

# Larval Flatfish Distributions and Drift on the Southern Grand Bank

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Ichthyoplankton and hydrographic surveys of the southern Grand Bank in September of 1986, 1987, and 1988 revealed substantial correspondence between the areal distributions of larvae of three flatfish species and temperature below the thermocline. Depth-averaged densities of American plaice (*Hippoglossoides platessoides*) were negatively correlated with temperature whereas yellowtail flounder (*Limanda ferruginea*) and witch flounder (*Glyptocephalus cynoglossus*) densities were positively correlated with temperature. In spite of large interannual differences in abundance, the larval distributions showed similar structure from year to year. Using estimates of larval age inferred from length frequency distributions and literature values for growth rate, in conjunction with moored current measurements, estimates of spawning times and locations were obtained for each species. These estimates were compared with historical information on the distribution of prespawning fish for each species to examine the hypothesis of passive larval drift. The results indicate that in most, but not all cases, the larval distributions and currents are consistent with passive larval drift for particular growth rates and vertical distributions. However, the observations are not adequate to rule out alternative mechanisms involving behaviour.

Des relevés de l'ichtyoplancton et des paramètres hydrographiques effectués dans le secteur sud des Grands Bancs en septembre 1986, 1987 et 1988 ont révélé une correspondance importante entre la répartition spatiale des larves de trois espèces de poissons plats et la température de l'eau sous la thermocline. Les densités, en fonction de la moyenne des profondeurs, des larves de plie canadienne (*Hippoglossoides platessoides*) étaient en corrélation négative avec la température, tandis que les densités de larves de limande à queue jaune (*Limanda ferruginea*) et de plie grise (*Glyptocephalus cynoglossus*) étaient en corrélation positive avec cette variable. Malgré d'importantes différences inter-annuelles de l'abondance, la répartition des larves présentaient une structure semblable d'une année à l'autre. À l'aide d'estimations de l'âge des larves établies à partir des distributions de la fréquence des longueurs, de taux de croissance tirés d'ouvrages publiés et de quantifications courantométriques, les auteurs ont obtenu des estimations du moment et du lieu de la fraie de chaque espèce. Ils ont ensuite comparé ces estimations à des données historiques sur la répartition de chaque espèce avant la fraie pour tenter d'étayer l'hypothèse d'une dérive passive des larves. Les résultats révèlent que dans la plupart des cas, mais pas tous, la répartition des larves et les courants appuient cette hypothèse dans le cas de certains taux de croissance et de répartition verticale. Toutefois, les observations ne suffisent pas à écarter d'autres mécanismes liés au comportement.

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A common approach in investigations aimed at understanding recruitment to marine fish populations and its variability is a search for and quantification of the factors that determine the distribution and survival of the early life stages. Hypotheses include those in which purely environmental factors such as water drift (or lack thereof) dominate (e.g. Myers and Drinkwater 1988) and those requiring significant behavioural components such as vertical migration in relation to currents (e.g. Sinclair 1988). The possibility of retention, or an extended residence time in a particular area, has been suggested for many species and has been attributed both to purely

physical processes (e.g. American plaice (*Hippoglossoides platessoides*), Nevinsky and Serebryakov 1973; silver hake (*Merluccius bilinearis*), Fahay 1974) and vertical migration in relation to depth-varying currents (e.g. Atlantic herring (*Clupea harengus harengus*), Sinclair and Iles 1988).

Two physical factors that affect the degree to which eggs and larvae are retained within an area are its horizontal extent and the rate of horizontal water exchange. Together, these factors determine the water residence time (extent/exchange rate). The Grand Bank of Newfoundland, a continental shelf region used as a spawning ground by numerous species, has both a broad

plateau and weak subtidal currents (except in the Labrador Current around its perimeter) (e.g. Petrie and Anderson 1983; Loder et al. 1988). Therefore, retention of early life stages might be expected to be a common feature on the Bank.

In this paper we report the distributions of the early life stages of three flatfish species on the southern Grand Bank, as observed in ichthyoplankton surveys conducted in September of 1986, 1987, and 1988. The species examined are American plaice, yellowtail flounder (*Limanda ferruginea*), and witch flounder (*Glyptocephalus cynoglossus*). There is limited information on the distribution of larvae and juveniles of these species in the area. However, extensive sampling of older juveniles (ages 1 and older), conducted since 1985, indicates that the southern Bank may be a juvenile nursery area for yellowtail

and plaice (Walsh 1991). We describe the distributions of larvae and 0-group juveniles in relation to the temperature field and use current measurements derived from moored instruments to estimate their movement and probable spawning sites, assuming that the dominant influence is water drift. We use the results of these analyses to assess the hypothesis that passive drift from spawning areas can account for the observed larval distributions.

## Materials and Methods

### Study Area

The study area (Fig. 1) was the Southeast Shoal (approximate centre 44°30'N, 50°W) of the Grand Bank, its

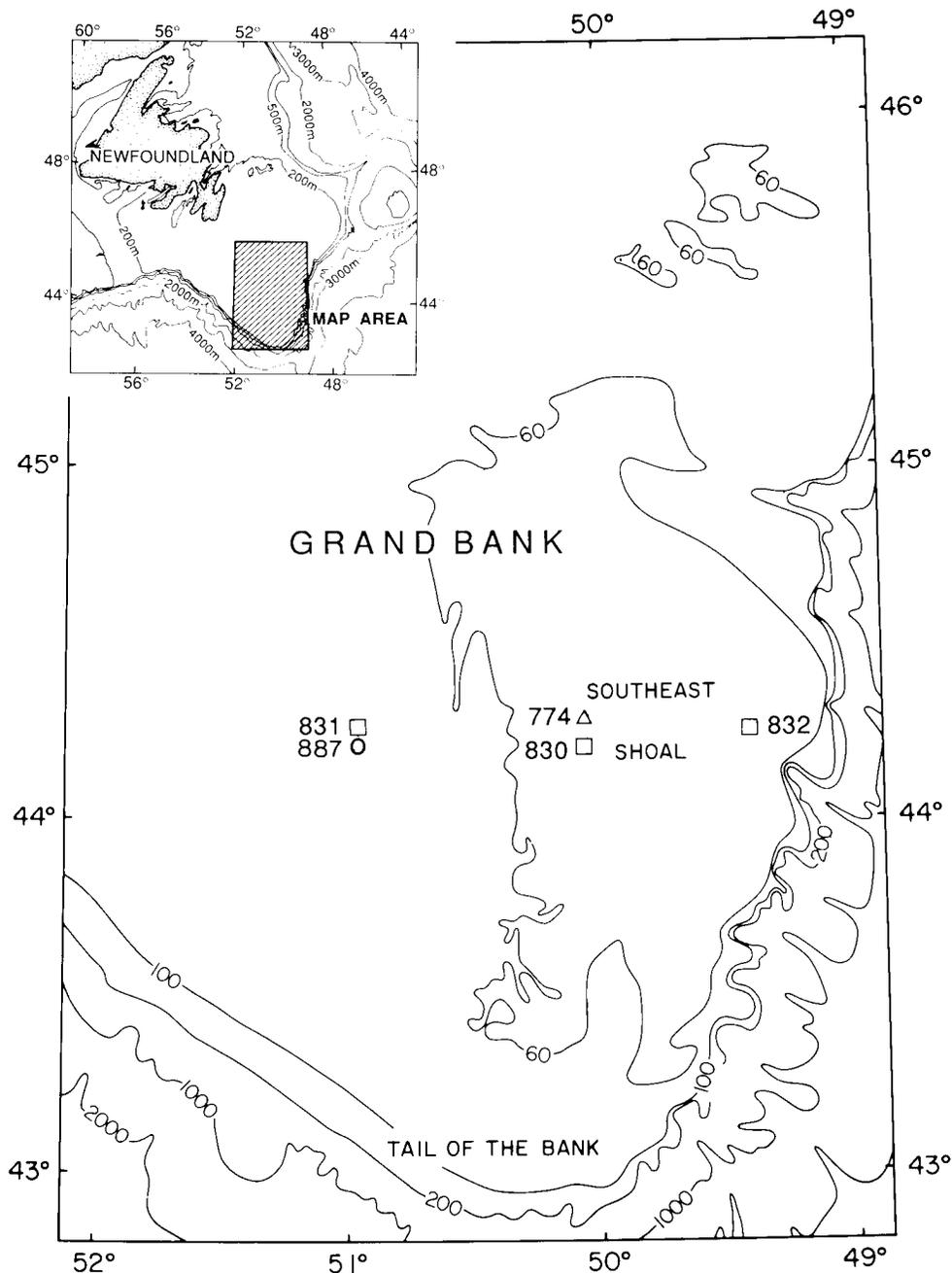


FIG. 1. Location map for the southern Grand Bank with the 1986-88 current meter mooring sites (see Table 1 for times and depths).  $\Delta$ , 1986;  $\square$ , 1987;  $\circ$ , 1988.

TABLE 1. Summary of positions, depths (below surface), and periods with reliable data for current meter measurements on the southern Grand Bank in 1986–88. Mooring No. refers to the Bedford Institute of Oceanography Consecutive Number.

Mooring No.	Latitude (N)	Longitude (W)	Water		Data
			depth (m)	Instrument depth (m)	return period (calendar days)
1986					
774	44°14.4'	50°04.2'	55	20 45	108–215 108–268
1987					
830	44°16.0'	50°05.3'	54	11 44	123–275 123–257
831	44°14.9'	50°58.8'	72	14 47	123–292 123–292
832	44°13.3'	49°19.5'	55	12 45	124–187 124–291
1988					
887	44°15.1'	50°59.9'	73	13 63	121–262 121–262

shallowest area. The Shoal is or has been the site of major domestic and international fisheries for capelin, cod, and flatfishes. It is a major spawning area for capelin and has been the site of studies on spawning (Carscadden et al. 1989) and early life stages (Frank and Carscadden 1989) of capelin and on juvenile stages of flatfish (Walsh 1991). The principal features of its spring–fall physical oceanographic regime are an approximate two-layer stratification (e.g. Loder 1991), weak subtidal currents, and a branch of the Labrador Current along the shelf break to the east (e.g. Petrie and Anderson 1983).

#### Physical Oceanography

The current and hydrographic fields in the Southeast Shoal region were monitored in 1986, 1987, and 1988 using moored sensors deployed from spring to fall (Ross et al. 1988) and hydrographic surveys. The returned data include time series from two Aanderaa current meters at each of one site in 1986, three sites in 1987, and one in 1988 (see Fig. 1 and Table 1, and Ross et al. 1988 for details). Temperature and salinity distributions were obtained during the 1986–88 September larval surveys from a CTD mounted on the BIONESS net system (Sameoto et al. 1980) and from XBT casts. Temperature and salinity data for other times during spring–fall of 1986–88 were obtained from dedicated hydrographic (CTD and XBT) surveys and from the Marine Environmental Data Service (MEDS). The MEDS data were screened for suspect values which were removed, and all the hydrographic data were subsequently grouped into time intervals of 1–2 wk duration which provided quasi-synoptic coverage of the region.

#### Adults

Spawning has never been directly observed for any of the three species studied. Published historical accounts of adult distributions, the approximate limits of the distribution of pre-spawners, and the relationship between these pre-spawning distributions and bottom temperatures were therefore used to a delimit the expected spawning times and locations.

#### Larvae and Juveniles (0-Group)

The sampling methods used are detailed in Frank and Carscadden (1989). Briefly, the horizontal and vertical distri-

butions of larvae of the three flatfish species were assessed from surveys conducted in September of 1986, 1987, and 1988. In 1986, a rectangular grid of 39 stations spaced at 10 nautical mile intervals along six transects was sampled. Eight additional stations were sampled along 44°15' centered on the shelf break. In 1987 the grid was expanded to the north, west, and south yielding a total of 71 stations. In 1988, another grid of 71 stations was sampled with slightly different spatial coverage. We used a small-scale version (0.25 m<sup>2</sup>) of the BIONESS, a multiple opening and closing net, fitted with seven 333- $\mu$ m-mesh nets. Seven discrete depths were sampled at each deployment and sample depths were spaced at 5-m intervals starting at 5 m (below surface). Each depth stratum was sampled for 10 min during which approximately 200 m<sup>3</sup> of water was filtered. Sensors positioned on the net frame provided real-time on-deck readouts of pitch, roll, and flow rate, as well as temperature, salinity, and depth (CTD). During the middle of each BIONESS tow, a horizontal tow of 10 min duration was made at 1 m depth with a 333- $\mu$ m, 0.75-m diameter net.

All samples were preserved in 4% formalin buffered with sodium borate. All fish larvae and macrozooplankton were sorted from the samples and counted. Total length measurements were made using an ocular micrometer for larvae <15 mm and a millimetre scale ruler for larger larvae ( $\geq$ 15 mm) and juveniles.

Variations in the depth distributions of larvae and juveniles of the three species were evaluated by calculating the vertical centre of mass of their distributions,  $z_{cm}$ :

$$(1) \quad z_{cm} = \sum_j (p_j z_j), \quad j = 1, m$$

where  $p_j$  is the proportion of larvae in the  $j$ th depth interval,  $z_j$  is its average depth, and  $m$  is the number of intervals. The centroids of the horizontal distribution of vertically averaged larval density were computed from

$$(2) \quad x_{cm} = \frac{\sum_k N_k x_k}{\sum_k N_k}, \quad y_{cm} = \frac{\sum_k N_k y_k}{\sum_k N_k}, \quad k = 1, n$$

where  $N_k$  is the larval density,  $x_k$  and  $y_k$  are the horizontal coordinates of the  $k$ th station, and  $n$  is the number of stations.

#### Inferred Spawning Areas

For an egg or larva released at horizontal position  $X_i$  at time  $t_i$ , its position at some later time  $t_f$  is

$$(3) \quad X_f = X_i + \int_{t_i}^{t_f} U_L(X_i, t) dt$$

where  $U_L(X_i, t)$  is its Lagrangian velocity (relative to the sea-floor) at time  $t$ . This velocity includes both the motion of the egg/larva relative to the water and the space- and time-dependent water velocity. To evaluate the influence of physical advection on larval distributions, we assumed that the individual larvae move with the ambient water and approximated this velocity by the velocity  $u_m(x_m, t)$  observed at a current meter position  $x_m$ . Taking  $t_f$  to be the midtime of the September survey, the mean release time can be approximated by

$$(4) \quad t_i = t_f - (l_f - l_i)/g$$

where  $l_f$  is the larval length from the September survey,  $l_i$  the length at release, and  $g$  its average growth rate. Thus, the release position can be estimated from

$$(5) \quad X_i = X_f - \int_{t_i}^{t_f} \mathbf{u}_m(\mathbf{x}_m, t) dt$$

with  $X_f$ ,  $t_f$ , and  $l_f$  specified from the September survey data,  $\mathbf{u}_m(t)$  from the moored current measurements, and  $l_i$  and  $g$  from literature values. The use of current observations from a single position assumes that there is limited horizontal structure in the subtidal currents which dominate long term drift on the Southeast Shoal. Cross-spectral analysis of the 1987 moored observations indicates that the spatial scale of the subtidal currents over the Shoal is of the order 50–100 km, although around the Shoal's perimeter, there is substantial structure associated with the Labrador Current and the steep bathymetry. Hence, the accuracy of  $X_i$  estimated from (5) will generally decrease for earlier release times (older larvae) if positions are considerable distances from the mooring site.

In the analysis presented here, the length at release was taken as the hatching length and the growth rate chosen to be appropriate to post-hatching. Strictly speaking, the inferred release times and positions are therefore appropriate to hatching. However, because the egg phase is short relative to the larval drift time, they also approximate the spawning times and positions.

## Results

### Physical Oceanography

The temperature distributions observed along  $44^{\circ}15'N$  during the September survey in each year (Fig. 2) indicate a

pronounced vertical stratification with a sharp thermocline near 20 m, consistent with historical observations (Loder 1991). Some interannual variability is apparent, including cooler temperatures and a less pronounced thermocline in 1986, and warmer near-surface waters and a slightly deeper thermocline in 1988. The vertical sections also show elevated near-bottom temperatures in the vicinity of the Shoal in each year, again consistent with historical observations (Loder 1991), and subzero temperatures along the Bank's eastern edge consistent with the presence of the cold intermediate layer associated with the Labrador Current (Petrie et al. 1988). Areal distributions of bottom temperature (Fig. 3) during early spring, early summer, and late summer (from the MEDS and hydrographic survey data) confirm the persistence of these features during spring and summer of each year, although with some variability in spatial structure and temperature from year to year (also see Carscadden et al. 1989).

The current measurements derived from the moored instruments revealed that, although the subtidal currents are important to long-term drift on the southern Grand Bank (Loder et al. 1988), they are generally weak. The mean currents have magnitudes of up to 0.04 m/s, while the standard deviations of the low-frequency current components are typically 0.02–0.05 m/s (Ross et al. 1988). The expected particle drifts resulting from the measured currents are illustrated in Fig. 4 which presents progressive vector plots for the central and eastern sites (Fig. 1) in 1987. Typical of the central and western sites in the other years, the central-site drift is generally westward and significantly stronger at the upper meter. In

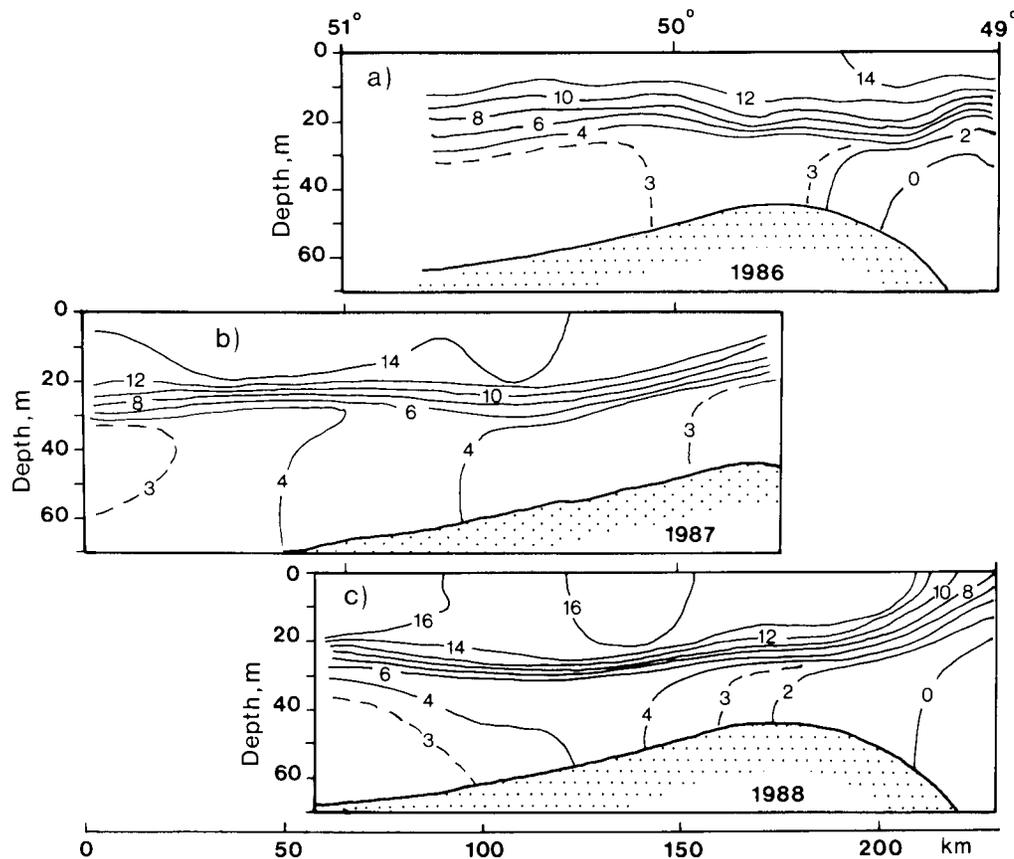


FIG. 2. West-east vertical sections of temperature along  $44^{\circ}15'N$  from the CTD mounted on the BIO-NESS during the September larval surveys of (a) 1986, (b) 1987, and (c) 1988.

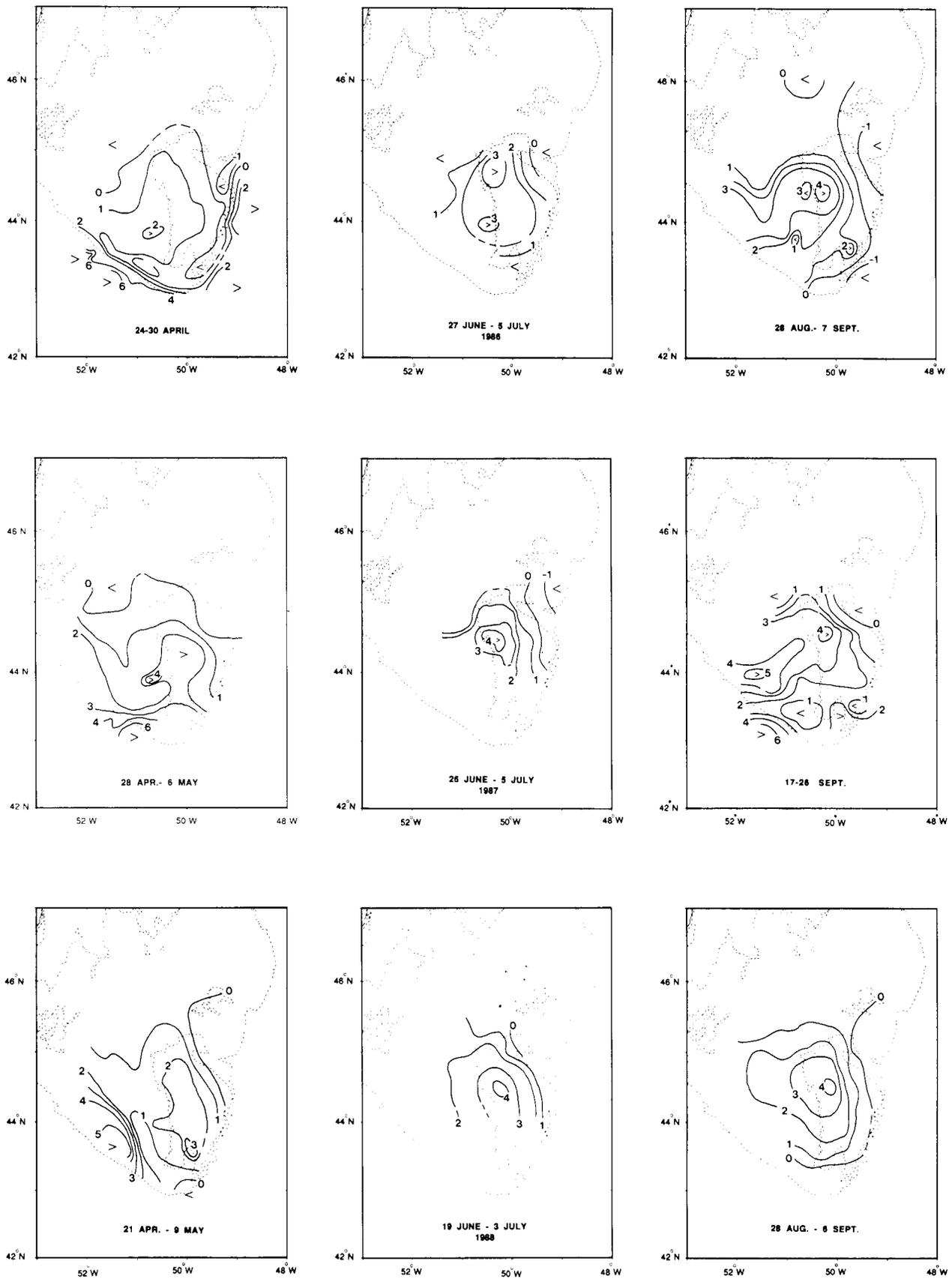


FIG. 3. Bottom temperature distributions on the southern Grand Bank during early spring, early summer, and late summer in 1986, 1987, and 1988. Data are from dedicated hydrographic surveys and MEDS and have been sorted into time intervals with broad spatial coverage.

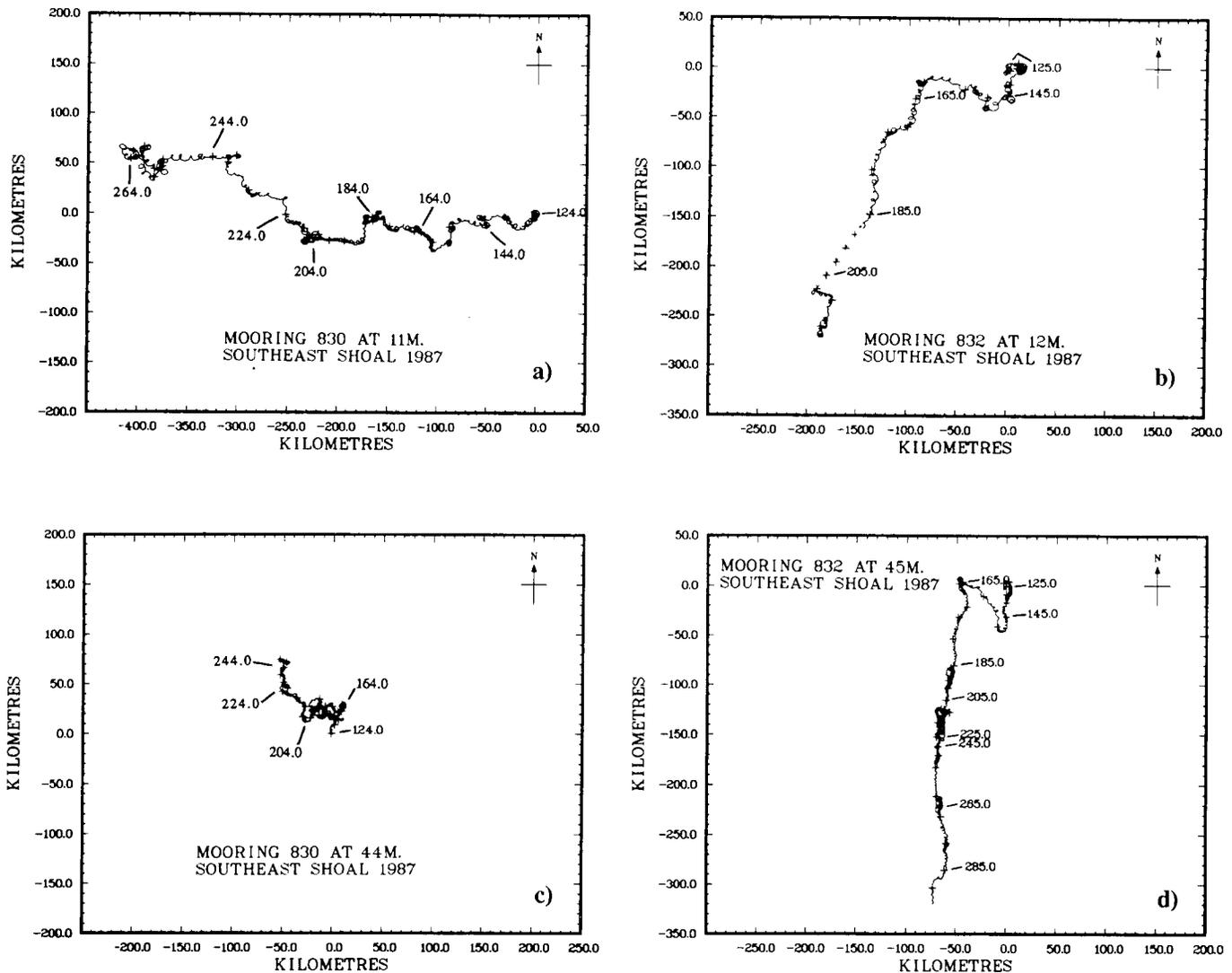


FIG. 4. Progressive vector plots from current meters at the (a, c) central (mooring 830) and (b, d) eastern (mooring 832) sites in 1987. Crosses denote 5-d intervals, labelled every 20 or 40 d.

contrast, the eastern-site drift is generally southward. These drifts are consistent with barotropic numerical model predictions (Greenberg and Petrie 1988; Hukuda et al. 1989) of a strong southward Labrador Current along the Bank's eastern edge and a weak west to northwestward drift across the Bank. The mean currents (Fig. 5) confirm the interannual persistence and large space scales of the characteristic drifts, but also indicate quantitative variations.

The moored measurements at the central site also revealed a large decrease in temperature over much of the water column in August 1986. This was associated with both vertical mixing and the displacement of Labrador Current water onto the Shoal during the passage of a tropical storm (Loder and Ross 1988; Frank and Carscadden 1989) and contributed to the relatively cool 1986 September temperatures (Fig. 2).

#### Adults

Commercial abundances of American plaice, yellowtail flounder, and witch flounder are common on the Grand Bank. As a result, their seasonal distributions and those of prespawners are documented. Of the three, yellowtail inhabits the shall-

lowest and warmest portions of the Bank. In fact, in this area, yellowtail is at the northern limit of its commercial range. As a result, temperature appears to be an important regulator of its distribution. In the early 1960's yellowtail abundance on the Bank increased coincident with a decrease in haddock abundance and an upward trend in bottom temperature (Pitt 1970). During the 1950's and 1960's, the greatest concentrations of yellowtail occurred at depths of 57–64 m, coincident with bottom temperatures of 3.1–4.8°C (Pitt 1970). Research trawl surveys conducted during the 1970's and 1980's revealed the largest concentration of yellowtail to be at depths less than 100 m where water temperatures exceeded 1°C (Wells et al. 1988). Fitzpatrick and Miller (1979) used research trawl data to delimit the distribution (Fig. 6) of ripe fish between 1952 and 1968. During this interval, peak spawning occurred during the latter half of June in areas where bottom temperatures exceeded 2°C (Pitt 1970). Since the warmest summertime bottom temperatures on the Grand Bank occur over the Southeast Shoal (Loder 1991; Fig. 3), the Shoal is probably the most important spawning area for yellowtail on the Bank.

In contrast with yellowtail, plaice occurs in deeper waters and is considered a cold-water species. It is reported to occur

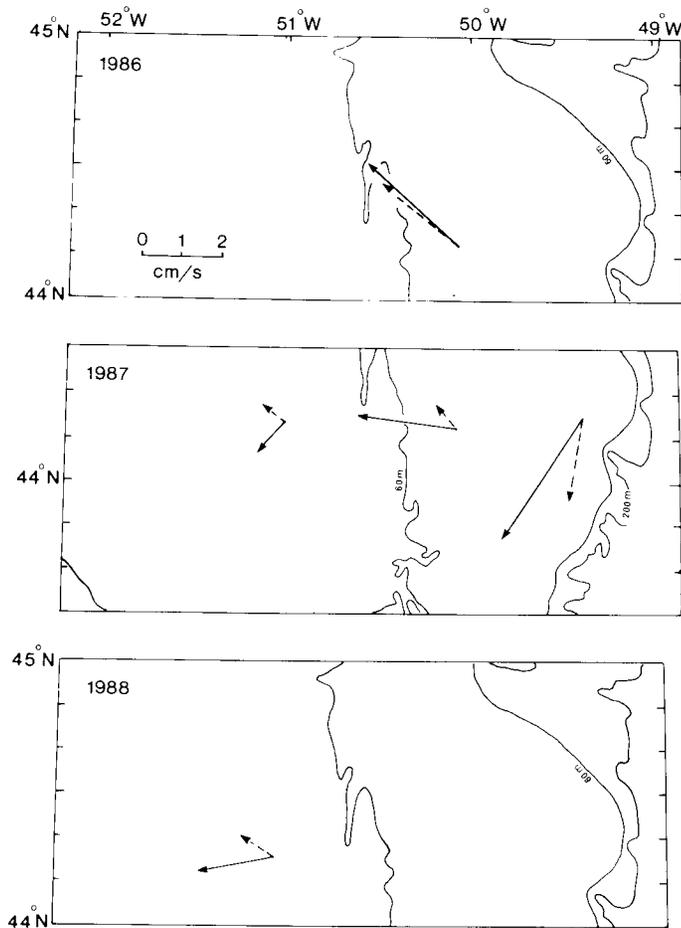


FIG. 5. Record-mean currents from moored measurements on the southern Grand Bank in 1986–88. Solid vectors are for upper instruments; broken vectors are for lower meters.

at depths ranging from 90 to 250 m and at temperatures from just below 0 to 1.5°C (Scott and Scott 1988; Wells et al. 1988). Plaice appears to spawn in most areas where the influence of the cold Labrador Current is apparent (Fig. 6). There is, however, some dispute concerning the relative importance of dif-

ferent areas. Pitt (1966) reported that the northern and eastern slopes of the Bank supported the greatest spawning activity. Nevinsky and Serebryakov (1973) also noted the importance of the northern Grand Bank but reported that spawning on the eastern, southwestern, and southern slopes was less intense. They concluded that spawning occurs from April to mid-May at bottom temperatures ranging from -1.3 to 3.5°C, with spawning being most intense at 0–2°C. Pitt (1966) reported that average spawning temperatures ranged from -1.3 to 2.8°C on the northern, southeastern, and southwestern areas of the Bank.

Witch is generally considered to be a deepwater species, residing in gullies where the bottom is clay and mud rather than on sand and gravel bottom typical of the banks and the inshore (McKenzie 1955). In the Grand Bank area, research trawl surveys conducted during 1958–74 have revealed that the greatest numbers of witch occurred at depths of 185–366 m and at bottom temperatures of 2–6° (Bowering 1976). On the basis of the relative frequencies of ripening and recently spent fish from research surveys, Bowering (1990a) concluded that spawning occurs during April–June (Fig. 6) on the southern Grand Bank at depths ranging between 100 and 200 m and temperatures between 2 and 3°C.

None of the three flatfish species discussed is reported to undergo extensive migrations, although yellowtail and plaice migrate seasonally, moving into shallow water in the spring and into deeper water during the winter (Scott and Scott 1988; Walsh 1991).

#### Larval Distributions and Size Composition

##### *Yellowtail flounder*

The depth of the centre of mass of yellowtail larvae and juveniles occurred at 24.2, 28.0, and 26.7 m during the day and 18.6, 23.9, and 25.1 m during the night in 1986, 1987, and 1988, respectively (Fig. 7). This diel pattern of depth distribution is similar to that described by Smith et al. (1978), but the day–night change in depth in the mid-Atlantic Bight was greater, exceeding 25 m. In view of the limited day–night change observed on the southern Grand Bank, we combined the centre of mass depths for day and night when estimating the direction and magnitude of larval drift (Table 2).

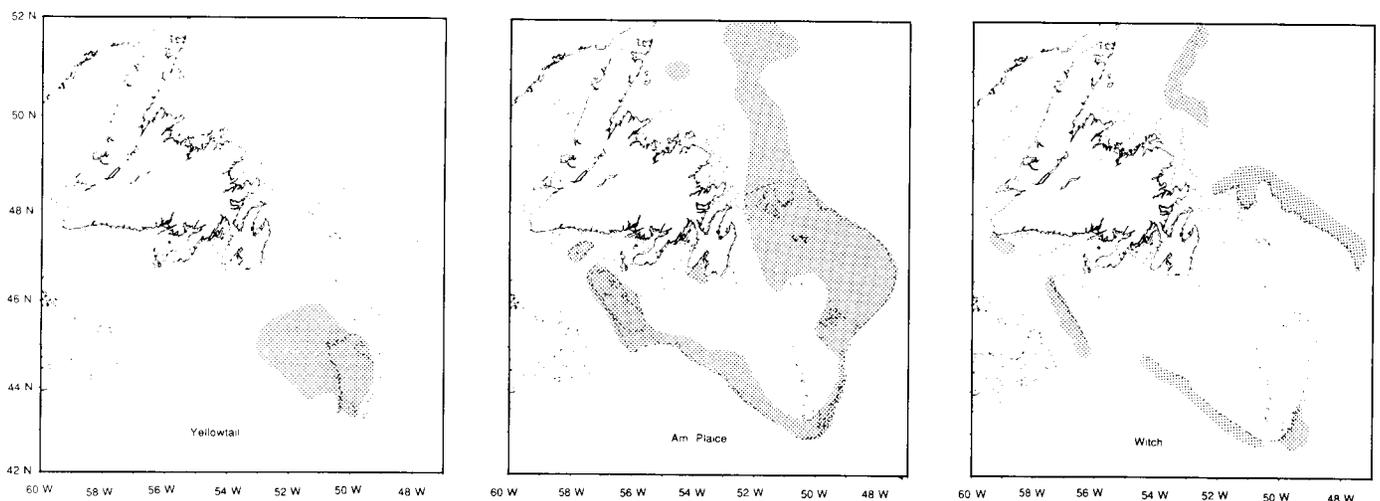


FIG. 6. Composite picture of spawning distributions of yellowtail and plaice (after Fitzpatrick and Miller 1979) and witch (after Bowering 1990a) in the Grand Banks region for April–July.

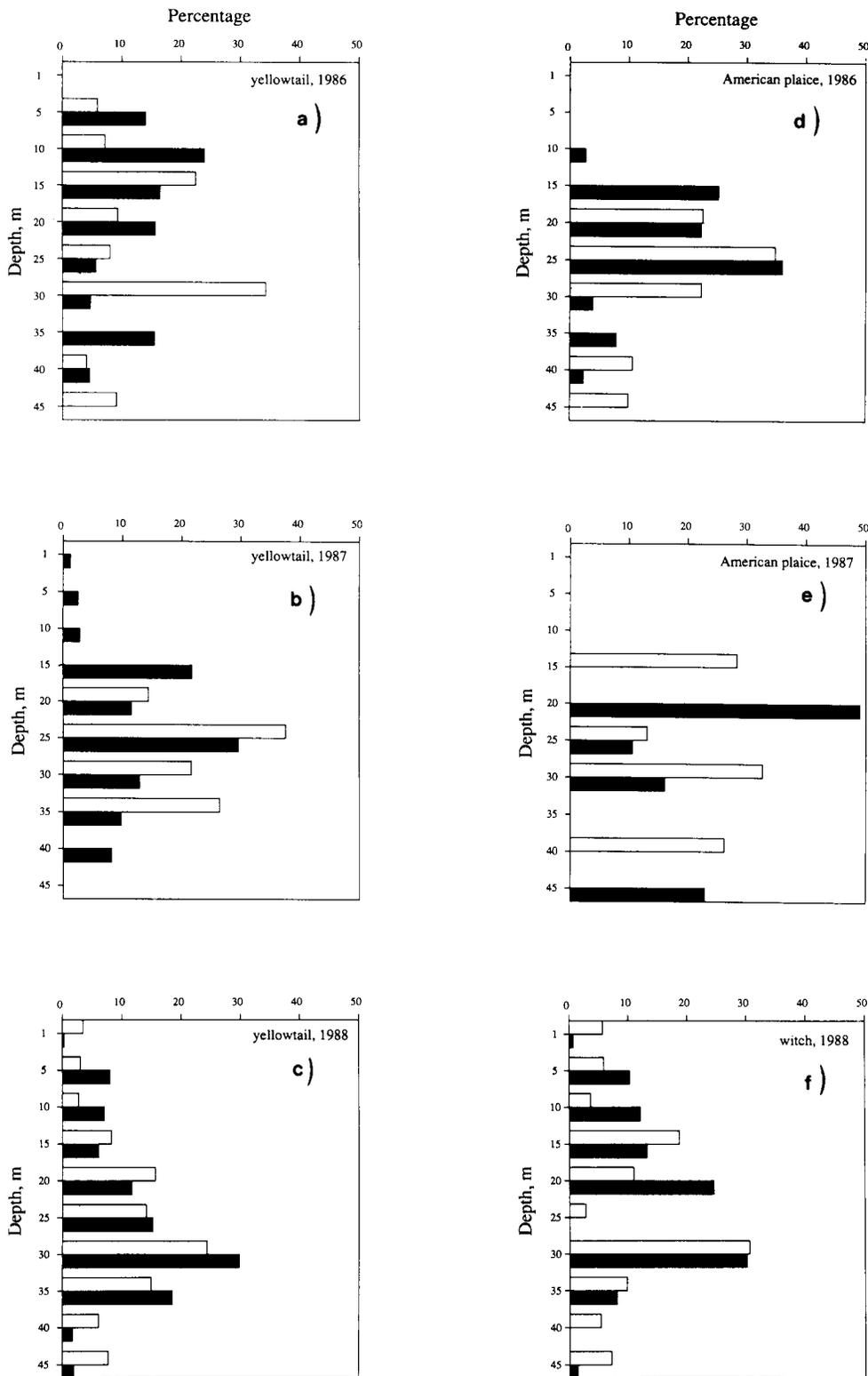


FIG. 7. Percentage of larvae in various depth intervals for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988. Distributions are shown for both day (open bars) and night (shaded bars) stations.

Furthermore, peak concentrations of yellowtail were observed at depths near or below the thermocline (Fig. 8). In 1986 and 1987, a majority of the yellowtail (>60%) were below the thermocline. Given the two-layer stratification, bottom temperature was taken as an index of the (lower-layer)

thermal regime principally experienced by the larvae and juveniles.

In 1986 the highest concentrations of yellowtail occurred over the western half of the survey area where bottom temperature generally exceeded 2°C (Fig. 9a, 9g, 10a). No yellowtail were

TABLE 2. Summary of midtimes ( $t_f$ ) of surveys, observed mean vertical positions ( $z_{cm}$ ) and larval lengths ( $l_f$ ), assumed hatching lengths ( $l_i$ ) and growth rates ( $g$ ), and calculated ages (post-hatching) and spawning dates ( $t_i$ ) for the larval cohorts observed in September of each year.

Cohort	$t_f$ (d)	$z_{cm}$ (m)	$l_f$ (mm)	$l_i$ (mm)	$g$ (mm/d)	Age (d)	$t_i$ (d)
Yellowtail							
1986	258	23.2	23.1	3.5	0.11	178	80
					0.25	78	180
1987	264	24.7	26.0	3.5	0.11	205	59
					0.25	90	174
1988	264	25.7	18.7	3.5	0.11	138	126
					0.25	61	203
Plaice							
1986	258	24.3	27.8	4.0	0.16	149	109
					0.25	95	163
1987	264	29.1	30.1	4.0	0.16	163	101
					0.25	104	160
Witch							
1988	264	22.8	18.3	4.5	0.09	153	111
					0.25	55	209

found on the eastern portion of the Bank where temperature was generally less than 2°C. The highest yellowtail concentrations occurred west of the peak temperatures, but the westward limits of the distribution were not resolved.

The 1987 yellowtail distribution (Fig. 9b) exhibited some similarity with that of 1986, although the average density was substantially lower. Maximum densities occurred on the northwestern portion of the Shoal. Very few individuals were collected in the eastern, southern, or southeastern sections of the grid. As in 1986, the highest catches were generally obtained at stations where bottom temperature (Fig. 9h, 10b) exceeded 2°C. However, the yellowtail and temperature maxima were again offset, with peak yellowtail densities to the north of the temperature peak. The northwestward limit of the yellowtail distribution was not resolved.

The average density of yellowtail in 1988 (Fig. 9c) was similar to that observed in 1986. Peak abundances were again coincident with bottom temperatures above 2°C (Fig. 9i, 10c), with densities declining from west to east. Unlike 1986 and 1987, the extent of the yellowtail patch was better defined and the patch coincided with the temperature maximum. There was also bimodality in the yellowtail-temperature relation, with highest densities occurring at temperatures between 0 and 1°C and above 2°C (Fig. 10c). The observations from all three years support a relation between the horizontal distributions of yellowtail and lower-layer temperature, although it is unclear whether or not there is a direct influence.

The lengths ( $l_f$ ) of yellowtail collected in September 1986 ranged from 10 to 33 mm with a mean of 23 mm (Fig. 11a; Table 2). Literature values for larval growth rate ( $g$ ) range from an average of 0.11 mm/d for larvae collected over the Grand Bank during June–August 1980 (Bonnyman 1983) to 0.25 mm/d for larvae reared in the laboratory at 10°C (Smigielski 1979). Hatching length ( $l_i$ ) is approximately 3.5 mm (Fahay 1983). Assuming that the growth rates were similar in all areas, as well as before and after metamorphosis, we estimate from (4) that the mean age (post-hatch) of yellowtail captured in 1986 was in the range of 78–178 d (Table 2). In September 1987, the mean length of yellowtail was 26 mm (Table 2), with most individuals lying between 22 and 34 mm (Fig. 11b), although

individuals as small as 5 mm were captured. In September 1988, yellowtail sizes ranged from 4 to 33 mm (Fig. 11c), with a mean of 19 mm (Table 2). For the above growth rates and hatching length, the mean ages of larvae sampled in 1987 and 1988 were in the ranges of 90–205 and 61–138 d, respectively (Table 2). While the uncertainty in the growth rate results in a wide mean age range, the historical data on spawning times (e.g. Fitzpatrick and Miller 1979) suggest that the lower ages are more probable. The wide range of sizes (and ages) coincident in time and space in each of the three years also suggests that there is some retention of the early life stages (larvae and pelagic juveniles) of yellowtail on the Southeast Shoal.

#### American plaice

There was little evidence of vertical migration by plaice larvae and juveniles in the 1986–88 observations. The average centres of mass for day and night generally occurred at depths exceeding 20 m (Fig. 7d, 7e). Since there are no other published data on the depth distribution of the early stages of plaice, we used the mean depth for the day and night observations combined to estimate drift (Table 2). Peak plaice concentrations were located near the thermocline, with greater than 70% of the larvae and juveniles below the thermocline in 1986 and 1987 (Fig. 8d, 8e). As with yellowtail, bottom temperature was used as an index of the lower-layer thermal regime in our evaluation of the horizontal distributions of plaice.

The horizontal distribution of plaice in September 1986 was inversely related to that of yellowtail (Fig. 9a, 9d). Plaice densities increased from west to east across the Shoal and peaked along its eastern flank where bottom temperatures were below 1°C (Fig. 9g, 10d). Only a few plaice were found in the western and central parts of the grid where temperatures exceeded 2°C (Fig. 9d, 9g).

The 1987 and 1988 plaice densities were approximately two orders of magnitude lower than those from 1986. However, the distributions were similar in all three years. In each of 1987 (Fig. 9e) and 1988 (not shown), plaice were captured at only 8 of 71 stations. These were located primarily along the eastern half of the grid where bottom temperatures were near or below 0°C. There were also some occurrences of plaice at stations with higher temperatures (Fig. 9e, 9h, 10e).

The ranges in length of plaice collected during the September surveys were 16–38 mm (Fig. 11d), 25–35 mm (Fig. 11e), and 10–38 mm (not shown) for 1986, 1987, and 1988, respectively. The mean lengths in 1986 and 1987 were 28 and 30 mm (Table 2). Growth rates of plaice larvae on the Grand Banks average 0.16 mm/d during May–September (Bonnyman 1983), while rates average 0.25 mm/d over the first 80 d in the Wadden Sea (Zijlstra et al. 1982). For these growth rates and a hatching length of 4.0 mm (Fahay 1983), the mean age of the 1986 and 1987 plaice cohorts was estimated to be in the ranges of 95–149 and 104–163 d, respectively (Table 2). Given the limited occurrence of plaice over the Southeast Shoal, we suggest that their distribution is primarily influenced by Labrador Current advection along the Bank edge to the northeast of the study region. The occurrence of plaice on the eastern Shoal may result from leakage of the Current onto the Bank followed by a weak westward drift.

#### Witch flounder

The depth of the centre of mass of witch larvae and juveniles in 1988 was 21 m at night, 26 m during the day, and 23 m for both combined (Fig. 7f; Table 2). Peak concentrations were in the thermocline (Fig. 8f). However, the larvae were broadly

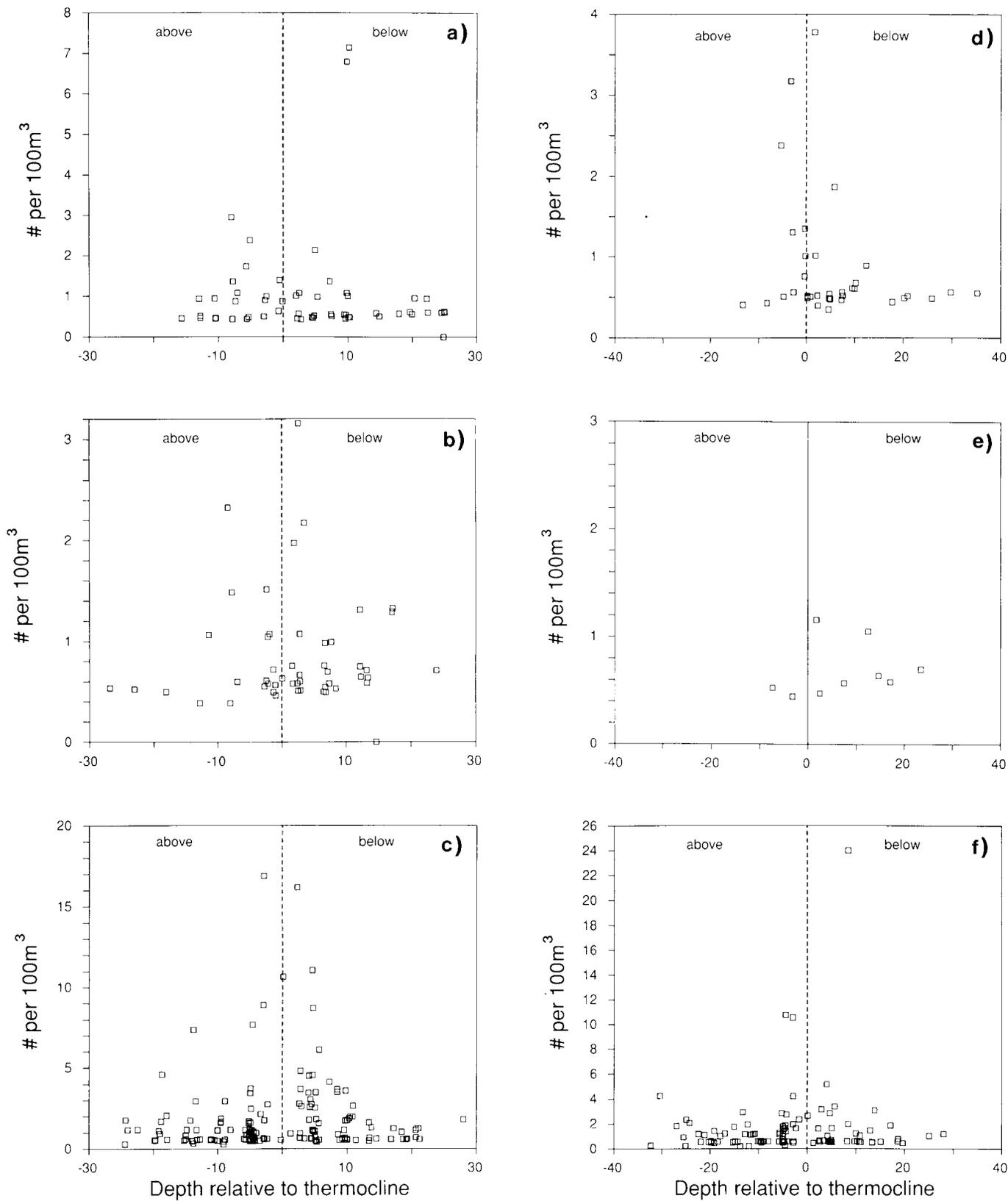


FIG. 8. Scatter plots of larval density versus depth (m) relative to the thermocline for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

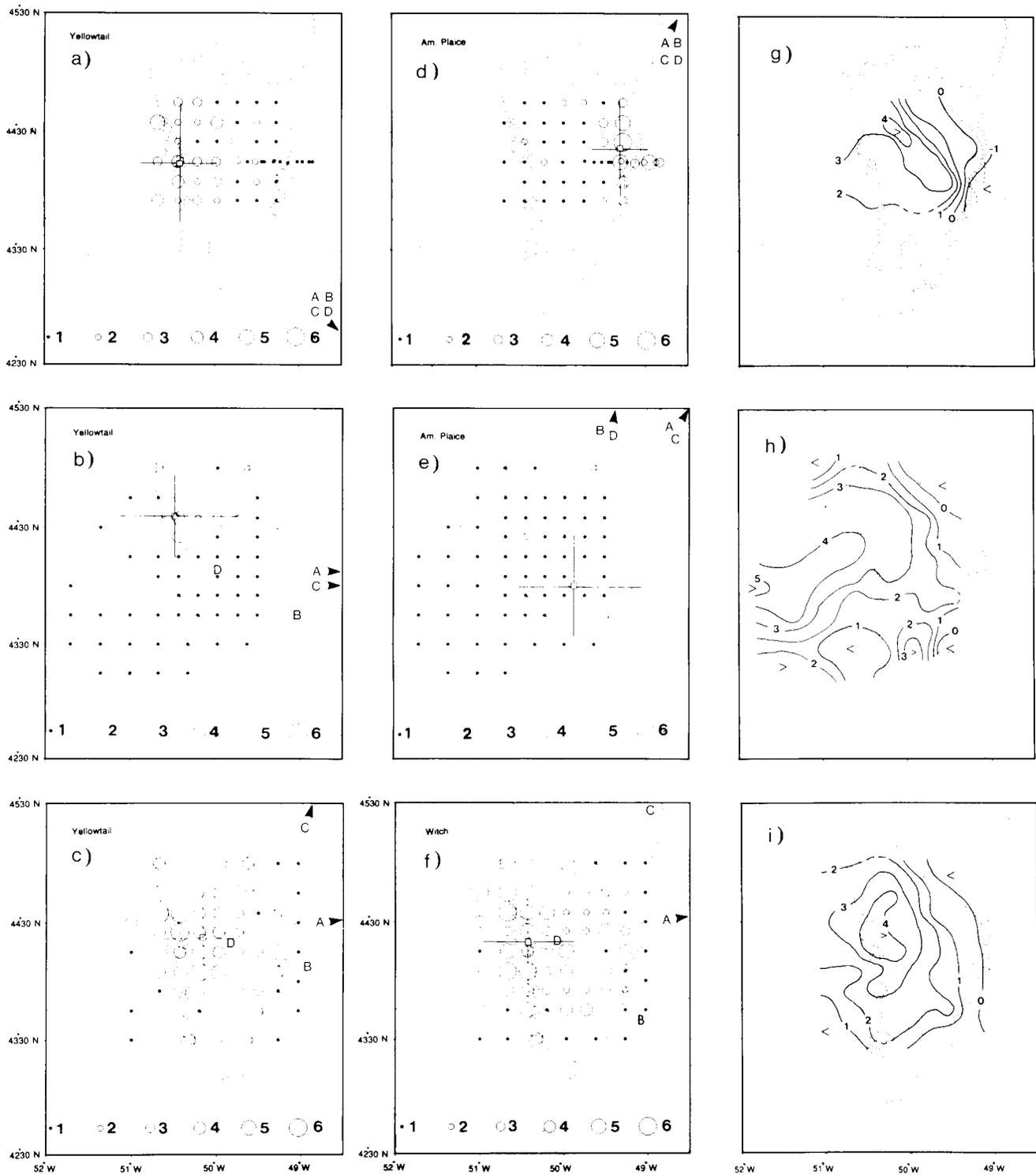


FIG. 9. Distributions of depth-averaged larval density and bottom temperature (g, h, i) from surveys during (a, d, g) 13–18 September 1986 (days 256–261), (b, e, h) 17–26 September 1987 (days 260–269), and (c, f, i) 17–23 September 1988 (days 261–267). Larval distributions are shown for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988. Keys to the expanding symbols: (a, b, c) 1: none, 2: 0.05–0.13, 3: 0.13–0.31, 4: 0.31–0.78, 5: 0.78–2.0, and 6: >2.0; (d, e, f) 1: none, 2: 0.05–0.1, 3: 0.1–0.2, 4: 0.2–0.4, 5: 0.4–0.8, and 6: >0.8, where all densities are numbers per 100 m<sup>3</sup>. Centroid positions and second moments of the larval distributions are also shown. The capital letters (A, B, C, D) indicate the inferred spawning locations presented in Table 3.

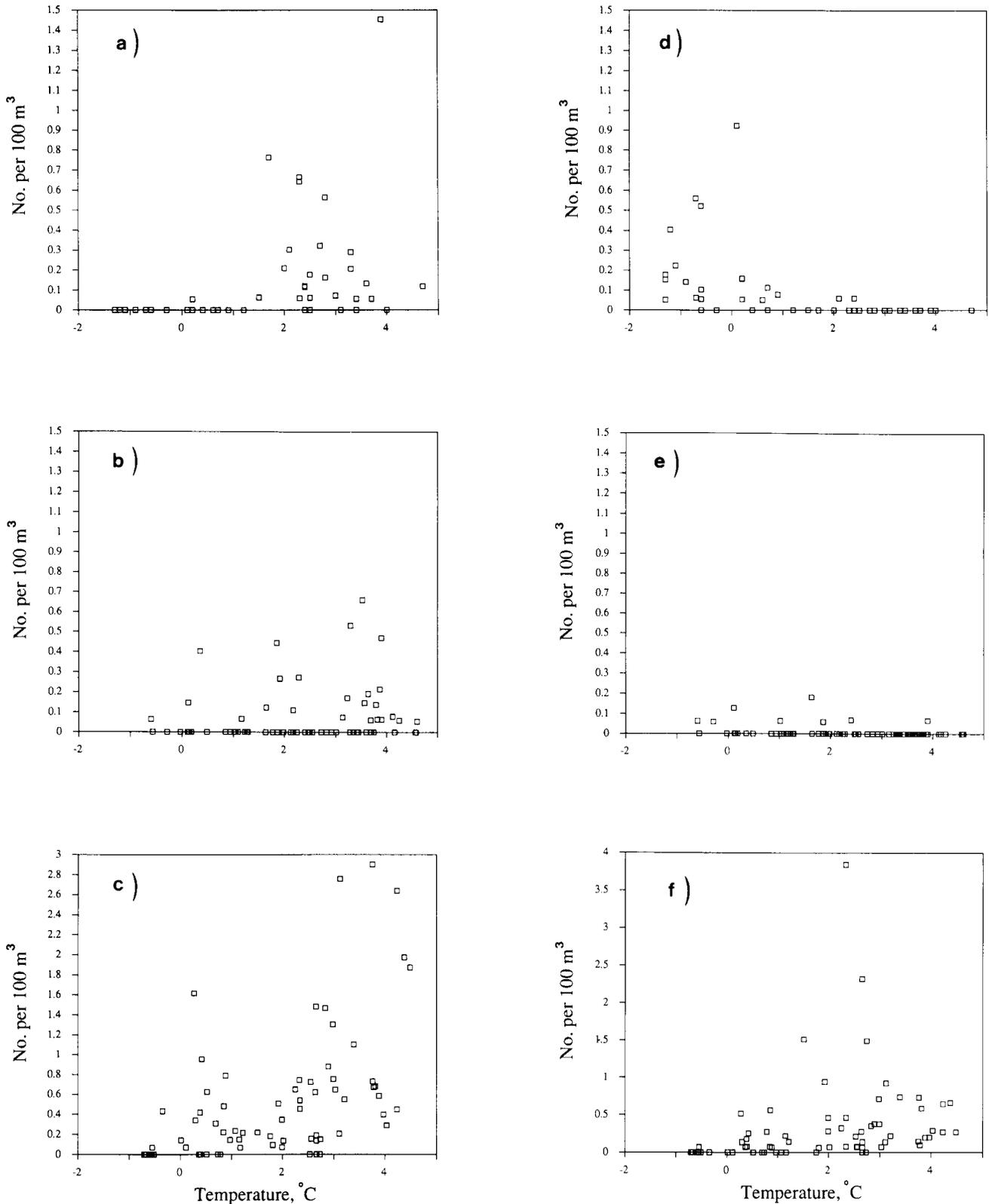


FIG. 10. Scatterplots of larval abundance versus bottom temperature for yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

distributed over the water column, with roughly equal proportions occurring above and below the thermocline. As with the other species, we used bottom temperature as an index of the lower-layer thermal regime in examining the horizontal distribution of witch.

Witch occurred as single individuals at only 2 of 47 stations in September 1986 and 3 of 71 stations in 1987. They were abundant during the 1988 survey (Fig. 9f) when their average density equalled that of yellowtail. In 1988, witch larvae and pelagic juveniles were most abundant over the central, western,

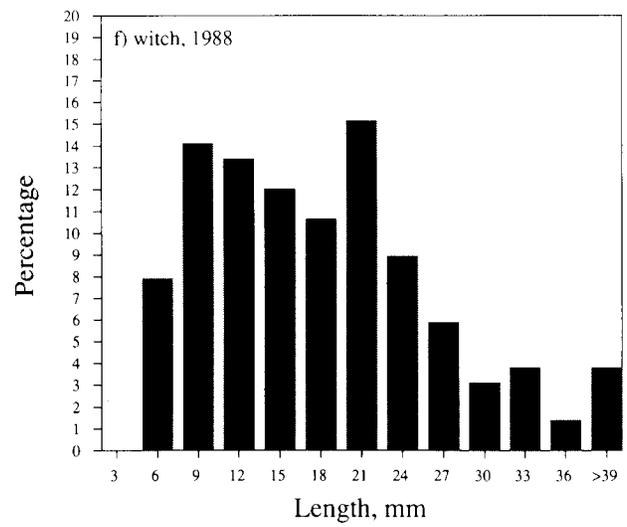
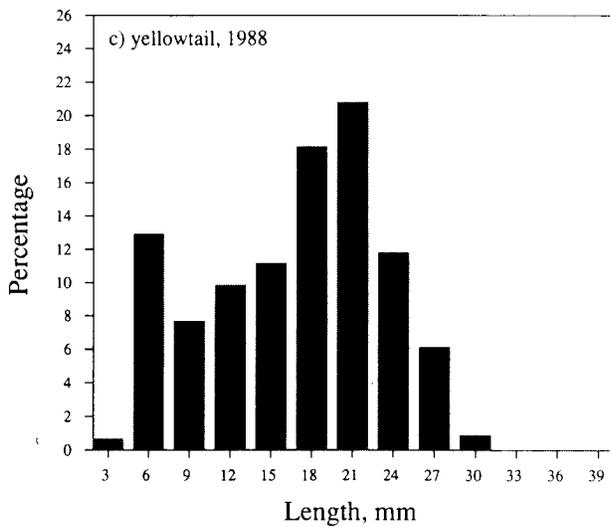
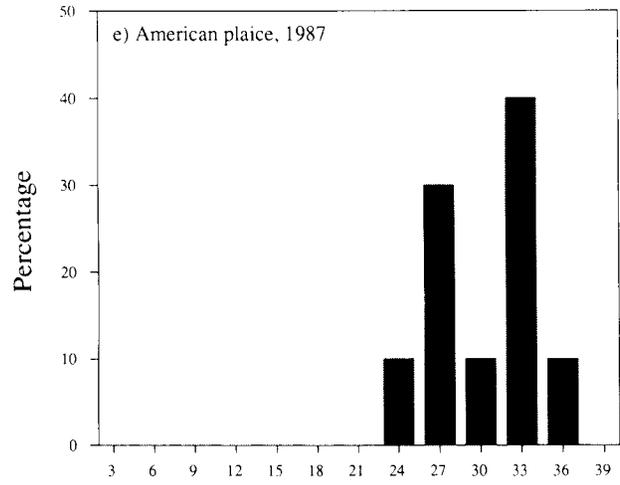
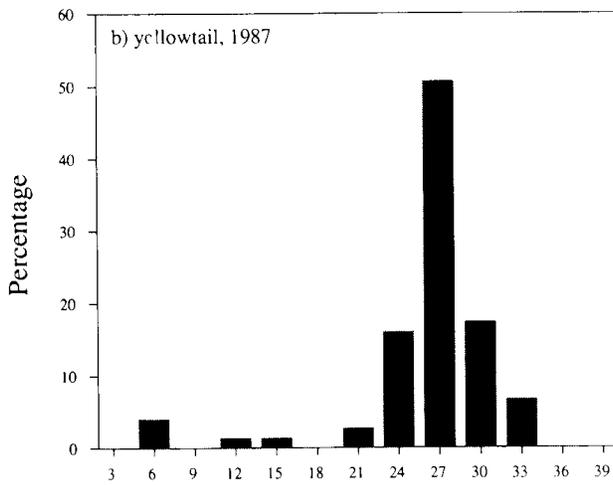
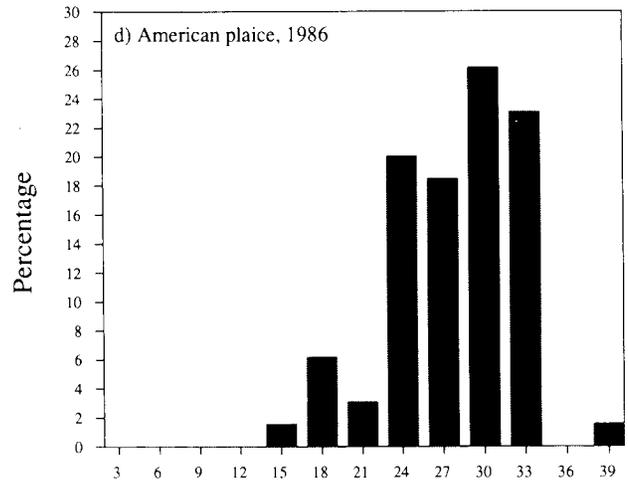
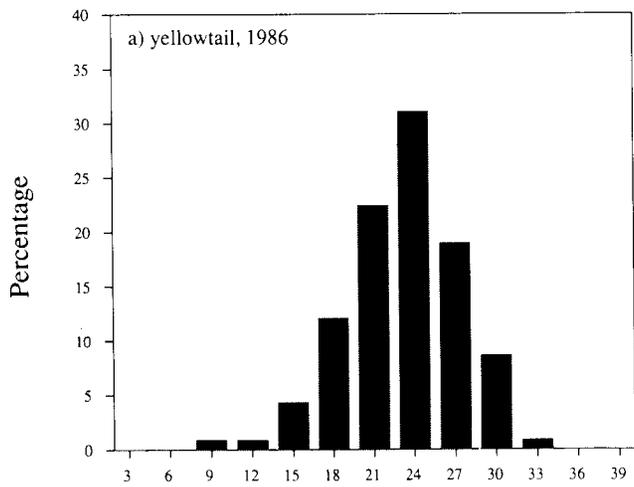


FIG. 11. Length frequency distributions of yellowtail in (a) 1986, (b) 1987, and (c) 1988, plaice in (d) 1986 and (e) 1987, and (f) witch in 1988.

and northwestern portions of the survey area, particularly where bottom temperatures exceeded 2°C (Fig. 9f, 9i, 10f). They were absent from the eastern edge of the survey where temperatures were near 0°C. The witch distributions were thus similar to those of yellowtail, with maximum densities occurring in relatively warm bottom waters (Fig. 9).

The length of witch collected in 1988 ranged from 5 to 50 mm, with a mean of 19 mm (Fig. 11f). The only published estimate of growth rate for witch (0.09 mm/d) is based on monthly collections from the southern Grand Bank (Bonnyman 1983). We assumed an upper limit growth rate of 0.25 mm/d consistent with that of the other two species. Given a hatching length of 4.5 mm and the above growth rates, we estimated a mean age for witch in our samples ranging from 55 to 153 d (Table 2).

### Inferred Spawning Positions

To examine whether the larval distributions and the estimated ages at capture are consistent with passive advection from sites with historical distributions of prespawning fishes, we used (5) to estimate the spawning (hatching) sites by species and year for a range of input values. Examination of (4) and (5) indicates that there will be uncertainty in the inferred sites associated with uncertainties in  $l_f$ ,  $l_i$ ,  $g$ ,  $X_f$ , and the horizontal and vertical structure of  $u_m$  (taking passive advection as a given). However, con-

sideration of the available information suggests that the largest contributors to this uncertainty are the growth rates, the depth of the larvae during the drift period, and horizontal structure in the currents near the Bank edge. To provide approximate bounds on the likely sites, we show in Table 3 the expected larval displacements ( $X_f - X_i$ ) for four cases (A, B, C, D) for each species and year. These are estimates based on the two different mean ages (or spawning dates) shown in Table 2 and estimates for currents typical of the upper (A, C) and lower (B, D) water columns (current meters). For yellowtail and witch, current measurements from the respective years are used, while the 1987 measurements from the eastern mooring site are used for plaice in both 1986 and 1987. The estimated spawning positions for the different cases are indicated in Fig. 9.

For most of the cases considered, the inferred spawning positions are off the Bank in areas which are represented poorly by the moored measurements. The specific positions in those cases have limited meaning, but the prediction of remote spawning sites under the assumed conditions should nevertheless be valid. In particular, the moored measurements of upper-layer currents strongly suggest that, if larvae occupy these surface waters through the summer and are transported passively, spawning must occur well away from the Southeast Shoal (cases A, C). In contrast, passive advection by lower-layer currents does allow for spawning sites in the vicinity of the Shoal, particularly if growth rates approximate 0.25 mm/d (case D).

TABLE 3. Estimated displacements of spawning positions ( $x_i, y_i$ ) from September observation positions ( $x_f, y_f$ ) for various species and years. Results are shown for four cases for each species/year: two different spawning dates (growth rates) taken from Table 2 and drifts as measured at the upper (cases A, C) and lower (cases B, D) current meters. A positive  $x$ -displacement denotes a spawning site to the east of the September larval position, and a positive  $y$ -displacement denotes a spawning position to the north of the September position. Where current measurements are available for the entire drift period, they are used; otherwise the record-mean currents are used. See Fig. 9 for estimated spawning positions.

Cohort	Case	Spawning date (d)	Drift depth (m)	$x_i - x_f$ (km)	$y_i - y_f$ (km)	Current source: period and mooring No.
Yellowtail						
1986	A	80	20	370	-370	Record mean ( $\bar{a}$ 774)
	B		45	290	-290	
	C	180	20	160	-160	
	D		45	170	-190	Days 180-258 ( $\bar{a}$ 774)
1987	A	59	11	490	-53	Record mean ( $\bar{a}$ 830)
	B		44	120	-90	
	C	174	11	280	-70	Days 174-264 ( $\bar{a}$ 830)
	D		44	39	-54	Record mean ( $\bar{a}$ 830)
1988	A	126	13	250	33	Days 126-262 ( $\bar{a}$ 887)
	B		63	94	-58	
	C	203	13	110	130	Days 203-262 ( $\bar{a}$ 887)
	D		63	21	4	
Plaice						
1986	A	109	12	280	420	Record mean ( $\bar{a}$ 832)
	B		45	64	280	
	C	163	12	180	270	
	D		45	41	180	
1987	A	101	12	310	460	
	B		45	70	310	
	C	160	12	200	290	
	D		45	25	230	Days 160-264 ( $\bar{a}$ 832)
Witch						
1988	A	111	13	280	40	Record mean ( $\bar{a}$ 887)
	B		63	110	-70	
	C	209	13	110	130	Days 209-262 ( $\bar{a}$ 887)
	D		63	28	2	

### *Yellowtail flounder*

For yellowtail, the observed 1987 and 1988 larval distributions are consistent with spawning over the Shoal if larvae drift with the lower-level currents and experience a high growth rate (case D) (Fig. 9b, 9c). The bottom temperature distributions (Fig. 3) during the late June/early July spawning times inferred for the high growth rate for 1987 and 1988 show values above 2°C in the vicinity of the inferred spawning sites. Although the measured (northwestward) lower-level currents in 1986 were stronger than in 1987 and 1988 (Fig. 5) and imply an off-bank spawning site, the bottom temperature (and salinity, not shown) distributions (Fig. 3) suggest persistence of relatively warm bottom water over the Shoal during spring–summer and an intrusion of water from the west. Given the suggested increased spatial structure of the near-bottom currents in 1986, the possibility that lower-layer residence times were greater than that implied by the current measurements cannot be discounted. For the other cases (A, B, C), the inferred yellowtail spawning sites were off the Bank, although the sites for lower-level drift and slow growth in 1987 and 1988 were close to the Shoal.

### *American plaice*

Given that the September plaice distributions were concentrated along the eastern edge of the Bank where the measured currents were southward, the inferred spawning positions are well to the north of the study area. Only the slower growth rate yielded spawning times (Table 2) consistent with historical information. The inferred spawning positions under these conditions are in the vicinity of historical spawning sites on the northern–northeastern Grand Bank (Fig. 6), but it is not possible to discriminate between upper- and lower-layer drift. However, passive advection in the core of the Labrador Current where the residual current speeds are substantially greater than those observed at the eastern mooring site (Mountain 1980; Greenberg and Petrie 1988) would not lead to the distribution observed. The bottom temperatures on the eastern Bank in the study years (Fig. 3) are consistent with a cold intermediate layer, with temperatures in the range observed historically for plaice spawning.

### *Witch flounder*

Given the low densities of witch observed in 1986 and 1987, we estimated spawning sites for 1988 only. In that year the range of expected growth rates generates spawning times that are consistent with historical observations and, assuming drift with the lower-level currents, implies spawning positions (Fig. 9f) which bracket the historical sites. In contrast, drift in the upper-level currents would require spawning positions well off the Bank. There are, however, some unresolved questions regarding the witch distributions (in addition to their occurrence in 1988 but not 1986 and 1987). Lower-level passive drift and a high growth rate (*D*) are unlikely, since they imply a Shoal spawning site inconsistent with the historical information presented in Bowering (1990a). Lower-level drift requires a slower growth rate (similar to B) in order to have an off-bank spawning site. However, our limited information on currents and hydrography on the eastern side of the Bank in 1988 makes the expected spawning position and its consistency with the temperature range of witch unclear. Thus, a witch spawning site on the eastern side of the Bank together with passive lower-layer drift cannot be discounted for 1988, although there is no direct evidence for this.

## Discussion

The horizontal distributions of larvae and juveniles of the three flatfish species show a striking correspondence to the bottom temperature distributions, suggesting a probable influence of the physical environment on the early life stages of flatfish on the southern Grand Bank. Correlation analyses between depth-averaged densities and temperature and salinity at various vertical levels generally yielded the highest (significant) correlations for bottom temperature. There are, however, several unresolved questions. In particular, the full extent of the flatfish and temperature features was not resolved by the survey grids, the flatfish and temperature maxima appear to be offset in some cases (yellowtail in 1986 and 1987), the flatfish distributions extend through the thermocline into the upper layer while the bottom temperatures are representative of depths below 25–30 m (Fig. 2), and the mechanism(s) underlying the correspondence is unclear. It is unclear whether there is a direct temperature influence on larval distributions or whether larval densities and temperature are indirectly related by some common correlate (e.g. different water masses). One possible scenario linking larval distributions directly to temperature is passive advection of the eggs and larvae in subthermocline waters followed by active seeking, by late-stage larvae and juveniles, of the adults' preferred bottom temperature.

The vertical distributions observed during the September larval surveys are of limited value in identifying the origin of the larvae–temperature relation. Plaice distributions were dominantly subthermocline, but yellowtail and witch were distributed over the range of sampled depths with centres of mass near the thermocline. It is possible that the dominant sampling above 40 m missed a significant number of older larvae and juveniles at depth and biased the centres of mass towards the surface. Some support for this comes from annual flatfish surveys conducted in September over the southern Grand Bank using bottom trawling gear which occasionally capture 0-group yellowtail and plaice as small as 2 cm standard length (S. J. Walsh, Department of Fisheries and Oceans, St. John's, Nfld., pers. comm.). On the other hand, the observed depth distributions, especially the high concentrations near the thermocline, may promote fast growth and high survival for those individuals occupying depths of maximum thermal gradients, as previously documented for fish larvae inhabiting oligotrophic lake systems (e.g. see Wurtsbaugh and Neverman 1988).

Comparison of spawning sites inferred from the observed distributions and measured currents with historical concentrations of mature fishes provides some support for the hypothesis of passive advection in some but not all cases, and then only with significant provisos. For two of the three years sampled (1987, 1988), the yellowtail distributions were consistent with passive advection from a Southeast Shoal spawning site provided that the survivors drift in the lower water column and the growth rate is near the maximum value considered (0.25 mm/d). The spawning times inferred from this growth rate approximate historical descriptions, and the bottom temperatures observed in the vicinity of the inferred spawning locations and times are consistent with reported temperature preferences of adult yellowtail. However, the 1986 inferred spawning site for yellowtail was implausible. This may have been due to increased spatial structure in the lower-layer drift. Observations of yellowtail egg and early-stage larval distributions in other years (May–June 1983 (J. Anderson, Department of Fisheries and Oceans, St. John's, Nfld., pers. comm.), July 1985) sup-

port their persistence over the Shoal in summer as well as their occurrence to the northwest.

The observed plaice distributions in all three years suggest spawning along the northern or northeastern Grand Bank followed by southward advection in the Labrador Current. For plaice the current data are not adequate to discriminate between upper- and lower-layer drift. The historical spawning times for plaice are consistent with the slower growth rate considered (0.16 mm/d), and the historical sites imply slow rates of larval drift in the bankward portion of the Labrador Current.

For witch, there was little evidence that the 1988 distribution on the Shoal was consistent with historical spawning sites, although the possibility that they resulted from passive lower-layer drift from the Bank's eastern edge and a relatively slow growth rate could not be discounted. Among the three species studied, witch has the longest pelagic phase (up to 1 yr) (Scott and Scott 1988), suggesting that slow growth is a reasonable approximation. Indeed, the cooccurrence of yellowtail (historical spawning on the Bank) and witch (historical spawning on the sides of the Bank) larvae on the Bank in 1988 requires either earlier spawning for witch (and subsequent drift through the yellowtail spawning area) or dominant behavioural influences for one of the species.

While most of the above evidence in support of the passive advection scenario is inadequate to exclude the possibility that the distributions result from behavioural mechanisms which act to govern the observed larval and juvenile distributions, the observations on diel pattern of depth distribution provide little support for retention via diel vertical migration. The centres of mass for the nighttime distributions were only about 5 m deeper than those for the daytime distributions, and larval drift trajectories computed on the assumption of a diel migration between the observed time-varying currents (linearly interpolated from the moored measurements) were little different from those generated by assuming drift at the average depth of the centre of mass.

The observations point to significant interspecies and inter-annual variations in larval abundance and distribution, as well as persistent features within species from year to year. The plaice larvae were consistently associated with the relatively cool bottom water along the Bank's eastern edge. They were also more abundant in 1986 coincident with an increase in the distribution of cooler water on the Bank. These conditions arose from displacement of Labrador Current water onto the Bank in August 1986 during the most energetic (summertime) wind event of the three years. The associated increase in plaice abundance is consistent with the inferred advection of plaice southward along the bankward edge of the Labrador Current. Yellowtail distributions were qualitatively similar in the three years. However, witch distributions differed greatly, being more abundant in 1988 than in 1986 and 1987 without any unusual environmental conditions having been detected.

It appears that changes in spawning stock biomass can be dismissed as a cause for the large interannual differences in larval and juvenile densities. For yellowtail, research vessel surveys showed a decline in age 5+ abundance from 189 (millions) in 1986 to 168 and 98 and 1987 and 1988, respectively, while commercial catch rates indicated no change in stock status (Brodie et al. 1990b). In contrast, our larval surveys suggest the lowest densities during 1987 and approximately equal and much higher densities during 1986 and 1988. All indicators for plaice (research vessel surveys, catch rates, and sequential population models) indicate that there was no detectable change in

adult abundance between 1986 and 1988 (Brodie et al. 1990a). Results from research vessel surveys for adult witch are inconclusive because of incomplete coverage of the expected distribution of adults (Bowering 1990b). However, commercial catch rates show a decline of about 40% between 1986 and 1988 (Bowering 1990b). If catch rates in the witch fishery are indicative of stock biomass, this implies a significant decline during this period, a result which contrasts with our ichthyoplankton surveys which yielded much higher catches of witch in 1988.

Overall, the larval distributions of plaice and yellowtail show similar patterns in the three years surveyed, apparently related to the bottom temperature variation across the southern Grand Bank. Although the mechanism underlying this temperature relation remains unclear, the available information on currents suggests that the distributions can be explained by passive advection, provided the larvae are in the lower water column and growth rates are close to maximum for yellowtail and close to minimum for plaice. Given the limited information available on vertical distributions of larvae and the horizontal structure of currents, it must be emphasized that this consistency does not exclude other scenarios requiring significant behaviour. The distribution of witch was not consistent in the three years (having a significant occurrence in only one year). There is more limited support for its distribution being consistent with passive advection, although it cannot be discounted.

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