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Temporal and spatial variability in growth and condition of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae in the Irish Sea

ORLA LEE,[1,2] BRET S. DANILOWICZ,[1,3]* AND MARK DICKEY-COLLAS[4]

[1]*Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland*
[2]*Department of Zoology, Trinity College, Dublin 2, Ireland*
[3]*Allen E Paulson College of Science and Technology, PO Box 8044, Statesboro, GA 30460-8044, USA*
[4]*Netherlands Institute for Fisheries Research (RIVO), PO Box 68, 1970 AB IJmuiden, The Netherlands*

ABSTRACT

Variability in the high mortality rate during early life stages is considered to be one of the principal determinants of year-class variability in fish stocks. The influence of water column stability on the spatial distribution of fish larvae and their prey is widely acknowledged. Water column stability may also impact growth through the early life history of fishes, and consequently alter the probability of survival to maturity by limiting susceptibility to predation and starvation. As a test of this concept, the variability in condition and growth of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae was investigated in relation to seasonal stratification of the water column in the north-western Irish Sea. RNA/DNA ratios and otolith microincrement analysis were used to estimate nutritional status and recent growth rates of larvae captured on four cruises in May and June of 1998 and 1999. Dab and sprat larvae were less abundant in 1999 and were in poorer condition with lower growth rates than in 1998. Dab larvae of <13 mm also exhibited spatial variability with higher RNA/DNA ratios at the seasonal tidal-mixing front compared with stratified and mixed water masses. However, the growth and nutritional status of sprat larvae was uncorrelated to water column stability, meaning the more favourable feeding conditions generally associated with the stratified pool and tidal-mixing front in the Irish Sea were not reflected in the growth and condition of these larvae. This suggests that the link between stability, production and larval growth is more complicated than inferred by some previous studies. The existence of spatio-temporal heterogeneity in the growth and condition of these larvae has implications for larval survival and the recruitment success of these species in the Irish Sea.

Key words: dab, Irish Sea, larvae, *Limanda limanda*, otoliths, RNA:DNA, sprat, *Sprattus sprattus*

INTRODUCTION

Variability in the high mortality rate during early life stages is considered to be one of the principal determinants of year-class variability in fish stocks (Heath, 1992). A rapid growth through the larval and juvenile stages should increase the probability of survival to maturity by limiting susceptibility to predation and starvation (Houde, 1997).

The distribution and growth of fish larvae have been shown to vary considerably both temporally and spatially due to a combination of biotic and abiotic factors. Several authors have recorded large differences in larval condition and growth on an interannual scale (Theilacker *et al.*, 1996; Amara and Galois, 2004) and between sampling dates within a year (Hovenkamp, 1990; Rilling and Houde, 1998; Amara and Galois, 2004). Significant spatial variability in growth and condition of fish larvae has also been shown to occur and this variability has often been linked to the presence of hydrographic features. The influence of water column stability on the spatial distribution of fish larvae and their prey is widely acknowledged (Munk *et al.*, 1995; Hays *et al.*, 2001), and a relationship between larval condition and stratification has been reported in a number of studies (Buckley and Lough, 1987; Munk, 1993; Nakata *et al.*, 1996).

Within the Irish Sea, a region of low tidal energy to the west of the Isle of Man results in the formation of thermally stratified waters from late spring through summer which are separated from mixed waters by

*Correspondence. e-mail: danilowicz@georgiasouthern.edu
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seasonal tidal mixing fronts, the western Irish Sea (WIS) fronts (Simpson and Hunter, 1974). Previous ichthyoplankton surveys have shown that the establishment of stratification in this region affects the distribution of fish larvae and their prey. Temporal variability in ichthyoplankton and zooplankton distribution has been linked to differences in the extent and duration of stratification on a seasonal and interannual scale (Scrope-Howe and Jones, 1985; Dickey-Collas *et al.*, 1997; Lee *et al.*, 2005). Dickey-Collas *et al.* (1996) suggested that fish larvae move offshore from coastal waters into the stratified water masses during the later stages of development where higher concentrations of larger prey items may be found. Several studies have recorded regional variation in feeding conditions for fish larvae in relation to water column stability with stratified waters of the WIS supporting a higher zooplankton biomass (Scrope-Howe and Jones, 1985) and allowing more efficient food transfer for fish larvae (Coombs *et al.*, 1994) than the coastal and mixed waters in the region. Based on these results, stratified (and frontal) waters would be expected to yield fish larvae in better nutritional condition and growing faster than those found in mixed water masses. However, the effect of wind- and tide-induced turbulence on the encounter rates between fish larvae and their prey was not considered in these investigations. Larval feeding and growth rates may be significantly increased by small-scale turbulence in mixed and frontal waters depending on wind and tidal velocities, prey density and distribution, and larval fish swimming speeds (MacKenzie, 2000).

Although extensive research has been carried out to examine feeding conditions for fish larvae within the WIS, few studies have investigated directly the spatial and temporal variability of larval growth and condition in this region. Hapette *et al.* (1991) examined the variation in nutritional condition (vitamin C content) of sprat (*Sprattus sprattus*) larvae along a transect in the Irish Sea. They found no significant differences in the vitamin C content per unit weight between larvae from stratified and mixed waters.

The spatial and temporal variability of recent growth rates and nutritional condition of dab (*Limanda limanda*) and sprat (*S. sprattus*) larvae in the northwestern Irish Sea were investigated in the current study. Dab and sprat larvae were chosen as target species as they are among the most widespread and abundant fish larvae in the Irish Sea (Conway *et al.*, 1997), with a similar diet and spawning distribution to other commercially important species (Russell, 1976). The principal objectives of the research were (i) to examine temporal variability in growth and condition of sprat and dab larvae and (ii) to compare larval growth and condition in stratified, frontal, and mixed waters.

MATERIALS AND METHODS

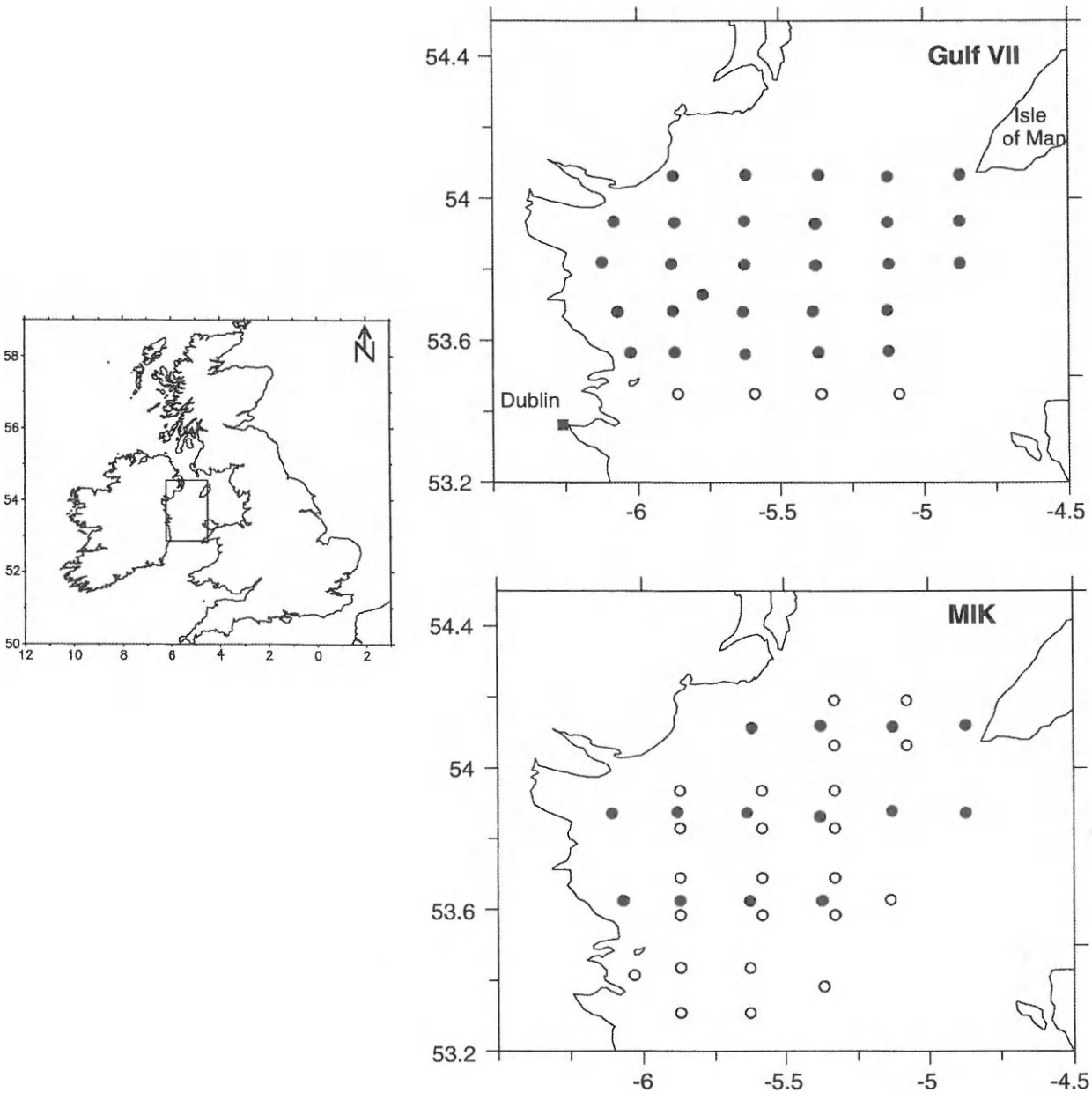
Field investigations

Dab (*L. limanda*) and sprat (*S. sprattus*) larvae were collected in the north-western Irish Sea from the *RV Lough Foyle* during four sampling cruises conducted in May–June 1998 and 1999. A total of 42 stations were sampled from 18 to 21 May and from 8 to 10 June in 1998, while in 1999 (24–27 May and 14–16 June), this grid was re-sampled along with several additional stations (Fig. 1). Ichthyoplankton sampling was conducted throughout the day and night. During daylight tows, a 70-cm Gulf VII high-speed plankton sampler (SPARTEL, Devon, UK) (Nash *et al.*, 1998) with a mesh size of 280 μm was deployed at 3–4 knots (1 knot = $\sim$1 m s^{-1}) in a double oblique tow from the sea surface to 2 m above the seabed. An estimate of the volume of water filtered was obtained using Valeport internal and external flowmeters (Valeport Ltd, Devon, UK). At night, a 5 m^2 Methot-Isaacs-Kidd (MIK) frame net with a mesh size of 5 mm was used to capture larger larvae. This net was fitted with a mechanical flowmeter and was deployed at three knots in a double oblique tow to 4 m above the seabed.

Upon recovery of the net, dab and sprat larvae were removed from the plankton sample and placed in labelled microtubes between blocks of dry ice (solid CO_2, melting point of −56°C). The time from sorting to freezing did not exceed 30 min, thus minimizing the activity of RNAses and DNAses within the larval tissue. Larvae that had stopped moving were assumed to be dead.

Temperature and salinity values were averaged for 1-m intervals down through the water column using a Pronet sensor (SPARTEL, Devon, UK) deployed at Gulf VII sampling stations. A fluorometer (SeaTech Wetlabs, Philomath, OR, USA) was used to record fluorescence profiles as a proxy for chlorophyll *a* abundance (Gowen and Bloomfield, 1996). A stratification parameter (ϕ) was derived from vertical profiles of density according to the equation used in Simpson *et al.* (1979). The value of ϕ represents a measure of the amount of energy required to mix the water column and thus increases with increasing stratification. The limits defining mixed and stratified waters from Simpson *et al.* (1979) were followed where mixed waters: $\phi < 10$ J m^{-3}; frontal waters: 10 J m^{-3} $\leq \phi <$ 20 J m^{-3}; stratified waters: $\phi \geq 20$ J m^{-3}. Stratification values were interpolated for

Figure 1. Gulf VII and MIK sampling stations in the Irish Sea in May–June 1998 and 1999. Filled circles represent stations sampled in both 1998 and 1999 while stations added to the sampling grid in 1999 are shown as empty circles.



MIK stations using Sigma Plot 5.0 (Systat Software Ltd, London, UK).

Laboratory analysis

The microtubes containing dab and sprat larvae were transferred from dry ice to a −80°C freezer back at the laboratory. The abundance of larvae of each species was estimated for each station from the volume of water filtered and water depth. Standard lengths of dab and sprat larvae were adjusted for shrinkage due to preservation on dry ice according to Lee (2002). Nucleic acid analysis was carried out on all dab and sprat larvae collected while a representative subset of these larvae from each water mass (mixed, frontal and stratified), over the entire size range, was chosen for otolith microincrement investigations.

RNA/DNA ratios have been used to determine the nutritional condition of fish larvae in numerous studies (e.g. Ferron and Leggett, 1994). The homogenization of fish larvae and the fluorimetric determination of

nucleic acid concentrations were carried out as described by Clemmesen (1993), except for the exclusion of the phenol-chloroform-isoamylalcohol purification from the nucleic acid extraction procedure based on the results of optimization studies (Lee, 2002) and on the recommendations of Grémare and Vétion (1994).

For otolith analyses, both sagittae and lapilli were dissected from dab larvae and were mounted convex side up in clear nail polish. The lapillus was chosen for analysis over the sagitta for several reasons. Sagittae in dab larvae have many accessory primordia and subdaily increments which make accurate increment measurements difficult. In contrast, the outer microincrements on dab lapilli were generally clear and could be analysed without further preparation or grinding of the otolith (Fig. 2a).

The use of otolith microincrement analysis is based on the assumption that the increments are formed at a rate of one per day. Although daily increment deposition has not been validated for dab otoliths, the deposition of daily growth rings has already been proved for several other pleuronectid species, such as plaice *Pleuronectes platessa* (Karakiri and von Westernhagen, 1989) and winter flounder, *Pseudopleuronectes americanus* (Sogard and Able, 1992). A good linear relationship between lapillus radius and standard length exists for dab larvae in the Irish Sea, making it suitable as an estimate of somatic growth (Fig. 3a). Therefore, the growth rate of individual larvae was estimated by back-calculation from otolith microincrement widths.

Lapilli were examined under oil immersion at ×1000 magnification through an Olympus compound microscope (Olympus America, Inc., Melville, NY, USA) attached to an image analysis system (Optimas 6.1, Media Cybernetics, Inc., Silverspring, MD, USA). The maximum radius was measured and the radius of

Figure 2. Dab (*Limanda limanda*) lapillus showing (a) microincrements clearly visible on outer edge of otolith and (b) position of nucleus and hatch check.

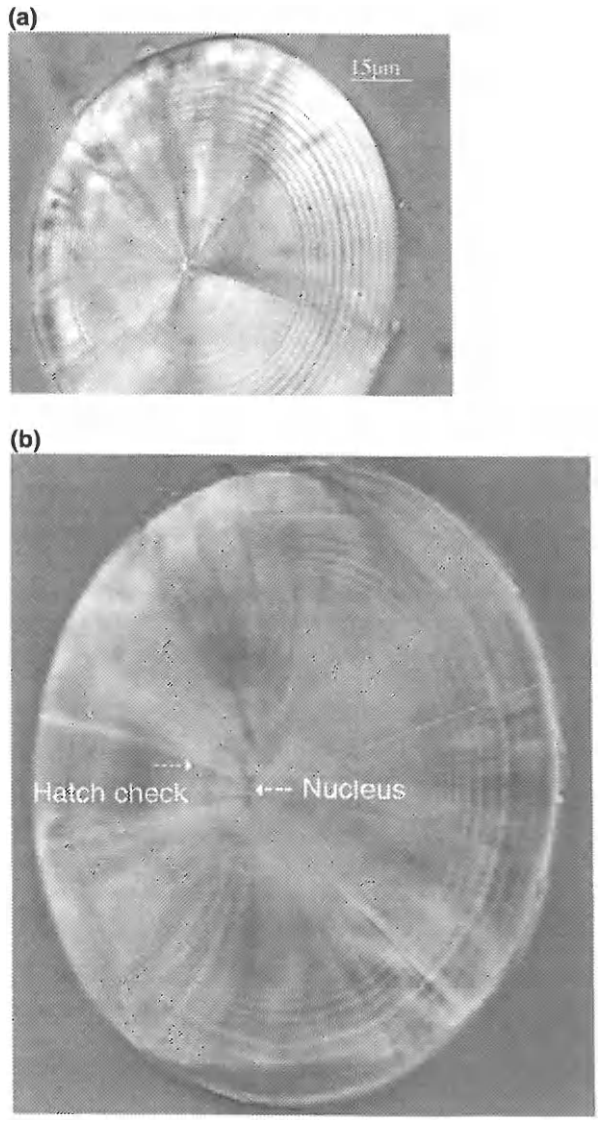
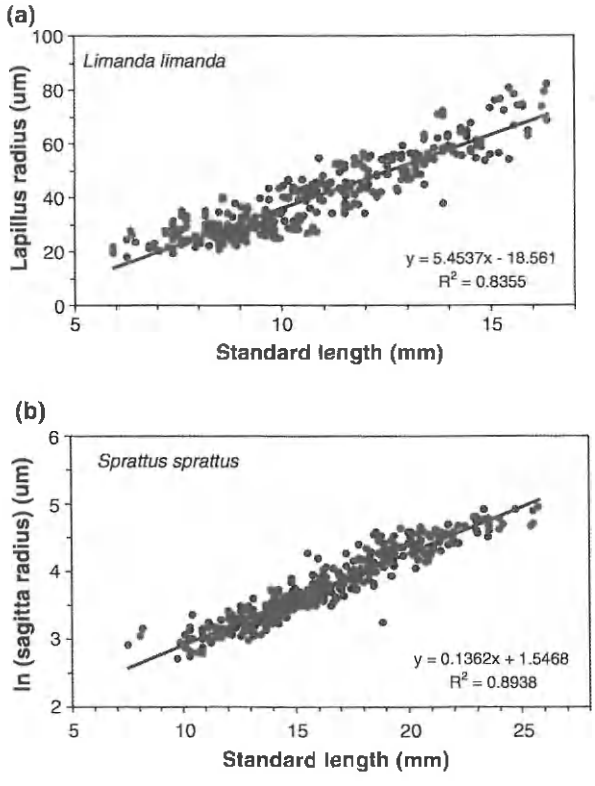


Figure 3. Relationship between otolith radius and standard length for (a) dab (*Limanda limanda*) and (b) sprat (*Sprattus sprattus*) larvae in the Irish Sea.



the hatch check along the longest axis was recorded. The widths of the outer increments, omitting the incomplete outermost increment, were also measured along the longest axis. Otoliths were excluded from the analysis when the increment widths could not be accurately measured due to unclear microstructure (26 of 281 otoliths). To prevent any bias due to potential differences between right- and left-side otoliths, left lapilli were consistently analysed. In the few instances where the left otolith was unreadable, the right otolith was analysed (nine of 255 otoliths) – the relationship between radius of right lapilli and standard length was not significantly different from that measured for the left lapilli (ANCOVA, $P = 0.341$) for the size range of larvae used within this study.

The biological intercept method (Campana, 1990) was used to back-calculate the length of dab larvae 3 days prior to capture and the recent growth rate of individual larvae (mm day^{-1}) was estimated. The lapilli of dab larvae have a check positioned close to the core (Fig. 2b) which was assumed to represent the otolith size at hatch as a similar hatch check has been recorded in other flatfish species (Al-Hossaini *et al.*, 1989; Lagardère, 1989) as well as numerous other species (Campana, 1989). The fish length at hatch (2.7 mm from Russell, 1976) was used, along with otolith size at hatch, as the biological intercept.

The sagittal otoliths were used for microincrement determinations in sprat larvae as they showed clear daily rings and core and did not require grinding prior to analysis. To prevent any bias due to potential differences between right- and left-side otoliths, the right otoliths were consistently analysed as far as possible. In the few instances where the right otolith was unreadable or was not obtained, the left otolith was examined (14 of 357 otoliths) – the relationship between radius of left sagittae and standard length was not significantly different from that measured for the right sagittae (ANCOVA; $P = 0.125$). Otoliths with unclear microstructure were omitted from the analysis (four of 360 otoliths).

The methods used for mounting and measuring the sprat sagittae were identical to those used for the dab lapilli. The biological intercept method was also used to back-calculate the length of sprat larvae. However, due to the slightly curvilinear relationship which existed between sagittal radius and standard length for sprat larvae, it was necessary to log-transform otolith measurements prior to back-calculating previous lengths (Fig. 3b). A similar relationship between otolith radius and age/length has been shown for sprat larvae in previous studies (Ré and Gonçalves, 1993; Dulčić, 1998). The deposition of the first daily growth ring in sprat larvae has been shown to occur 6 days after hatching at the onset of exogenous feeding (Alshuth, 1988). Therefore, the fish length and otolith size at first-feeding (5.5 mm, Russell, 1976) was used as the biological intercept. As daily increment formation has been validated for sprat larvae (Alshuth, 1988), it was possible to age larvae in the current study by counting the number of rings from the first feeding check to the outer edge of the sagitta.

Data analysis

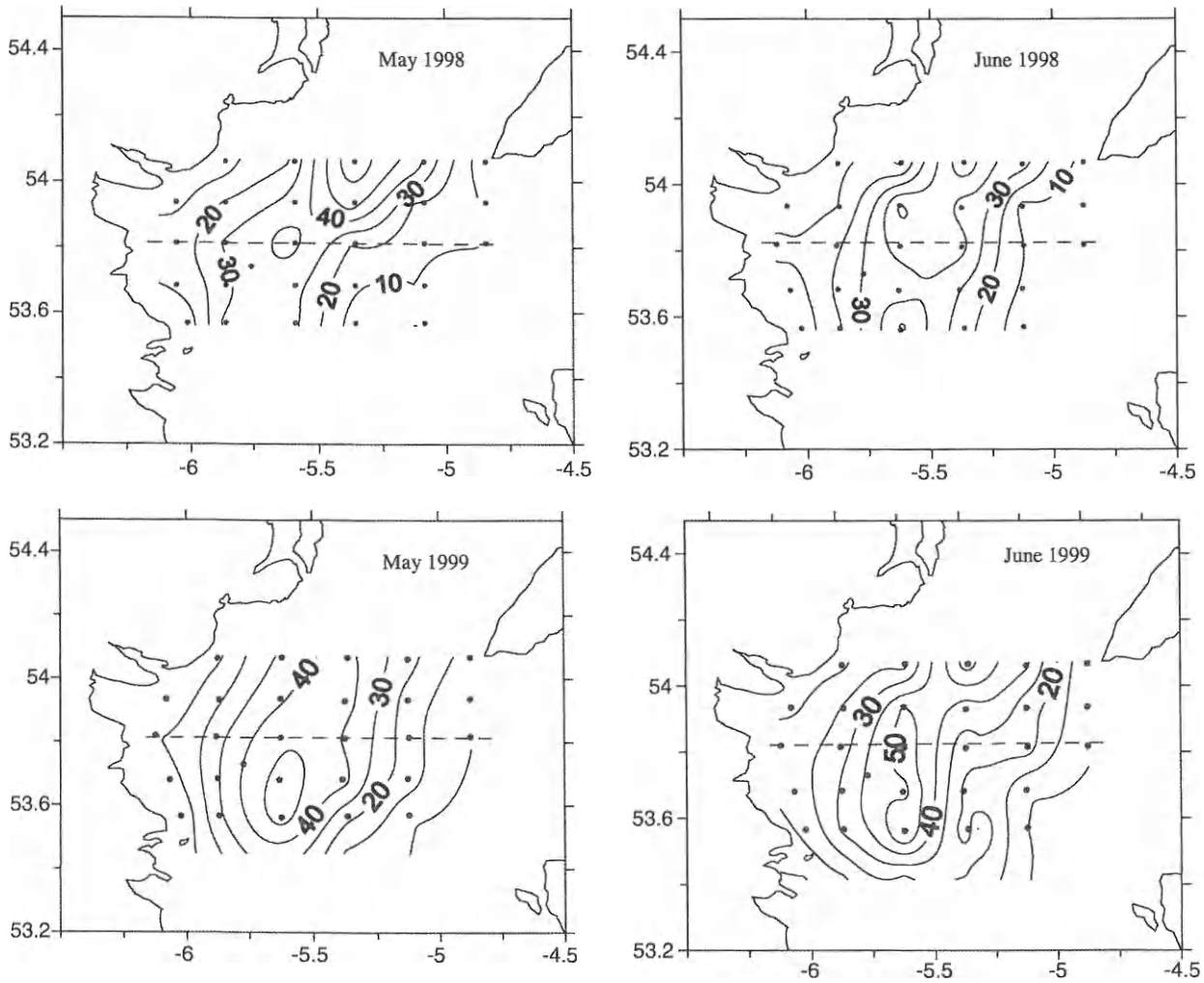
Contour maps were plotted by kriging the data using Surfer 7.0 (Golden Software Inc., Golden, CO, USA). Data were tested for normality and homogeneity of variances prior to analysis and log transformations were carried out as required. Any outliers detected were winsorised to the next highest value or removed from the analysis (one outlier winsorised and one removed in dab data set, three outliers winsorised in sprat data set). Pearson's product–moment correlation was used (with Bonferroni-adjusted probabilities for multiple comparisons) to test for significant correlations between continuous environmental parameters and larval abundance, growth and condition for the Gulf VII samples. However, such analyses will be limited by the sampling techniques used. Vertical samples were not taken down through the water column; therefore, the depth at which the larvae were located and, hence, the exact environmental conditions they were experiencing are unknown. The effect of categorical variables (stratification, date of sampling and other covariables) on RNA/DNA ratios and recent growth estimates was tested using analysis of variance (ANOVA) or analysis of covariance (ANCOVA) with standard length or age as a covariate. Both continuous and categorical factors were treated as independent variables and were examined one at a time. All significant factors were then included into a general linear model (complete estimate GLM) initially and their significance was re-assessed – variables with low partial effects (P-values <0.150) were excluded from the final GLM.

RESULTS

Hydrography

The pattern of water column stratification within the sampling grid was closely linked to the bathymetry of the region with highest values recorded in the deeper waters (Fig. 4). Values of the stratification parameter (ϕ) observed within the study area did not vary significantly among cruises (ANOVA, $P = 0.902$),

Figure 4. Distribution of the stratification parameter, ϕ, in the Irish Sea in May–June 1998 and 1999 (contoured at intervals of 10 J m^{-3}). Gulf VII sampling stations are represented by black circles and the position of the transect of stations at 53.8° latitude is shown using a dashed line.



though higher values were observed within stratified waters in 1999 than in 1998 and in June than in May. Surface temperatures recorded within the study area ranged from 9.6 to 13.4°C and were significantly higher in 1999 than in 1998 (ANOVA, $P = 0.027$) and in June than in May of each year (ANOVA, $P < 0.001$). Average chlorophyll *a* concentrations were significantly lower in 1999 than in 1998 (ANOVA, $P = 0.044$). Variability in chlorophyll *a* concentrations was not closely linked to the distribution of the stratification parameter except in June 1999 when higher concentrations were recorded in the surface waters of the front than in stratified waters (ANOVA, $P < 0.001$, frontal versus stratified).

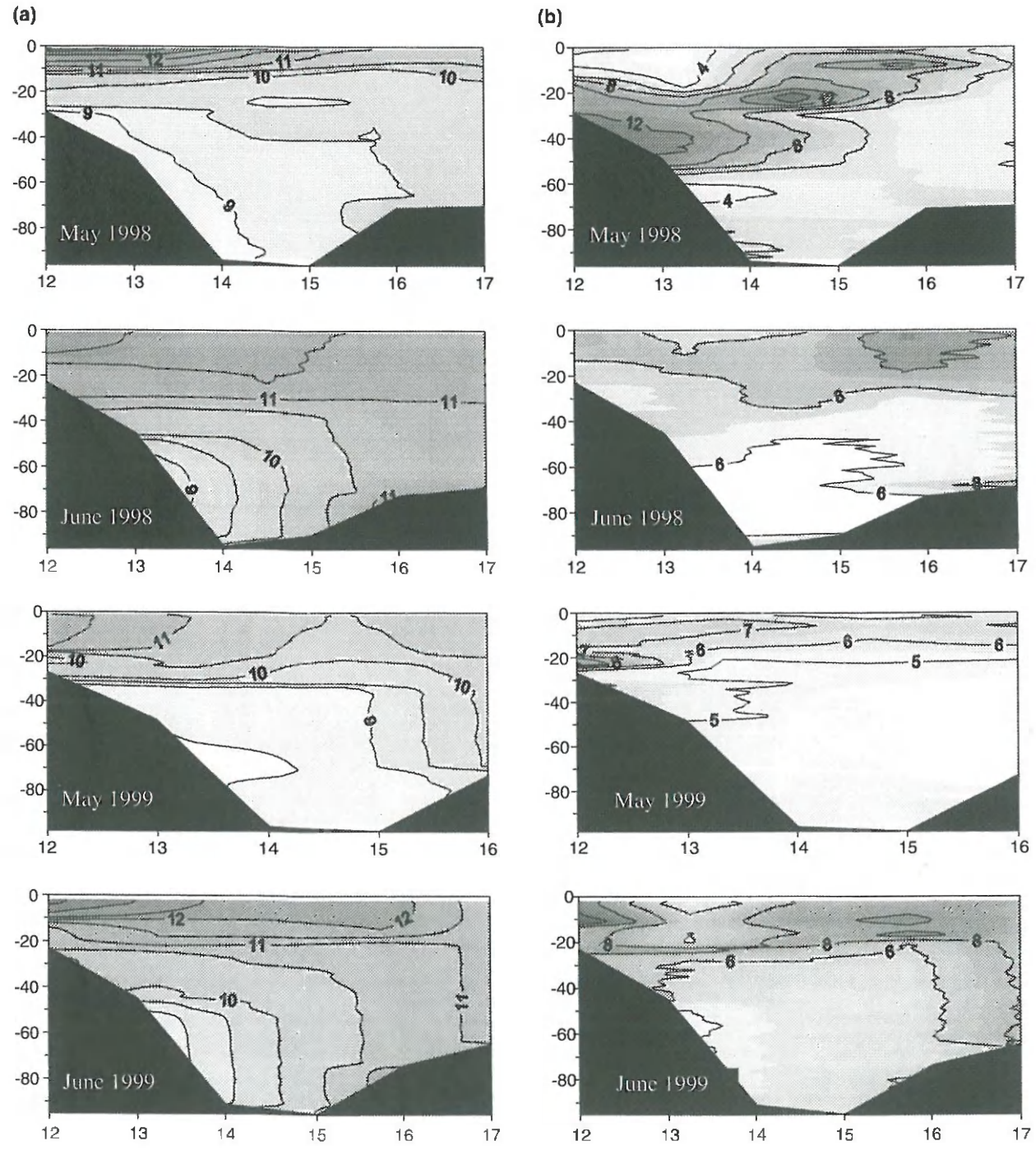
Stratification of the water column resulted from temperature differences of up to 4°C between surface and bottom waters (Fig. 5a). The depth of the thermocline varied between stations but was generally recorded between 10 and 30 m on all sampling dates. Chlorophyll *a* concentrations generally peaked at approximately 10 m but high concentrations extended down to 30 m at some stations (Fig. 5b).

Wind speeds were relatively low during all cruises (Fig. 6) particularly in May 1998 (mean = 5.4 knots, SD = 3.1) and June 1999 (mean = 7.9 knots, SD = 3.5). Average values in May 1999 and June 1998 were slightly higher at 12.3 knots (SD = 5.1) and 11.3 knots (SD = 3.5) respectively. There were no major storm events during the sampling period.

Abundance and distribution of dab

A total of 511 dab (*L. limanda*) larvae were collected in the north-western Irish Sea in May–June 1998 and 1999 (Table 1). The abundance of dab larvae was

Figure 5. Vertical (a) temperature (°C) and (b) chlorophyll *a* profile (mg m^{-3}) profiles for a transect of stations in the Irish Sea (53.8° latitude) in May–June 1998 and 1999 (temperature contoured at 0.5°C and chlorophyll *a* contoured at 2.0 mg m^{-3} intervals apart from May 1998 which is contoured at 1.0 mg m^{-3}). The positions of the transect on each date are shown in Fig. 3 in relation to the pattern of water column stratification.



generally higher in 1998 than in 1999 (ANOVA, Gulf VII: $r^2 = 0.026$, $P = 0.077$; MIK: $r^2 = 0.052$, $P = 0.018$) and in May than in June (ANOVA, Gulf VII: $r^2 = 0.155$, $P < 0.001$, MIK: $r^2 = 0.074$, $P = 0.004$). The distribution of dab larvae was not significantly correlated to degree of stratification during any of the

Figure 6. Variation in wind speeds (knots) recorded in the Irish Sea 5 days before and during surveys in May–June 1998 and 1999 (Ronaldsway Airport, Isle of Man data). Average daily values are shown using black circles and maximum gusts are represented by white squares.

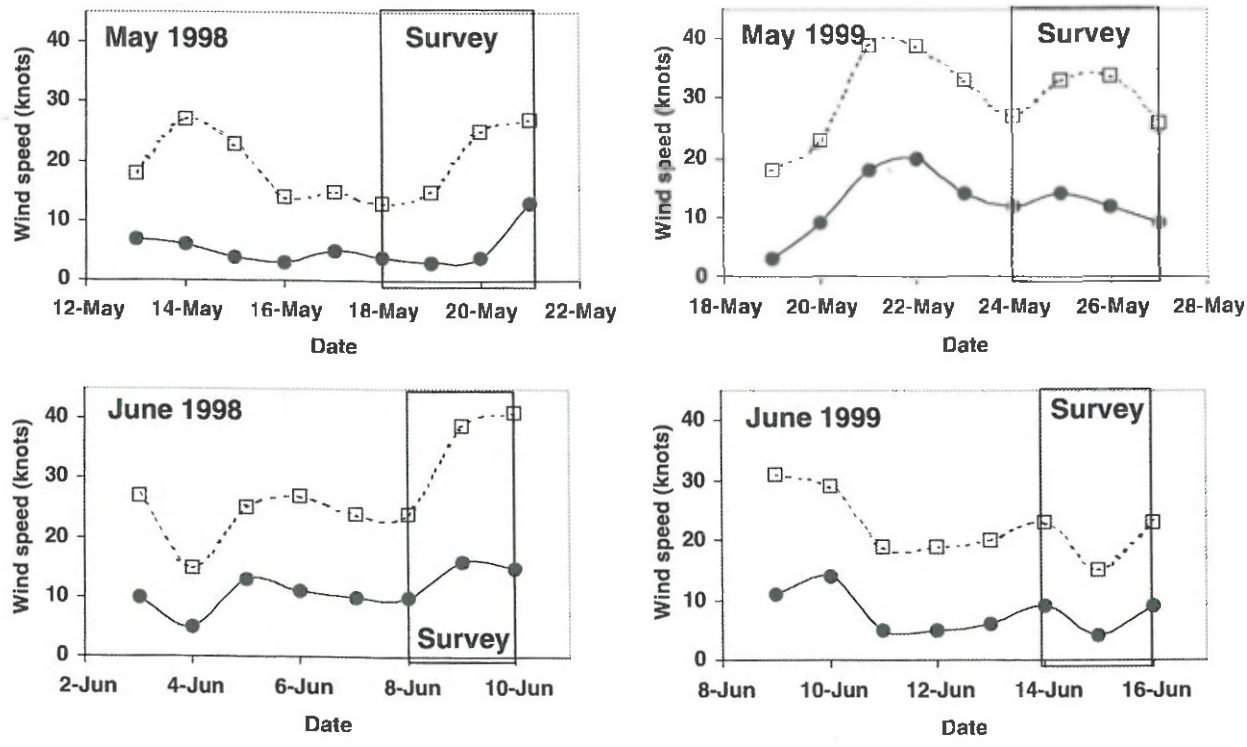


Table 1. Details of dab (*Limanda limanda*) and sprat (*Sprattus sprattus*) larvae collected using Gulf VII and MIK nets in the Irish Sea in May–June, 1998 and 1999.

Cruise	No. captured (n)		% Stations present	Max conc. (m^{-2})		Length (mm)	
	Gulf	MIK		Gulf	MIK	Gulf	MIK
Limanda limanda							
18–21 May 1998	77	142	66.7	24.2	1.0	4.7–13.4	8.8–16.4
8–10 June 1998	32	14	50.0	11.2	0.3	6.3–12.8	9.2–13.2
24–27 May 1999	111	115	64.9	21.6	1.5	4.0–13.2	10.6–18.3
14–16 June 1999	10	9	34.2	3.6	0.1	5.8–11.5	10.3–17.9
Sprattus sprattus							
18–21 May 1998	125	50	85.7	26.8	0.5	5.8–27.0	13.1–26.8
8–10 June 1998	116	55	87.5	23.6	0.8	10.1–30.0	13.3–31.2
24–27 May 1999	113	26	60.8	14.7	1.0	9.0–24.2	17.6–28.5
14–16 June 1999	40	12	51.3	3.8	1.1	9.9–24.0	18.0–25.8

ichthyoplankton surveys. There was no significant correlation between larval concentration and measured environmental variables [depth, surface (at 5 m) and bottom temperature, salinity, and chlorophyll *a*].

Condition and growth of dab larvae

RNA/DNA ratios of dab larvae captured in the northwestern Irish Sea in May–June 1998 and 1999 were variable ranging from 1.7 to 18.8 (Fig. 7a). However, 76% of all larvae analysed had ratios in the range of 5–11. Nutritional condition increased with length up to approximately 11 mm when RNA/DNA ratios levelled off and began to decrease with increasing standard length after 13 mm (Fig. 7b). The growth rates of dab larvae collected ranged from 0.15 to 0.76 mm day^{-1} (Fig. 8a). Recent growth of dab

Figure 7. Relationship between (a) RNA/DNA ratios and standard length for dab (*Limanda limanda*) larvae collected in the Irish Sea in May–June, 1998 and 1999; (b) average RNA/DNA ratios (±SD) for each 1 mm length category between 5 and 17 mm (<11 mm: $y = 1.028x - 1.511$; 11–13 mm: $y = -0.004x + 10.204$; ≥13 mm: $y = -1.320x + 27.35$).

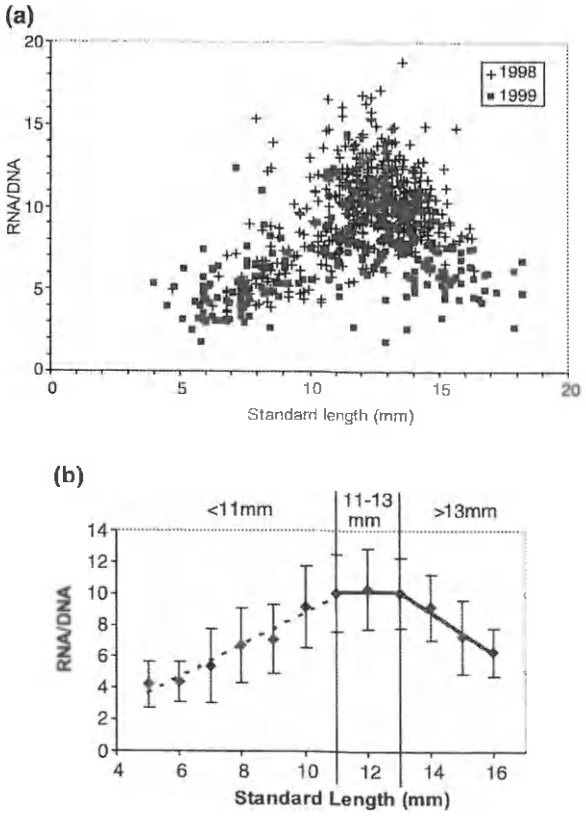
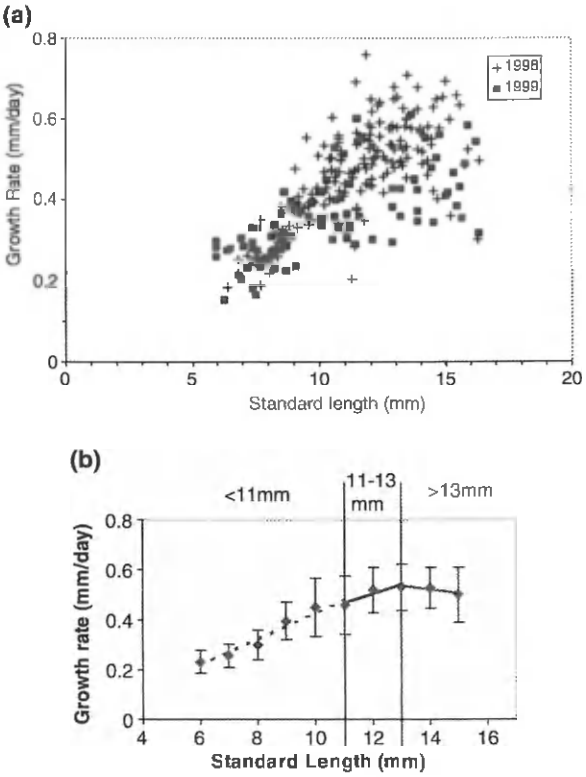


Figure 8. Relationship between (a) growth rates and standard length for dab (*Limanda limanda*) larvae collected in the Irish Sea in May–June, 1998 and 1999; (b) average growth rates (±SD) for each 1 mm length category between 6 and 16 mm (<11 mm: $y = 0.052x - 0.094$; 11–13 mm: $y = 0.036x + 0.076$; ≥13 mm: $y = -0.015x + 0.732$).



increased with increasing standard length up to 13 mm after which growth rates started to decrease as length continued to increase (Fig. 8b). As a result of this relationship between condition and growth of dab larvae with standard length, it was necessary to divide larvae into three separate length categories (<11, 11–13 and ≥13 mm) prior to further statistical analyses.

Factors affecting condition and growth of dab larvae are shown in Table 2. Several potential covariables were found to have no significant effect on RNA/DNA ratios and recent growth rates. Dab larvae that were damaged upon capture did not have lower RNA/DNA ratios than undamaged larvae. The effect of using the right lapillus (when left otolith unavailable) on estimated recent growth rate was also insignificant. Therefore, it was possible to exclude these variables from subsequent analyses. The effect of gear type (Gulf VII versus MIK nets) on RNA/DNA ratios was found to be insignificant for dab larvae in the mid-length category. It was not possible to accurately compare condition of larvae ≥13 mm from both net types as very few larvae were captured using the Gulf VII sampler (four of 158). These four larvae were omitted from further analyses. For dab larvae <11 mm, the effect of gear type and time of capture (i.e. day versus night) was significant – larvae caught using MIK nets had significantly higher growth rates and those caught at night time had higher RNA/DNA ratios and growth rates. As most larvae in this length category were captured during the day using the Gulf VII sampler, larvae caught in MIK nets at night time were omitted from further analyses (26 of 201 larvae). Dab larvae ≥13 mm had higher RNA/DNA ratios when caught live compared with those which were dead upon capture (live = 19, dead = 139), so live larvae were removed prior to analysis for compatibility with the remainder of the data set.

Dab larvae were in significantly better condition and were growing at a faster rate in 1998 than in 1999 (Figs 7a and 8a). Monthly variability in condition and

Table 2. Relation of factors to RNA/DNA ratios and recent growth rates of dab (*Limanda limanda*) in the Irish Sea in 1998–1999.

	Small <11mm		Medium 11–13mm		Large ≥13mm	
	$\log_{10}$ RNA/DNA	Growth	RNA/DNA	Growth	RNA/DNA	Growth
N	201	125	143	70	158	60
Length	$r = 0.639$, $P \leq 0.001$	$r = 0.802$, $P \leq 0.001$	$r = 0.018$, n.s.	$r = 0.353$, $P \leq 0.001$	$r = -0.534$, $P \leq 0.001$	$r = -0.281$, $P = 0.030$
Depth	$r = 0.044$, n.s.	$r = 0.090$, n.s.	$r = -0.259$, $P = 0.002$	$r = -0.371$, $P = 0.002$	$r = -0.209$, $P = 0.009$	$r = -0.187$, n.s.
Year	$P = 0.013$	$P = 0.078$	$P \leq 0.001$	$P = 0.003$	$P \leq 0.001$	$P \leq 0.001$
Month	$P \leq 0.001$	$P = 0.204$, n.s.	$P \leq 0.001$	$P \leq 0.001$	N/A	N/A
Stratification	$P = 0.069$, $f > m \approx s$	$P = 0.897$, n.s.	$P = 0.035$, $f > m > s$	$P = 0.080$, $m \approx f > s$	$P = 0.759$[a], n.s.	$P = 0.620$[a], n.s.
Day/night	$P = 0.049$, night > day	$P \leq 0.001$, night > day	$P = 0.349$, n.s.	$P = 0.738$, n.s.	$P = 0.314$, n.s.	$P = 0.553$, n.s.
Live/dead	$P = 0.766$, n.s.	N/A	$P = 0.186$, n.s.	N/A	$P \leq 0.001$, live > dead	N/A
Net	$P = 0.096$, MIK > Gulf	$P \leq 0.001$, MIK > Gulf	$P = 0.702$, n.s.	$P = 0.555$, n.s.	$P = 0.023$, Gulf > MIK	$P = 0.195$, n.s.
Damaged/undamaged	$P = 0.493$, n.s.	N/A	$P = 0.709$, n.s.	N/A	$P = 0.918$, n.s.	N/A
Left/right	N/A	$P = 0.772$, n.s.	N/A	All left otoliths	N/A	$P = 0.978$, n.s.

[a]Effect of stratification tested on larvae collected in 1998 only.
Relationship between continuous variables was investigated using Pearson's correlation. Effect of categorical variables was tested using ANCOVA (with length as a covariate) in all cases where RNA/DNA ratios and growth rates were significantly correlated with length. When length was not significant ANOVA was used (i.e. for RNA/DNA ratios of 11–13 mm larvae). *n*, number of larvae analysed (stratification parameter values were not interpolated for all MIK stations, therefore numbers of larvae analysed for stratification was lower, see Table 3); n.s., not significant; N/A not applicable; m, mixed waters; *f*, frontal waters; s, stratified waters.

growth of dab larvae differed with length category and year of sampling. When significant monthly variability was present, RNA/DNA ratios and growth rates of dab larvae were higher in May than in June 1998, while in 1999 this pattern was reversed with growth and condition of larvae higher in June than in May. However, no significant yearly or monthly differences were found for growth rates of dab larvae <11 mm. Because of insufficient numbers of larger larvae collected in June it was not possible to reliably test monthly variability in the largest length category (≥13 mm).

RNA/DNA ratios were affected by stratification in the medium length category (11–13 mm) where larvae were in significantly better condition in the frontal waters than in the stratified and mixed water masses (Table 3). Although dab larvae <11 mm were also in better condition at the front this difference was not statistically significant (ANCOVA, $P = 0.069$). Growth rates for larvae <13 mm were not statistically correlated to water column stability. In the large length category (≥13 mm) almost all larvae were collected from the stratified waters in 1999, therefore, it was not possible to test spatial variability for that year. In 1998, no significant relationship was found between water column stability and growth or condition of dab larvae ≥13 mm.

A significant negative correlation was observed between depth and growth and condition for larvae 11–13 mm and between depth and condition for larvae ≥13 mm. A positive correlation was observed between growth rates of dab, 11–13 mm, and bottom temperatures and bottom and average chlorophyll *a*. There was no significant effect of temperature or chlorophyll *a* on growth or condition of dab <11 mm in Gulf VII samples. It was not possible to test these relations for larvae ≥13 mm as very few larvae were caught using the Gulf VII sampler in this length category.

Table 4 shows the factors included in the final general linear model used to explain the variability in condition and growth of dab larvae for each of the length categories. The variance explained ranged from 26% to 55% for RNA/DNA ratios and from 31% to 44% for recent growth rates. In general, standard length was included as a covariate to account for significant variation in both indices with larval size. Temporal (interannual and monthly) differences in growth and condition also accounted for a large proportion of the explained variability. The relative importance of each of these factors varied between length categories and differed with growth index used (RNA/DNA ratios or recent growth rate).

	Small <11 mm	Medium 11–13 mm	Large ≥13 mm
	$\log_{10}$ RNA/DNA	RNA/DNA	RNA/DNA
Mixed	6.19 ± 2.26 (33)	10.50 ± 2.79 (21)	10.13 ± 1.13 (16)
Frontal	7.42 ± 2.91 (33)	11.65 ± 2.59 (10)	9.56 ± 1.72 (5)
Stratified	6.33 ± 2.91 (131)	9.63 ± 2.51 (94)	9.98 ± 1.72 (51)
	Growth rate		
Mixed	0.332 ± 0.095 (29)	0.520 ± 0.101 (21)	0.551 ± 0.074 (15)
Frontal	0.363 ± 0.104 (26)	0.529 ± 0.090 (10)	0.515 ± 0.144 (4)
Stratified	0.348 ± 0.101 (70)	0.462 ± 0.112 (39)	0.563 ± 0.068 (18)

Table 3. RNA/DNA ratios and growth rates (mean ± SD) of *Limanda limanda* larvae in mixed, frontal and stratified waters in the Irish Sea in May–June 1998 and 1999 (the number of larvae analysed for each water mass is given in parentheses).

Table 4. Significance levels of independent factors included in general linear models (GLMs) for dab (*Limanda limanda*) larvae in the Irish Sea in May–June 1998 and 1999 with RNA/DNA ratios and growth rates as dependent variables. Factors with significance values >0.15 were excluded from the models.

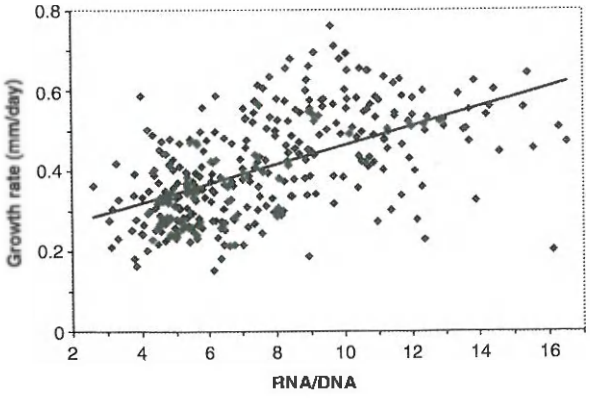
	Small (<11 mm)		Medium (11–13 mm)		Large (≥13 mm)	
	$\log_{10}$ RNA/DNA	Growth	RNA/DNA	Growth	RNA/DNA	Growth
N	175	108	143	70	137	49
r^2	0.395	–	0.261	0.442	0.546	0.314
Length (P)	≤0.001	≤0.001 $r = 0.774$	–	0.039	≤0.001	–
Year (P)	0.067	–	≤0.001	0.075	≤0.001	≤0.001
Month (P)	0.011	–	–	0.005	–	–
Depth (P)	–	–	0.056	0.030		
Stratification (P)	0.105	–	–	–	–	–

There was a highly significant positive correlation between RNA/DNA ratios and recent growth rates measured for individual dab larvae (Fig. 9; $r = 0.557$, $P < 0.001$).

Abundance and distribution of sprat

A total of 537 sprat (*S. sprattus*) larvae were collected in the north-western Irish Sea in May–June 1998 and 1999 (Table 1). The abundance of sprat larvae collected using the Gulf VII sampler was significantly higher in 1998 than in 1999 (ANOVA, $r^2 = 0.167$, $P < 0.001$) and in May than in June ($r^2 = 0.032$, $P < 0.001$). Concentrations of larvae captured using the MIK net did not exhibit significant interannual or monthly variability. Sprat larvae showed a patchy distribution within the sampling grid, and larval concentrations were not significantly different between mixed, frontal, and stratified water masses. The distribution of sprat larvae was not correlated with measured environmental variables during any of the ichthyoplankton surveys [depth, surface (at 5 m) and bottom temperature, salinity, and chlorophyll *a*]. A significant positive correlation was observed between the concentration of sprat and dab larvae collected in the Gulf VII samples ($r = 0.385$, $P < 0.001$).

Figure 9. Regression of recent growth rates on RNA/DNA ratios measured for individual dab (*Limanda limanda*) larvae captured in the Irish Sea in May–June 1998 and 1999 ($y = 0.024x + 0.225$; $r = 0.557$, $P < 0.001$).



There was a strong positive correlation between standard length and number of daily microincrements (Fig. 10, $r = 0.856$; $P < 0.001$). Standard length increased steadily with age up to approximately 46 days (40 microincrements) and then levelled off as age continued to increase. The average daily growth rate of sprat larvae with 0–40 daily rings was calculated to

Figure 10. Relationship between number of sagittal daily increments and standard length of sprat (*Sprattus sprattus*) larvae from the Irish Sea (<40 rings: 1998, $y = 0.432x + 6.590$, $r = 0.904$; 1999, $y = 0.300x + 8.887$, $r = 0.822$).

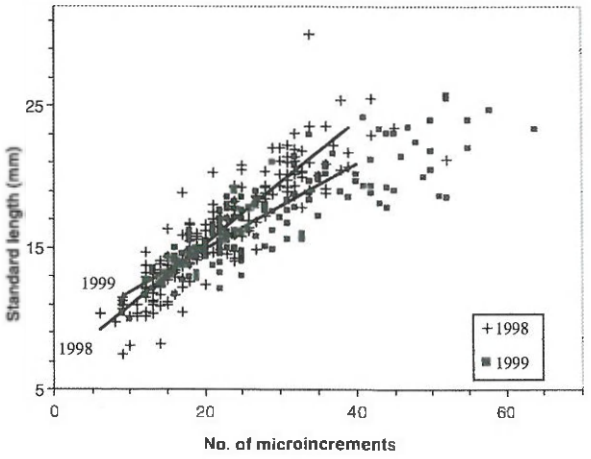
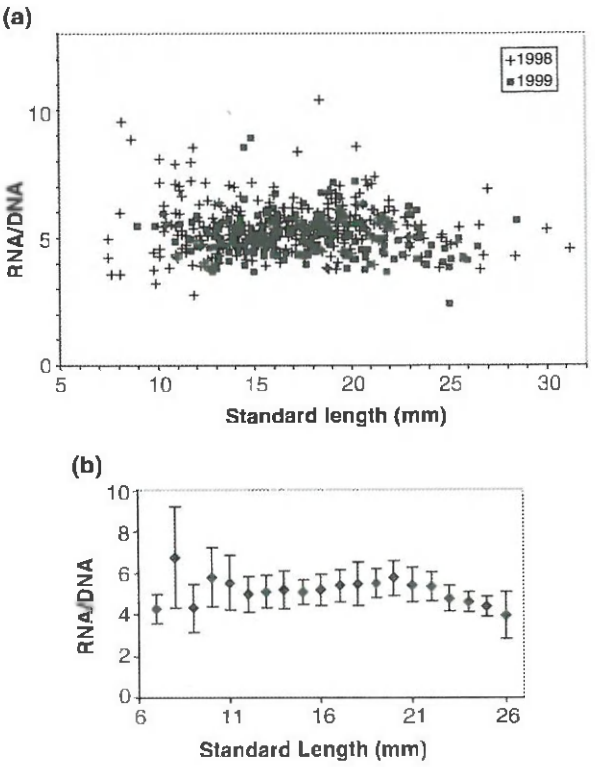


Figure 11. Relationship between (a) RNA/DNA ratios and standard length for sprat (*Sprattus sprattus*) larvae collected in the Irish Sea in May–June, 1998 and 1999 and (b) average RNA/DNA ratios (±SD) for each 1 mm length category between 7 and 27 mm.



be 0.382 mm day^{-1}. Larvae captured using the Gulf VII sampler ranged from 12 to 70 days while those collected in the MIK nets were aged between 34 and 64 days.

Condition and growth of sprat larvae

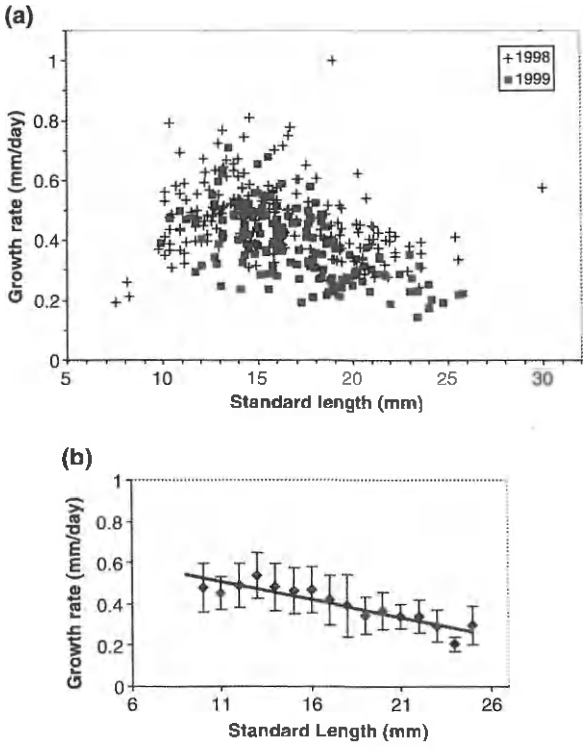
The RNA/DNA ratios of sprat larvae captured in the north-western Irish Sea in May–June 1998 and 1999 were relatively variable ranging from 2.4 to 10.4 (Fig. 11a). However, 89% of all larvae analysed had ratios between 5 and 7. Recent growth rates of sprat larvae ranged from 0.14 to 1.00 mm day^{-1} (Fig. 12a). Nutritional condition was not related to larval age or standard length while recent growth rates decreased significantly with increasing age and length (Figs 11b and 12b respectively).

Factors affecting growth and condition of sprat larvae are shown in Table 5. Variables which did not exert a significant effect on RNA/DNA ratios (time of capture i.e. day versus night) and growth rate (left versus right otolith, time of capture) of sprat larvae were excluded from the GLM analysis. As almost all larvae were dead upon capture, larvae caught live (five of 530 larvae) were removed from the data set prior to analysis. There was no significant effect of net on the recent growth rates of sprat larvae but larvae collected using the Gulf VII sampler had significantly higher RNA/DNA ratios than those captured in the MIK nets. Undamaged sprat had higher RNA/DNA ratios than damaged larvae.

Sprat larvae showed significant interannual variation in nutritional condition and growth rates with higher values observed in 1998 than in 1999 (Figs 11a and 12a). This was reflected in length at age of larvae – larvae captured in 1998 were larger at a given age than those collected in 1999 (ANCOVA, $r^2 = 0.760$, $P < 0.001$; Fig. 10) with an average daily growth rate of 0.432 mm day^{-1} in 1998 compared with 0.300 mm day^{-1} in 1999 for sprat larvae <46 days old. The RNA/DNA ratios also showed significant monthly variation between May and June which was consistent with that observed for dab larvae 10–13 mm (1998: May > June, 1999: June > May). However, differences in condition from May to June were not reflected in the growth of sprat larvae which did not vary monthly. RNA/DNA ratios and recent growth rates of sprat larvae did not differ significantly between mixed, frontal, and stratified water masses on any of the sampling dates (Table 6).

A significant positive correlation was observed between larval growth and depth. The relationship between temperature and chlorophyll *a* and RNA/DNA ratios and growth rates did not show a consistent pattern and varied depending on condition index used

Figure 12. Relationship between (a) growth rates and standard length for sprat (*Sprattus sprattus*) larvae collected in the Irish Sea in May–June, 1998 and 1999; (b) average growth rates (±SD) for each 1 mm length category between 10 and 26 mm ($y = -0.017x + 0.701$).



and on where environmental measurements were taken (surface, bottom, or average values).

Table 7 shows the factors included in the final general linear model used to explain variability in condition and growth of sprat larvae in the northwestern Irish Sea. The variance explained for RNA/DNA ratios was very low at 7.6% and was attributed to differences due to year of sampling and net type. In contrast, 54% of the variability in growth rates could be explained by larval age, year of sampling, and depth. There was no significant correlation between nutritional condition and recent growth estimates measured for individual sprat larvae (Fig. 13; $r = 0.021$, $P = 0.689$).

DISCUSSION

Temporal variability in growth and condition

Yearly fluctuations in the distribution of dab and sprat larvae were recorded with lower concentrations of both species found in 1999 compared with 1998. Condition and growth of dab larvae ≥11 mm and all sprat larvae also showed significant interannual variability with higher RNA/DNA ratios and faster growth rates in 1998 than in 1999. Similar differences were also observed in dab larvae <11 mm but were not as significant. Interannual variations in condition and growth of ichthyoplankton has been widely recorded in the literature and has been attributed to differences

Table 5. Relation of factors to RNA/DNA ratios and recent growth rates of sprat (*Sprattus sprattus*) in the Irish Sea in 1998–99.

	$\log_{10}$ RNA/DNA	Growth
N	530	356
Age	$r = 0.012$, $P = 0.821$	$r = 0.802$, $P \leq 0.001$
Length	$r = -0.069$, $P = 0.114$	$r = -0.431$, $P \leq 0.001$
Depth	$r = -0.082$, $P = 0.058$	$r = 0.144$, $P \leq 0.001$
Year	$P \leq 0.001$	$P \leq 0.001$
Month	$P = 0.006$	$P = 0.089$.
Stratification	$P = 0.214$	$P = 0.213$
Day/night	$P = 0.535$	$P = 0.251$.
Live/dead	Live removed	Live removed
Net	$P \leq 0.001$, Gulf > MIK	$P = 0.742$
Damaged/undamaged	$P = 0.018$, undamaged > damaged	N/A
Left/right	N/A	$P = 0.996$

Relationship between continuous variables was investigated using Pearson's correlation. Effect of categorical variables was tested using ANOVA (for RNA/DNA) and ANCOVA using age as a covariate (for growth). *n*, number of larvae analysed (stratification parameter values were not interpolated for all MIK stations, therefore numbers of larvae analysed for stratification was lower, see Table 6); n.s., not significant; N/A, not applicable.

Table 6. RNA/DNA ratios and growth rates (mean ± SD) of *Sprattus sprattus* larvae in mixed, frontal and stratified waters in the Irish Sea in May–June 1998 and 1999 (the number of larvae analysed for each water mass is given in parentheses).

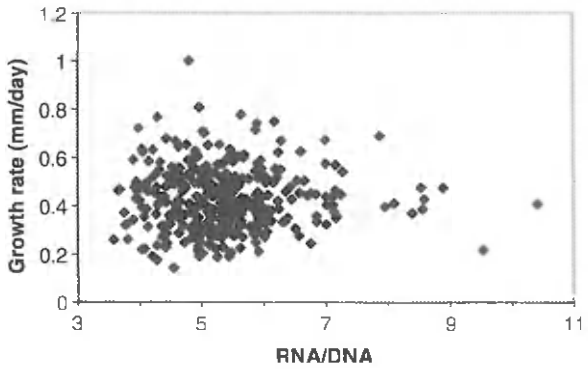
	$\log_{10}$ RNA/DNA	Growth rate
Mixed	5.17 ± 1.19 (149)	0.424 ± 0.118 (116)
Frontal	5.30 ± 1.13 (136)	0.427 ± 0.131 (103)
Stratified	5.32 ± 0.83 (225)	0.441 ± 0.134 (137)

Table 7. Significance levels of independent factors included in general linear models (GLMs) for sprat (*Sprattus sprattus*) larvae in the Irish Sea in May–June 1998 and 1999 with RNA/DNA ratios and growth rates as dependent variables.

	RNA/DNA	Growth
N	525	354
r^2	0.076	0.541
Age (*P*)	–	≤0.001
Year (*P*)	≤0.001	≤0.001
Depth (*P*)	–	≤0.001
Net (*P*)	≤0.001	–

Factors with significance values >0.15 were excluded from the models.

Figure 13. Regression of recent growth rates on RNA/DNA ratios measured for individual sprat (*Sprattus sprattus*) larvae captured in the Irish Sea in May–June 1998 and 1999.



in temperature and prey concentrations (Theilacker *et al.*, 1996). The interannual differences observed in the current study are most likely because of poor feeding conditions in 1999 compared with 1998. There were no significant differences in average temperature of the water column between years although the waters had a significantly higher surface temperature in 1999. The pattern of stratification was also quite similar in both years. In contrast, the average chlorophyll *a* concentrations (proxy of primary productivity) were found to be significantly lower in 1999 than 1998. Low primary productivity could ultimately affect secondary production (Gowen *et al.*, 1998) thus yielding larvae in poorer condition and growing at a slower rate. In an investigation modelling copepod egg production in the Irish Sea, Prestidge *et al.* (1995) concluded that the use of surface chlorophyll concentrations was a promising first approach to predicting copepod egg production. The WIS does exhibit annual differences in phytoplankton dominance (e.g. diatoms versus dinoflagellates, R.J. Gowen, pers. comm., Department of Agriculture, Northern Ireland, UK) and the dominance of copepod species (Nash and Geffen, 2004). In light of the results of the present study, an investigation of larval growth rates for years of contrasting food availability and quality would give a valuable insight into factors affecting larval survival and potentially recruitment variability. Interannual differences in condition may also be related to differences in predator concentrations – ctenophore densities were significantly higher in 1998 than in 1999 (M. Dickey-Collas, unpubl. data). A more comprehensive investigation of predator pressure would be necessary to fully assess their influence on larval condition.

In the present investigation, the average growth rate of sprat larvae captured in 1998 (0.432 mm day^{-1} for larvae with <40 daily rings) is similar to that recorded in previous studies. Shields (1989) found integrated somatic growth rates that varied from 0.37 to 0.49 mm day^{-1} for sprat (*S. sprattus*) larvae in the same age bracket in the Irish Sea. Ré and Gonçalves (1993) reported an integrated growth rate of 0.41 mm day^{-1} for sprat (*S. sprattus*) larvae with <40 daily rings in the German Bight of the North Sea. In contrast, in 1999, the average larval growth rate is significantly lower than in 1998 and at 0.30 mm day^{-1} is well below the ranges observed by Shields (1989) and Ré and Gonçalves (1993) for *S. sprattus*. These results support the hypothesis that these larvae are experiencing less favourable feeding conditions in that year.

Significant variability in growth and condition of larvae between sampling dates within each year was observed in the current investigation. Monthly variations were consistent for sprat and dab larvae of <13 mm with higher RNA/DNA ratios in May than in June 1998 and in June than in May 1999. Dab larvae 11–13 mm also showed a similar pattern for growth rates. Rilling and Houde (1998) recorded seasonal differences in condition of bay anchovy

(*Anchoa mitchilli*) larvae and attributed the variation to a combination of food availability and temperature differences. Water temperature has been shown to have a significant effect on otolith microincrement widths (Karakiri and von Westernhagen, 1989) and on RNA/DNA ratios (Buckley, 1984). Hovenkamp (1990) found that plaice (*Pleuronectes platessa*) larvae in the North Sea were growing faster on 22 March when compared with 8–9 March. He concluded that temperature differences were too small to explain this difference, and that temporary food limitation may have occurred. In the present investigation it is likely that the monthly variability in growth and condition of dab and sprat larvae may be primarily attributed to food availability. There was no clear relationship between larval condition and temperature. These properties are difficult to measure within the temporal and spatial scales that affect fish larvae (Dower *et al.*, 2002). As vertical sampling was not conducted in the present study, it is unclear where in the water column and under what environmental conditions (e.g. temperature) the larvae were residing.

It is possible that some monthly variation in larval condition may be related to wind-induced turbulence. Although average wind speeds did not reach storm levels during the surveys, dab and sprat larvae were in better condition in May 1998 when wind speeds were low compared with May 1999 when average wind speeds were higher. This would suggest that some environmental stability is required for good feeding conditions (Bergeron, 2000).

Spatial variability in growth and condition

Within the WIS, stratified waters have been associated with more favourable feeding conditions for fish larvae (Scrope-Howe and Jones, 1985; Coombs *et al.*, 1994; Dickey-Collas *et al.*, 1996). Therefore, larvae from stratified waters would be expected to be in better condition than those captured within the frontal and mixed waters. However, in the current study, seasonal stratification of the water column was found to vary in its effect on larval growth and condition. Dab larvae <13 mm in length were in better nutritional condition in the frontal waters than in the stratified and mixed water masses. In contrast, the degree of water column stability had no influence on the RNA/DNA ratios of sprat larvae in the northwestern Irish Sea.

Frontal structures have been shown to provide more favourable feeding conditions for fish larvae in a number of studies (Munk *et al.*, 1995; Hays *et al.*, 2001) yielding larvae in better condition and with higher growth rates. Nakata *et al.* (1996) recorded higher RNA/DNA ratios for Japanese sardine (*Sardinops melanostictus*) larvae in the Kuroshio frontal region than in the offshore waters. The growth of sprat (*S. sprattus*) larvae was found to be significantly related to distance from a tidal front in the North Sea with highest growth rates observed close to the frontal zone (Munk, 1993).

In the present investigation, dab larvae <13 mm were in better condition in the frontal zone than those found in the stratified or mixed waters. This may be because of improved feeding conditions associated with the tidal-mixing front. If this is the case, condition of dab larvae <13 mm is food limited, or influenced, and larvae must be located in frontal waters long enough to be distinguished from larvae in stratified waters based on their nutritional condition. Scrope-Howe and Jones (1985) recorded zooplankton maxima at the front on two occasions (July 1980 and May 1981) during their survey of the WIS, April 1980 to November 1981. As the copepod population within the frontal zone contained significantly higher numbers of nauplii than in adjacent waters, they attributed these higher zooplankton concentrations to increased copepod production rather than mechanical aggregation. It was not feasible to test growth and condition of dab ≥13 mm in 1999 in relation to water column stability as almost all larvae of this size were collected from the stratified waters. However, this distribution pattern implies that stratified waters provide a more favourable feeding environment for the larger dab larvae as they can survive here, or less likely, that they can actively select their habitat of choice.

There was no significant difference in growth or condition of sprat larvae between stratified, frontal, and mixed water masses. This contrasts with the results of Munk (1993) for sprat larvae in the eastern North Sea and also with the results for dab larvae <13 mm from the present investigation. Therefore, growth and condition of sprat larvae must be influenced by different factors in comparison with those affecting growth of dab larvae of that size. Dab and sprat larvae in the North Sea have been shown to have very similar diets dominated by the copepodites of *Pseudocalanus minutes*, *Temora longicornis* and *Oithona helgolandica* (Last, 1980). These results correspond with those recorded by Coombs *et al.* (1992) for sprat larvae in the Irish Sea. However, although they share similar feeding preferences, it is possible that sprat growth is not limited by food availability to the same extent as dab larvae (<13 mm). Hapette *et al.* (1991) found no significant differences in condition (vitamin C content per unit weight) of sprat larvae from stratified and mixed sites despite the presence of higher

prey concentrations in the stratified waters. Furthermore, research conducted on sprat larvae in the German Bight of the North Sea recorded no significant differences in growth rates in stratified and mixed sites (Ré and Gonçalves, 1993) and found no relationship between sprat larval condition and available food using lipid and elemental analysis (Håkanson *et al.*, 1994). If only small differences in suitable prey availability exist between the frontal zone and stratified and mixed waters, these may not be detected in the growth of sprat larvae. Although sprat have a similar diet to dab larvae, it is possible that they are more efficient foragers and cope well with interspecific competition. This could explain why the variability in dab growth in relation to the frontal zone is not observed in the growth of sprat larvae.

RNA/DNA ratios and otolith microincrement widths

This study gave an insight into the use of both RNA/DNA ratios and otolith microincrement widths as an index of condition and growth of dab and sprat larvae. Spatio-temporal patterns in larval condition identified using RNA/DNA ratios generally agreed with those found from recent growth rates. However, some inconsistencies did occur between condition and growth estimates. These differences are most likely due to the variability in latency periods for both indices and may identify periods of temporary starvation. RNA/DNA ratios reflect conditions over the previous day (Martin and Wright, 1987) while the last 3 days of growth were measured using otolith microincrement widths. In general, both indices appear to give a good indication of the nutritional status of both dab and sprat larvae. Laboratory studies on RNA/DNA ratios of dab and sprat larvae would improve their predictive capacity as a critical ratio could be determined to identify larvae prone to starvation. The relationship between RNA/DNA ratios and recent growth rate could also be clarified.

SUMMARY

The existence of consistent temporal variations in growth and condition of dab and sprat larvae within the Irish Sea was demonstrated in the current study. Both species showed similar patterns on an interannual and monthly scale. Such temporal variability in larval growth and condition has implications for the recruitment success of these species in the Irish Sea. The influence of water column stratification on larval growth and condition was found to be more complex than has been suggested in previous studies. Although dab larvae were in better condition in frontal waters, no significant differences in condition of sprat larvae was observed in relation to water column stability. Therefore, the more favourable feeding conditions associated with frontal and stratified waters in the Irish Sea are not necessarily reflected in improved nutritional status of fish larvae.

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