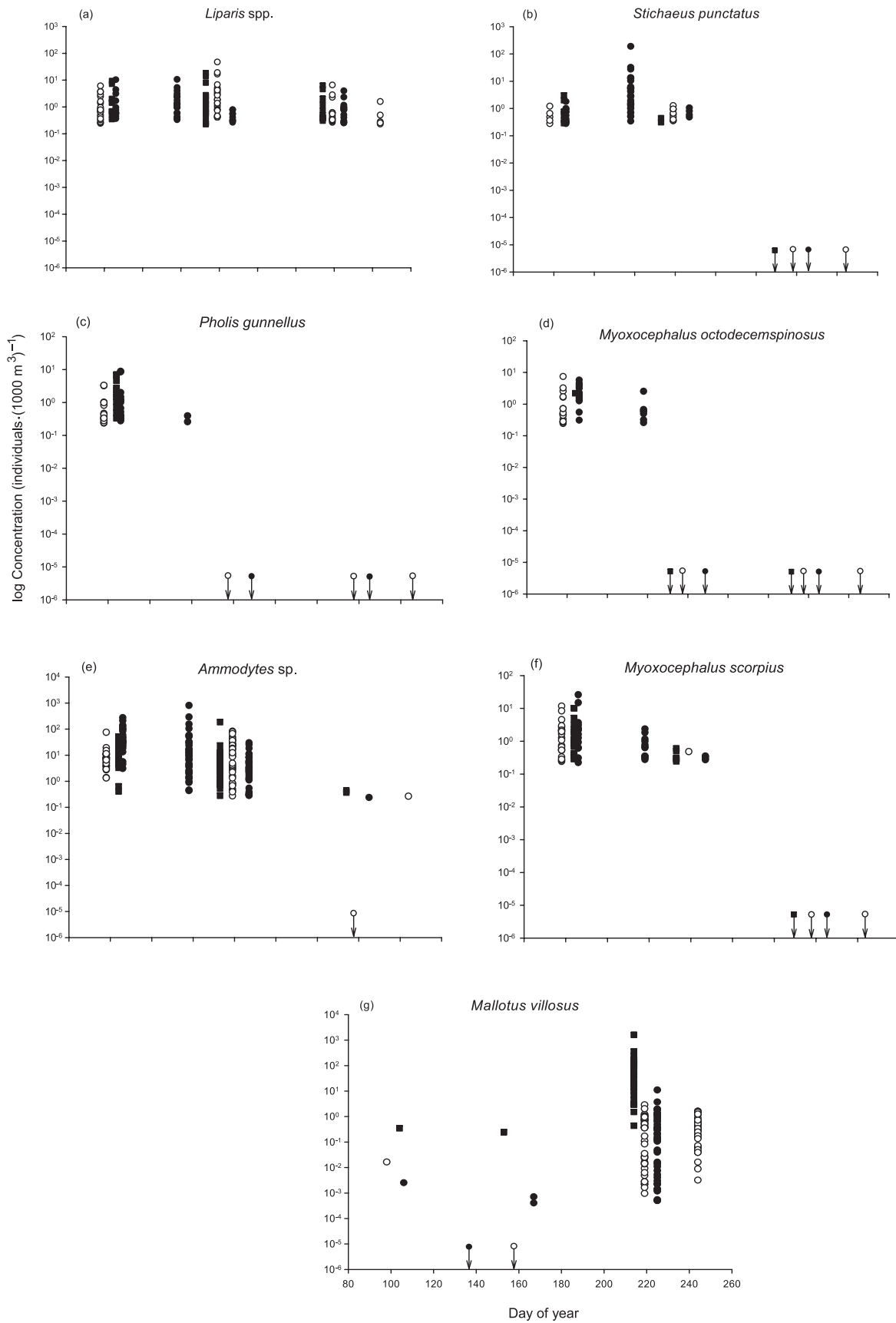


spawners was much greater than that observed in bottom spawners, which varied spatially among species (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). The linkage be-

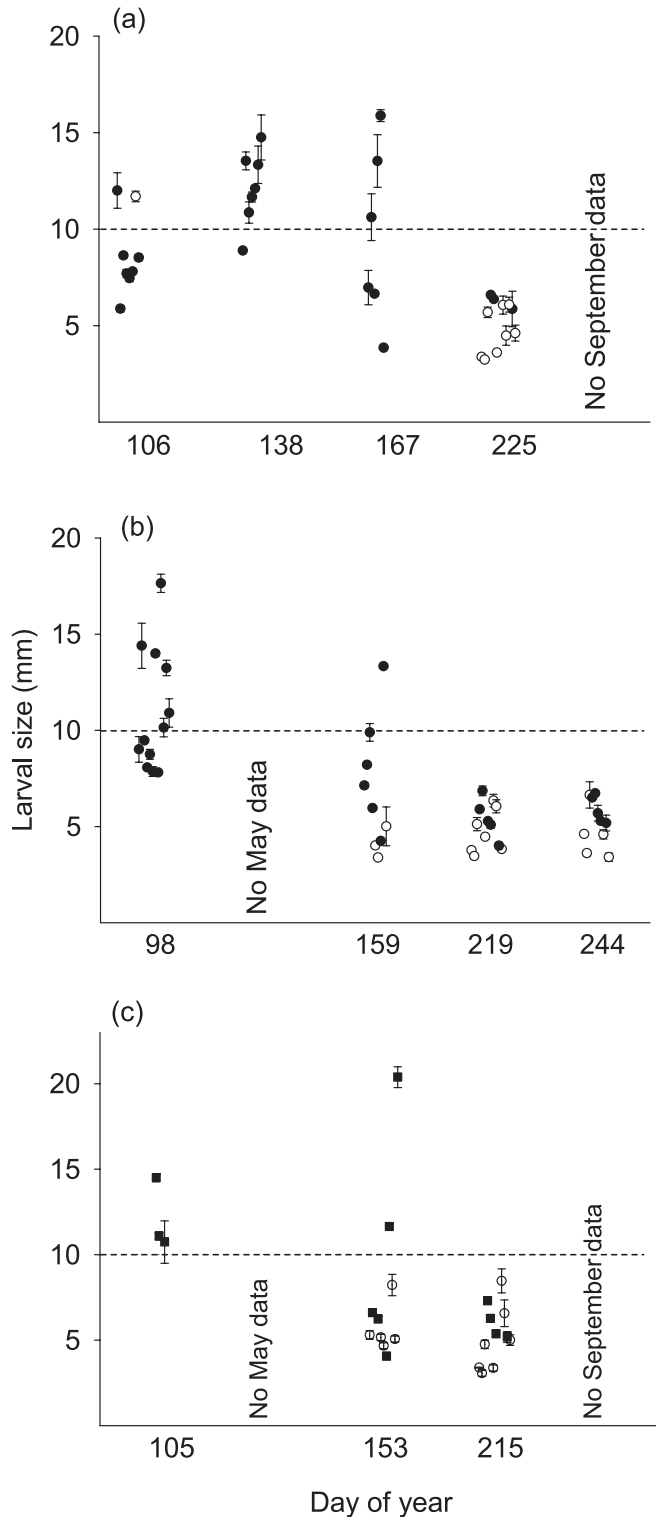
tween presumed spawning location and advection for pelagic spawners was generally consistent in August, in that peak numbers in eggs and larvae were in similar areas of the bay in



**Fig. 5.** Concentrations of larvae of dominant species of bottom spawners at all stations sampled for 1997 (solid circles), 1998 (open circles), and 1999 (solid squares). Arrows above horizontal axes indicate sampling times where no individuals were collected at any stations.



**Fig. 6.** Station means of larval size for each taxon for which more than five individuals were collected within a given sampling trip. Lines around points denote 1 standard error. Open points denote larvae from pelagic spawners; solid points denote larvae from bottom spawners. (a) 1997, (b) 1998, (c) 1999. Broken horizontal line indicates the 10 mm threshold identified by Bradbury et al. (2003) as a developmental stage where swimming ability is sufficient to contribute substantially to larval distributions.



all years. August was the only time when late stages and larvae were abundant. Early stages were typically most abundant near the head of the bay, whereas late stages were concentrated along the western side toward the outer part of the bay (Figs. 7–10).

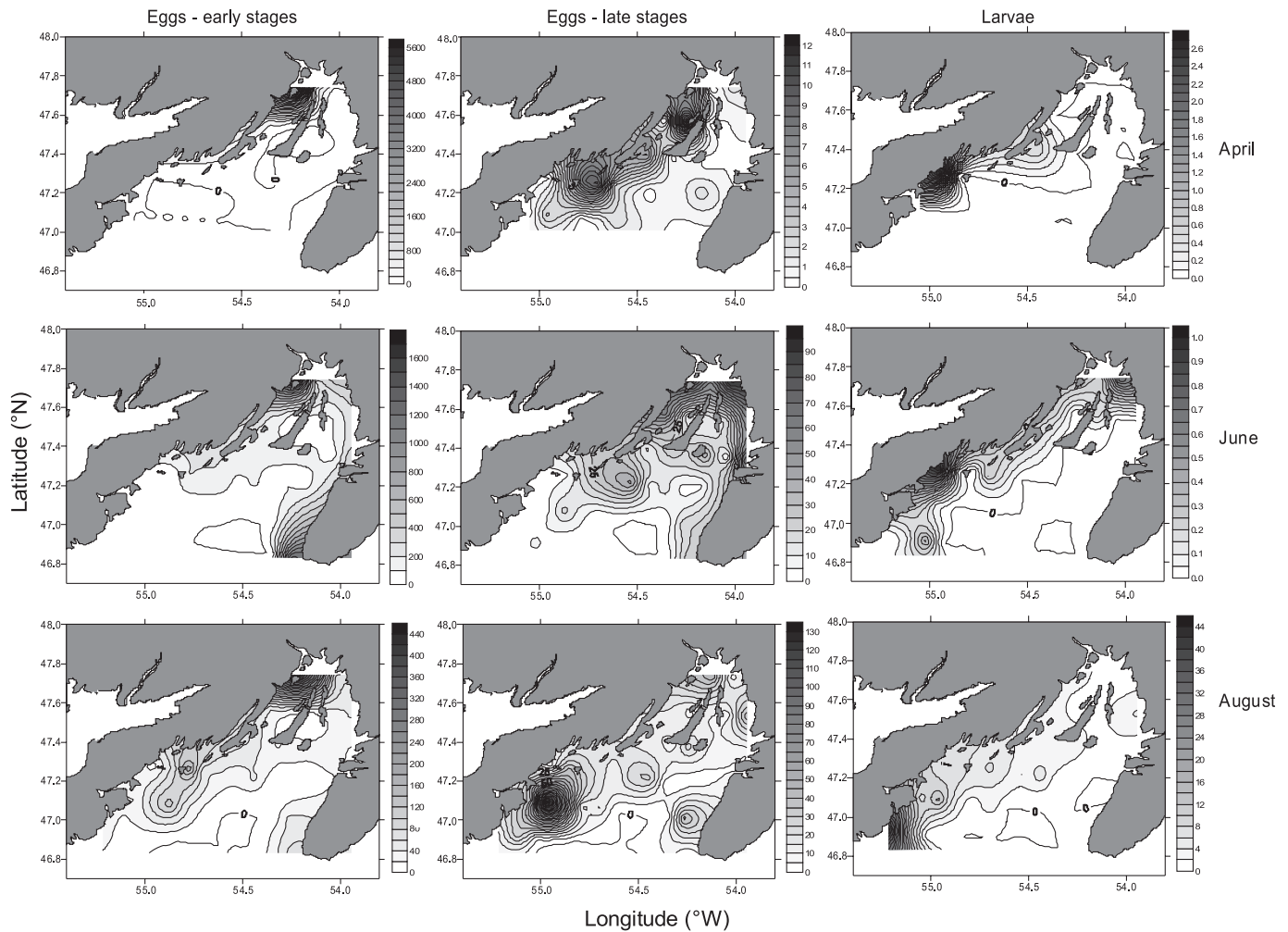
### Environmental data

Mixed-layer temperatures at the head of the bay or averaged over the full bay in April were 0–1 °C (Fig. 11) and showed little spatial variability. By August, mixed-layer temperatures were typically 6–9 °C with corresponding surface temperatures of 13–17 °C. The head and outer southeast parts of the bay were generally warmest, whereas the coolest area was the southwest side where upwelling was observed (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Chlorophyll in the bay exhibited considerable temporal and spatial variability. High concentrations of chlorophyll were observed in April and September. In terms of spatial variability, the center and outer areas of the bay were typically lowest in chlorophyll, whereas highest values were observed at the head of the bay and along the western side (Bradbury et al. 2000), as was also observed with zooplankton (Fig. 12). SeaWiFs images were consistent with our estimates based on chlorophyll extraction (Bradbury et al. 2000). Zooplankton abundance was highest in August and lowest in June (Fig. 12), and within-cruise spatial variability in abundance was also highest in August when the hydrographic structuring of the bay was strongest (Bradbury et al. 2000). As with phytoplankton, highest zooplankton abundances were observed on the western side of the bay, where, in August, larvae were most concentrated.

### Discussion

Placentia Bay ichthyoplankton display strong temporal variability in abundance that is related to spawning strategy, advection, and areas of elevated production. For pelagic spawners in particular, it is likely that the strong directional flow observed in Placentia Bay creates a retention problem that is strongest when water temperatures are low. In open systems, or bays with strong directional flow, transport out of a suitable environment is more likely to occur during cooler periods when egg and larval development rates are slow (e.g., Pepin 1991). In gyre systems (e.g., O'Boyle et al. 1984; Werner et al. 1993), where flushing is less of an issue, egg development time creates less of a constraint. This flushing problem is particularly exacerbated in areas with very short development seasons (Conover 1992). Placentia Bay is a complex spawning environment not only because of the directional flow, but also because of the short period when water temperatures are warm. Although substantial numbers of pelagic eggs were spawned in the spring by several taxa, late-stage eggs and hatched larvae were rare or completely absent until late in the summer, suggesting that they were flushed from Placentia Bay and (or) experienced high rates of mortality. Larvae of bottom spawners, by contrast, were abundant in April through August and were found over a broader geographic area than larvae from pelagic spawners. Thus, timing and spatial distributions of larvae for bottom spawners, in which developing eggs are affixed to the bottom, may be less influenced by water temperature,

**Fig. 7.** Linear kriging plots of concentrations (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) of early- and late-stage eggs and larvae of Atlantic cod (*Gadus morhua*) for April, June, and August cruises 1997–1999. Note change in scale among panels.



flushing, and temperature-dependent mortality. Larvae of both types of spawners were associated with times and locations of high zooplankton abundance, suggesting that food availability may also play a role in seasonal and spatial dynamics.

#### Flushing rates for Placentia Bay

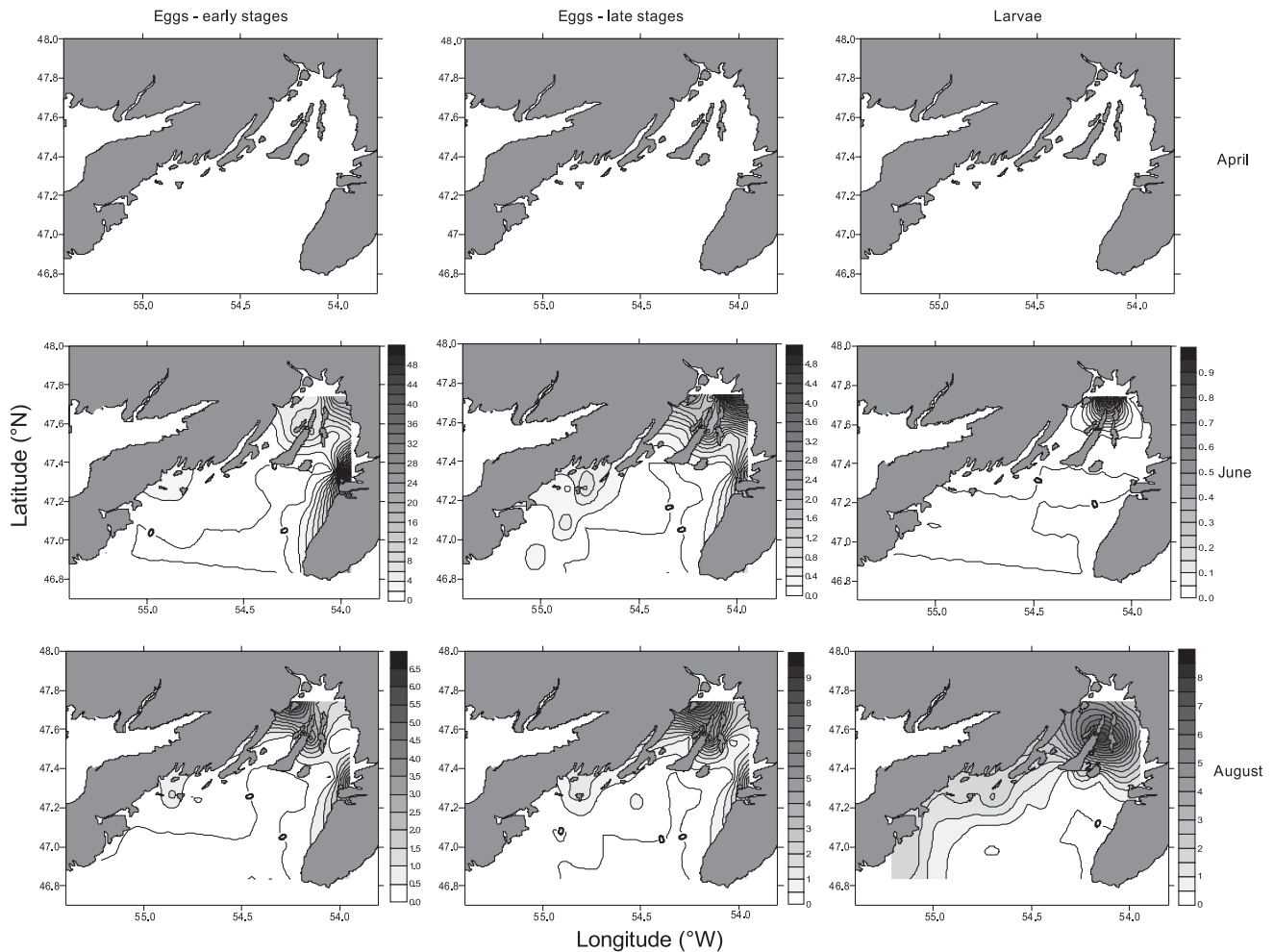
The mean circulation in Placentia Bay is influenced by inflow of the inshore branch of the Labrador Current and wind forcing. The cold Labrador Current water is carried around the Avalon Peninsula in a deep nearshore channel (Petrie and Anderson 1983) and enters on the eastern side of Placentia Bay, where it is the primary forcing term that generates the strong, mean counterclockwise circulation of the near-surface waters (Schillinger et al. 2000). The water has the characteristics of the Labrador Current in that it is relatively cold and fresh with a well-understood, depth-dependent seasonal cycle (Petrie et al. 1991). Studies of the coastal embayments on the northern side of the Avalon Peninsula (cf. deYoung and Sanderson 1995; Davidson et al. 2001) have shown that Trinity Bay, which is similar in scale to Placentia Bay, has a similarly well-developed mean circulation, whereas Conception Bay, which is substantially smaller, lacks a well-defined mean circulation (deYoung and Sanderson 1995).

The near-surface mean currents in Placentia Bay are roughly 10–12 cm·s<sup>-1</sup> at 20 m depth (Schillinger et al. 2000). These current measurements were made during the summer, from May to September, during the same period as for the egg and larval surveys. Although the calculation of mean residence time should consider the influence of wind forcing (e.g., deYoung et al. 1994, for Conception Bay), the much greater strength of the mean current in Placentia Bay allows a reasonable analysis for transport times through the bay based on circulation data. Considering the length of Placentia Bay to be about 120 km and taking a mean transport of 10 cm·s<sup>-1</sup> (based on measurements from the four quadrants of the bay) yields an along-bay transport of 14 days and a similar time for transport out of the bay on the western side. Thus, the total time of transit for eggs or larvae that are released in the surface water near the mouth on the eastern side of the bay would be roughly 28 days.

#### Pelagic egg development times and transport

Given that the approximate flushing time from the head of the bay to the southwest extremity of the bay is ~14 days and the complete flushing time from the southeast extremity to the southwest extremity is ~28 days, there are important im-

**Fig. 8.** Linear kriging plots of concentrations (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) of early and late stage eggs of fourbeard rockling (*Enchelyopus cimbricus*) and larvae for April, June, and August cruises 1997–1999.



plications for pelagic egg loss as a function of temperature-dependent development rate. Simple modeling of Atlantic cod development rates suggests that in April, hatch may not occur for as long as 41 days, whereas in August this time is reduced to ~8 days (Bradbury et al. 2001). Both American plaice and Atlantic cod produce substantial numbers of eggs in April (and to some extent June) near the head of the bay when water temperatures are comparatively low. These eggs were likely spawned near the head of the bay given that cod are known in that area in spring (Lawson and Rose 2000), and in both species the eggs are predominantly stage 1. Based on flushing time estimates outlined above, there is a strong likelihood that during spring, when water temperature are ~1 °C, the eggs would be flushed from the bay prior to hatching. The low numbers of late-stage eggs and larvae in April are consistent with this interpretation. The other common pelagic spawners, fourbeard rockling and cunner – yellowtail flounder, were absent in April, but early stages through late stages were present in low numbers in June. During June, fourbeard rockling showed a progression of stages from the head of the bay towards the southwest.

In August, when water temperatures were warmest, larvae and late-stage eggs of pelagic spawners were most abundant, and concentrations were often highest “downstream” of sites

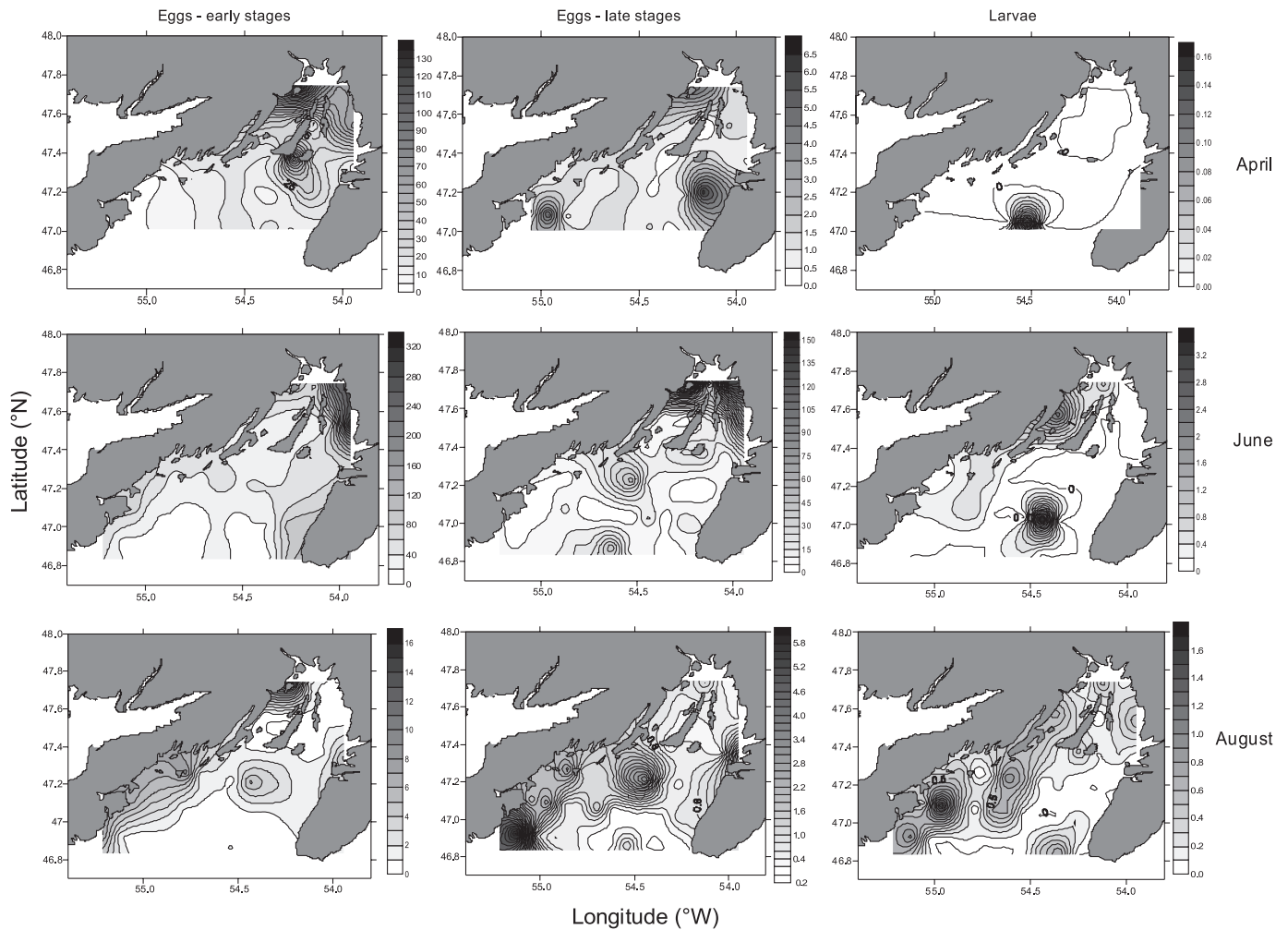
along the western side and head of the bay, where early stages were most abundant.

Temperature and wind were both found to be critical factors in the timing of spawning for pelagic and bottom spawners in Conception Bay (Laprise and Pepin 1995), which is just north of Placentia Bay. Given the similarity in temporal patterns in Placentia Bay in 1997, 1998, and 1999, our data are consistent with this interpretation, but spawning strategy also plays a key role.

#### Larval growth and swimming

Warmer temperatures not only decrease egg development time but also increase larval growth (Pepin 1991), thereby providing a double advantage to late summer spawning by pelagic species. Thresher (1984) noted that recently hatched larvae from pelagic eggs have undeveloped fins and unpigmented eyes that may make them more vulnerable to dispersal than larvae from bottom spawners (see Suthers and Frank 1991), so that largely passive transport is an issue for recently hatched pelagic larvae as well as for eggs. Our size data suggest that larvae from pelagic spawners were indeed typically much smaller than those produced by bottom spawners. Thus, although the same spawning sites were often used throughout extended periods by pelagic spawners,

**Fig. 9.** Linear kriging plots of concentrations (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) of early- and late-stage eggs and larvae of American plaice (*Hippoglossoides platessoides*) for April, June, and August cruises 1997–1999.



successful development and hatching within the bay was largely a late summer phenomenon.

#### Zooplankton availability

Total zooplankton abundance was highest in August, with highest concentrations typically found at the head of the bay. Thus, in terms of spatial pattern, the spawning strategy for pelagic taxa was appropriate for placing hatching larvae in a food-rich environment (e.g., Hjort 1914; Cushing 1990). In fact, total pelagic egg concentrations were highest in August at a time when development times were shortest. Nonetheless, high levels of spring egg production in some taxa (Atlantic cod, American plaice) may have resulted in flushing and (or) high rates of mortality, given the low numbers of late-stage eggs and larvae prior to August.

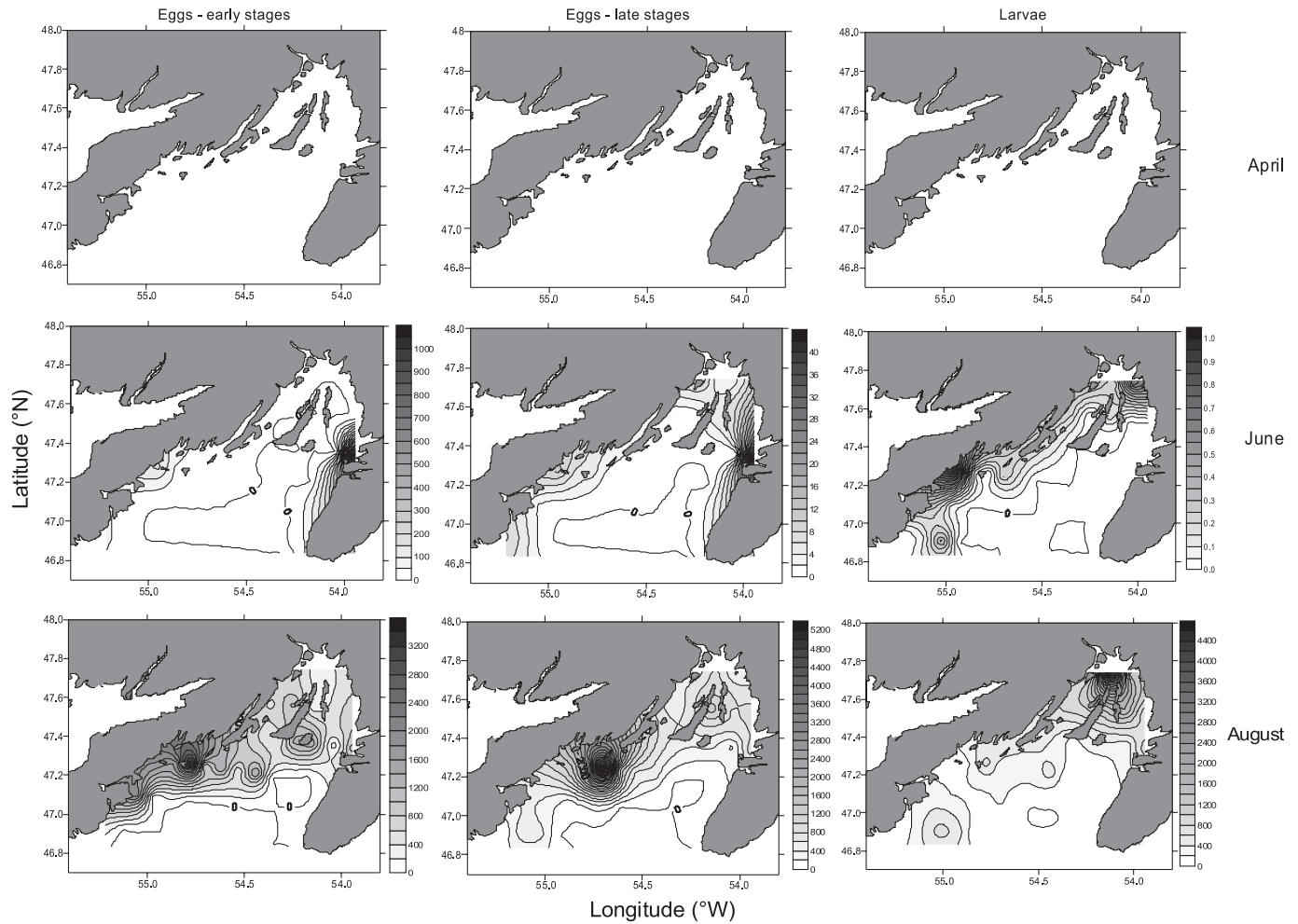
Not all pelagic spawners utilized the same strategy with respect to timing. Some species (fourbeard rockling, cunner, yellowtail flounder) spawn so that peak concentrations occur in August, whereas other taxa (Atlantic cod, American plaice) spawn over a broader period when food availability and temperature change considerably (see Hutchings and Myers (1994) for discussion on variability in cod spawning). The variability in timing of peak copepod abundance that has

been described for the broader area of the North Atlantic may be a contributing factor to this variability. Thus, different species utilize different strategies with respect to timing (Sherman et al. 1984), with different degrees of bet-hedging. Sherman et al. (1984) noted widespread larval distribution for some taxa and suggested that species such as Atlantic cod may adhere to tighter spawning locations to match larvae spatially to available food. Spawning upstream of productive areas by cod had been noted by other authors (e.g., Munk et al. 1995), as has association of high egg concentrations in areas with high zooplankton abundance (Doyle and Ryan 1989; P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Indeed, many studies have proposed downstream drift by larvae to appropriate nursery grounds (Harden Jones 1969; deYoung and Rose 1993).

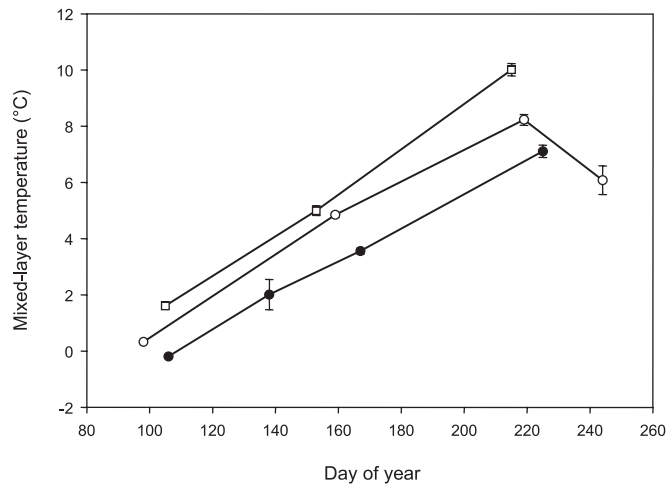
#### Bottom spawners

Unlike pelagic species, peaks in larval abundance of bottom-spawning species were highest in spring and early summer (with the notable exception of capelin). Because larvae of bottom spawners have a greater capacity to regulate their distribution than pelagic eggs or recently hatched larvae (Thresher 1984) and can begin feeding soon after they

**Fig. 10.** Linear kriging plots of concentrations (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) of cunner (*Tautogalabrus adspersus*) – yellowtail flounder (*Limanda ferruginea*) early- and late-stage eggs and cunner larvae for April, June, and August cruises 1997–1999. Note the differences in scale among plots.

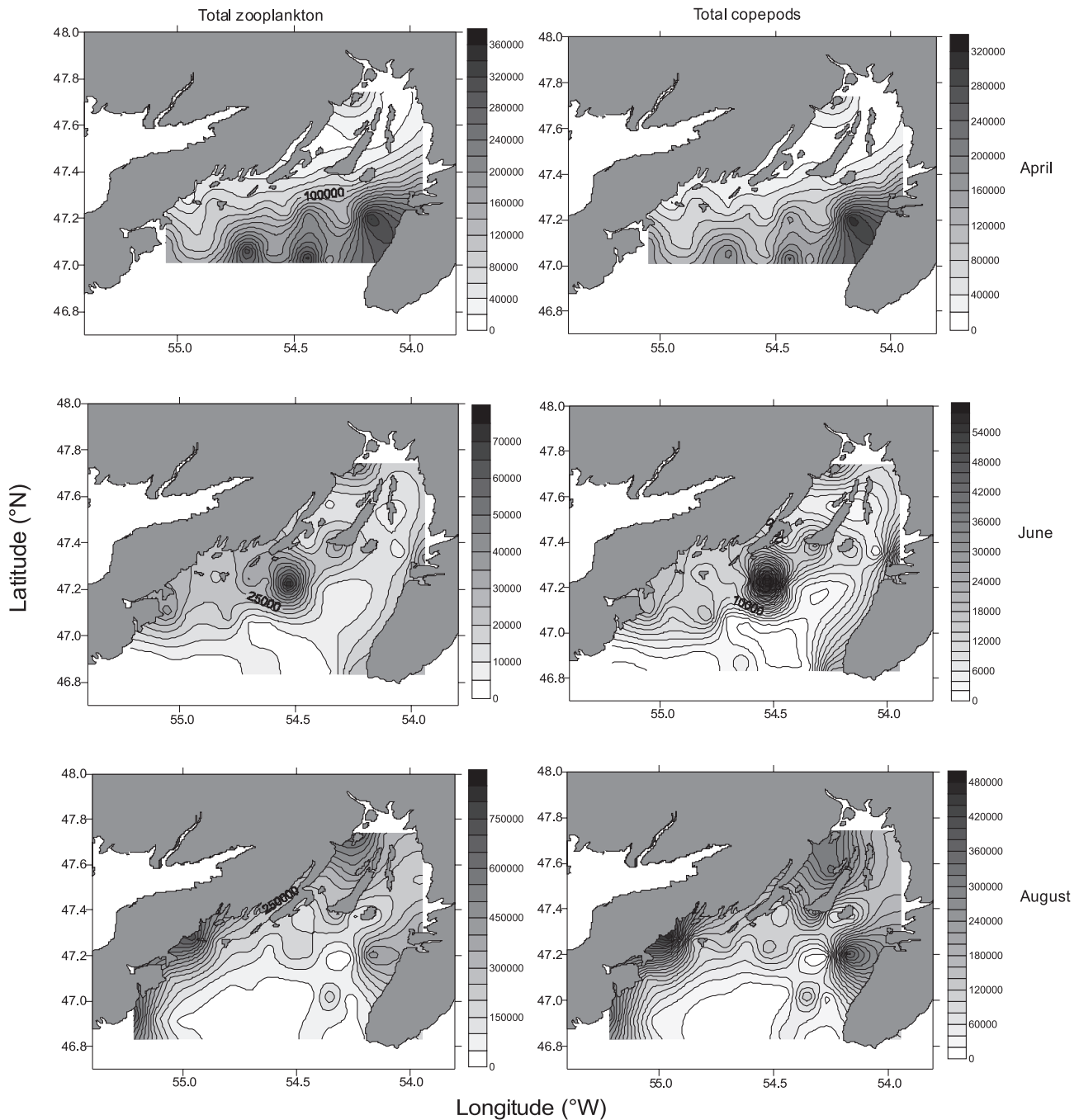


**Fig. 11.** Mean mixed-layer temperatures averaged for all stations during each cruise in 1997 (solid circles), 1998 (open circles), and 1999 (open squares).



are planktonic, their vulnerability to flushing in cold water is greatly reduced. For example, swim speeds of recently hatched Atlantic cod larvae are only 1.18 cm·s<sup>-1</sup>, whereas those of recently hatched shorthorn sculpin, *Myoxocephalus scorpius*, are 5.56 cm·s<sup>-1</sup> (Guan 2007). Moreover, our size data suggests that the larvae produced by bottom spawners in spring were larger than the larvae collected later in the year. We have argued elsewhere, based on scaling and changes in patch size with larval development (Bradbury et al. 2003), that 10 mm represents a critical size transition for fish larvae; individuals larger than this threshold have sufficient swimming capacity to contribute considerably to their distribution. Those larvae that were present in spring were near or above this size threshold, whereas those present in summer were almost invariably much smaller. The spring bloom in Placentia Bay results in high abundances of zooplankton; larvae hatching in spring may therefore be able to utilize some of these food resources. Because zooplankton are also abundant over a broader area in April than in August, larvae from bottom spawners may not face the same constraint of having to place hatching larvae in a particular area of the bay. The greater swimming ability and reduced

**Fig. 12.** Linear kriging plots of average total zooplankton abundance (individuals·(1000 m<sup>3</sup>)<sup>-1</sup>) for April, June, and August cruises 1997–1999. Note the differences in scale among plots.



dependence of larvae of bottom spawners on specific areas of the bay may also explain why they are present over a broader time period than pelagic larvae, which are heavily concentrated in the August sampling period. Larval patterns of bottom-spawning species are therefore dictated more by availability of suitable spawning habitat than by physical transport or peak zooplankton concentrations (P. Snelgrove, I. Bradbury, and S. Fraser, unpublished data). Temperature is thought to be a key factor in terms of emergence of bottom-spawned larvae (Frank and Leggett 1983) and may explain the temporal synchrony among most species.

*Mallotus villosus*, the only bottom spawner with a late summer larval peak, has shown unseasonably late spawning in recent years (Carscadden et al. 2001).

In conclusion, different taxa use different spawning strategies in the strongly seasonal Placentia Bay environment. Some pelagic spawners release eggs over a broad time period from spring through fall, resulting in advective loss or high mortality in the spring and greater hatching success in late summer. Other pelagic spawners are more confined to the late summer, when temperatures are more favourable for rapid egg and larval development. Pelagic spawning often

occurs coincident with or upstream of the most productive areas of the bay, and larval abundance peaks when zooplankton are most abundant. Larvae of bottom spawners typically emerge in the spring, likely reflecting the superior swimming ability of larvae that have hatched from bottom-spawned eggs and allowing them to take advantage of zooplankton associated with the spring bloom.

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