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Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship

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Abstract The significance of hatch date for the growth and survival of the sandeel, *Ammodytes marinus*, was investigated using otolith microstructure. Hatch dates of 2 to 6 mo-old juvenile *A. marinus* caught near Shetland were compared between 1990 and 1992, during which period year-class strength varied by more than an order of magnitude. The hatch-date distribution of juveniles in the 1992 year-class was compared with that estimated directly from the abundance of newly emerged larvae on the spawning grounds. The extent of larval hatching periods in 1990 and 1991 was also estimated from continuous plankton-recorder data. There were significant differences in hatching periods between all three years, hatching in 1990 and 1992 being markedly earlier than the long-term mean peak in hatching indicated from archival data. Most individuals from the 1991 year-class attained a larger size by July than those in other year-classes, despite hatching later. Variation in individual growth rates both within and between year-classes indicated that there was a seasonal cycle of growth opportunity in all years investigated. The study suggests that the degree of coupling between hatching and the onset of spring secondary production may be an important contributory factor to year-class variability in this species.

Introduction

The discrete timing of spawning and hatching in many temperate fishes is believed to be adaptive, reflecting the phase of the mean seasonal cycle of environmental conditions most favourable for egg and larval survival (Cushing 1975; Sinclair and Tremblay 1984; Cury and Roy 1989). Deviations in either the phase of the seasonal cycle or the timing of spawning and hatching are assumed to have consequences for the survival of the annual cohort of pre-recruits (Cushing 1975; Rothschild 1986). Hypotheses proposed to explain the need for precise timing of life-history events have emphasised the relative importance of temporal variability in either food-chain processes (Cushing 1975, 1990), predation pressure (Heath 1992), physical dispersive patterns of an area (Sinclair 1988) or the interaction between physical forcing and conditions favourable for larval growth (Cury and Roy 1989).

Asychrony between the time when larvae occur and favourable environmental conditions would be expected to lead to differences in the temporal distribution of hatch dates between surviving recruits and newly hatched larvae. Such a comparison of hatch-date compositions is possible through the analysis of daily otolith increments (Campana and Jones 1992). Applications of this technique to the northern anchovy *Engraulis mordax* (Methot 1983) and the Atlantic herring *Clupea harengus* (Moksness and Fossum 1992; Fossum and Moksness 1993) have demonstrated differences between the observed production schedule of newly hatched larvae and the subsequent surviving population. Early growth histories have also been investigated from otolith microstructure, and these together with hatch-date analyses may make it possible to examine how sources of mortality act, e.g. whether they are growth-dependent, size-specific, or dependent on the timing of certain physical or biological phenomena.

The present study forms part of an investigation into recent year-class variability in the lesser sandeel *Ammodytes marinus* and its effect on seabird populations around the Shetland Isles, UK. Surveys in this region found an order of magnitude variation in sandeel year-class strength during the period 1990 to 1992 (Wright 1996). This variability could only be explained

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by changes in early (egg to 6 mo post-hatch) survivorship as there was no parallel change in the size of the spawning stock (Anonymous 1994). In common with some other species of *Ammodytes*, *A. marinus* spawn demersal eggs in winter. The pelagic larvae hatch 1 to 3 mo later (Winslade 1971), often well in advance of the peak in plankton production (Macer 1965; Inoue et al. 1967; Sherman et al. 1984; Monteleone and Peterson 1986; Fortier et al. 1995). All winter-hatching sandeel species have larvae that are able to begin feeding prior to resorbing their large yolk-sacs (Yamashita and Aoyama 1986). These traits enable them to go without food for relatively long periods in relation to most other marine fish larvae (up to 20 d in *A. americanus*, Smigielski et al. 1984). Nevertheless, studies on winter-hatching *A. marinus* larvae in Hudson Bay have indicated that low prey availability at the time of hatching can lead to reduced growth (Fortier et al. 1995) or even a high mortality of first-feeding larvae (Gilbert et al. 1992). This would suggest that the degree of synchrony between hatching and prey production may be an important contributory factor to year-class variability in winter-hatching *A. marinus*.

The present study investigates the influence of variability in hatching time on the growth and mortality of *Ammodytes marinus*. Variability in the hatch date and growth rate of 2 to 6 mo-old juveniles from the 1990–1992 year-classes from Shetland waters was examined using otolith microstructure. Otolith increments are deposited daily from hatching in this species, and microstructural features provide a record of events in the life-history such as yolk-sac absorption and metamorphosis (Wright 1993). Data on juvenile hatch dates were compared with information on hatching periods derived either from a continuous plankton recorder (1990, 1991) or repeated larval surveys (1992).

Materials and methods

Study area

The study area was located near the south coast of Shetland, and included three spawning grounds previously identified by the presence of ripe adults and eggs of *Ammodytes marinus* in grab surveys (J. Gauld unpublished data; and present Fig. 1). The spawning grounds are in waters of < 50 m depth and within 1 to 2 km of the shore. These grounds also constitute the centres of sandeel distribution within this region (Wright 1996). The two southern grounds are influenced by a fast tidal race, known as the Sumburgh Røst, which flows around the southern tip of Shetland in an easterly or westerly direction. Owing to tidal mixing and the lack of thermal stratification from February to April (Turrell et al. 1991), there is little spatial variation in sea temperature near Shetland during this period. Temporal changes in sea temperatures around Shetland between February and April are typically < 2C°, with mean monthly temperatures ranging from 7 to 8°C (Turrell and Slesser unpublished data). Large-scale sea circulation in the Shetland–Orkney region is dominated by two features: the Fair Isle current, which flows between Orkney and Shetland; and the East Shetland inflow, which is generally a south-flowing current of Atlantic origin to the east of Shetland. During the February to May larval phase of *A. marinus*, the direction and strength of both these currents are largely wind-driven (Turrell et al. 1991). Model simulations of particle transport from around Shetland predict that advective losses of sandeel larvae from this region were between 10 and 40% for the period 1974 to 1990 (Berntsen et al. 1994). The presence of larvae at all stages of development, together with the early appearance of juveniles in the coastal waters of south Shetland suggest that recruitment to this region is initially from locally hatched larvae (Wright and Bailey unpublished data).

Hatching periods

Inter-annual variation in the timing of sandeel hatching was investigated using continuous plankton-recorder (CPR) data. Data from this survey are useful because sandeel larvae frequently concentrate near the surface, where the plankton sampler operates (Henderson 1961; Ryland 1964), and are therefore regularly sampled. Monthly

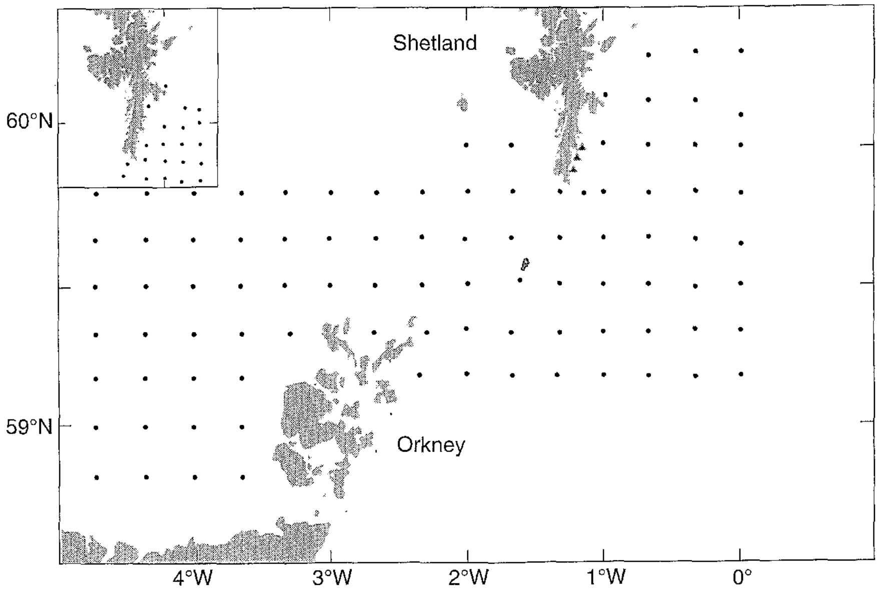

Fig. 1 Chart of Shetland–Orkney study area and location of large-scale plankton sampling grid (●, 1992 only) and three *Ammodytes marinus spawning* grounds where trawling was conducted (▲) [*Inset* areas near south-east Shetland that were sampled four times for hatch-date analysis (i.e. 25 February 1992; 3, 19 and 24 March 1992)]

records of larvae of < 6 mm total length (TL) for the periods 1953 to 1980 and 1989 to 1991 were obtained for the Aberdeen to Lerwick cruise track, between Stations 8 and 16 (which is part of CPR Area B2). The length range of < 6 mm TL corresponds to < 15 d post-hatch larvae (see "Results – Inter-annual variability in hatching date"). The duration of hatching in 1990 and 1991 was inferred from the numbers of larvae of < 6 mm TL in samples collected from 8 to 10 February, 20 to 25 March and 10 to 14 April. Monthly records of zooplankton standing stock were used to infer the approximate timing of the seasonal increase in secondary production, which is presumed to increase 1 to 2 wk before the rise in standing stock (Fransz et al. 1991).

Larval sampling

Larvae were collected between 25 February and 27 March 1992, during two cruises (conducted with the MV "Seaboard Invincible", 25 February to 6 March 1992, and MV" British Enterprise IV", 18 to 27 March 1992). Larvae were sampled using a Gulf III high-speed plankton sampler with a 250 µm-mesh net and cod end. The sampler was deployed in a single oblique tow at 2.5 $\mathrm{m\,s^{-1}}$ to within 5 m of the seabed, and was continuously lowered/raised at $\simeq$ 10 $\mathrm{m\,min^{-1}}$. A remote depth-sensor (SCANMAR) was used to monitor the depth of the Gulf III sampler during deployment. A 9 km grid of 23 stations was sampled four times during this period (25 February, 3, 19 and 24 March 1992: see inset Fig. 1). No larvae of > 10 d old were found during the first survey, suggesting that the start of the sampling period was close to the onset of the hatching period. All larvae were > 4 d old in the final sample, suggesting that local larvae had hatched by the end of the sampling period. During the study period, larvae were also collected from a 18 km grid of 108 stations extending from north Shetland to the Scottish mainland (Fig. 1). This larger-scale sampling programme made it possible to assess the extent and geographical isolation of larval patches near Shetland.

Larvae were preserved in 75% propan-2-ol immediately after capture. The propan-2-ol was replaced with fresh preservative within 48 h, and the samples were sorted in the laboratory. The total length of all larvae was measured to the nearest 0.05 mm with the aid of a digitising table, and was corrected for average shrinkage in preservative using a pre-determined factor (0.92). The numbers of larvae in each sample were then converted to numbers per $\mathrm{m^2}$ of the water column. Sub-samples of 10 to 25 randomly-chosen sandeel larvae were taken from each sample for age analysis. Details of sample sizes are given in Table 1.

Juvenile sampling

Samples (N = 12 to 16) of 0-group sandeels were obtained in June, 1990 to 1992 by bottom trawling at the three spawning grounds. A commercial net with a 4 to 7 mm-mesh cod-end and 20 t capacity was used. This gear is capable of capturing 40 mm TL post-larvae (maximum body width = 3.5 mm), although its size selectivity is not known. Based on the size compositions of sandeels caught with a 2 mm mesh Methot–Isaac–Kidd net (Methot 1986), > 97% of 0-group sandeels were > 60 mm TL (maximum body width = 7 mm) at the time of sampling in all three years, and consequently were likely to be fully retained by the gear. Catch weight was estimated from the number of full baskets (one basket = 33.5 ± 3.75 kg). A sample of 300 to 500 fish was measured to the nearest 5 mm TL at sea, a subsample of juveniles was frozen for later otolith analyses. The total numbers of fish per length class were calculated from a mean length–weight relationship for the Shetland sandeel grounds (Coull et al. 1989) and the estimated total catch weight. The number of 0-group sandeels in the catch was then estimated using an age–length key and total catch weight.

Age analysis

The sagittae of larvae were excised from the head and cleared in immersion oil. Daily increments were counted at × 1000 magnification. Sagittae of juvenile sandeels were prepared according to the methods given in Wright (1993), and were examined at × 400 or × 1000 magnification. Counts were made with the aid of a viewing tube. Hatch dates of juvenile 0-group sandeels caught around south Shetland were determined from the number of otolith increments between the date of capture and the larval primordium. The number of increments deposited between the primordium, post-rostral secondary growth centre and outermost increment provided estimates of the duration of the larval phase and timing of metamorphosis, respectively.

The age composition for each aged subsample of larvae was determined and used to apportion the numbers per sample into 5 d age classes. In 82% of samples, all larvae fell within a single age class, 13% samples contained two age classes, and only 5% samples contained three age classes. In order to compensate for the problem of differential cumulative mortality when calculating the hatch-date distributions, a correction factor for cumulative mortality was applied to the total numbers of each age class collected. A daily mortality rate of 0.07 was used to correct for the effect of differential cumulative mortality on the larval hatch-date distributions. This mortality rate was based on a previous field estimate of sandeel larval mortality for a related species, *Ammodytes personatus* (Fujiwara et al. 1990). However, as nearly all larvae examined were < 5 d old in the first two samples and < 10 d old in the third and fourth surveys, even a higher daily mortality rate of 0.10 would not have altered the relative sizes of the two larval cohorts identified in 1992. A combined hatch-date frequency distribution was derived from all subsamples using a weighting factor to account for the relative contribution of each sample to the estimated total abundance of larvae.

An age composition was derived for each juvenile sub-sample from daily increment counts. Annual age compositions were then derived from the sub-sample age compositions with a weighting factor based on the relative contribution of each catch to the total. An estimate of natural mortality (M) for sandeels derived from a local tagging study was used to correct the juvenile hatch-date distributions (M = 1.6; Kunzlik et al. 1986). Multi-modality within age compositions of larvae and juveniles was investigated using MacDonald and Pitcher's (1979) MIX programme (interactive programme for fitting mixtures of distributions). Differences among hatch-date distributions of larvae and juveniles in 1992 and of

Table 1 *Ammodytes marinus.* Number of samples collected, fish measured, fish aged and fish used in otolith back-calculations

Stage	Year	Site	Samples (N)	Measured	Aged	Back-calculation
Juveniles	1990	Sandeel grounds	(16)	2826	151	14
Juveniles	1991	Sandeel grounds	(16)	7792	120	14
Juveniles	1992	Sandeel grounds	(12)	476	93	10
Larvae	1992	Shetland–Orkney	(108)	28607	941	0
Larvae	1992	East Shetland	(92)	5390	600	0

juveniles in all years were tested for using a Kolmogorov–Smirnov test.

Growth-rate analysis

Age-at-length data were used to compare growth rates between year-classes. Specific growth rates (Ricker 1979) of individual juveniles from the 1992 year-class were estimated from length-at-age measurements and an assumed initial length at hatching of 5 mm TL. A sagitta otolith radius:total length relationship was determined from fresh specimens to enable back-calculation of length-at-age, thus enabling the construction of individual growth histories. Post-rostral radius to within ± 5% precision and increment counts were determined with the aid of a video-measurement system. Post-rostral radius did not exhibit a linear relation with total length over the range in length considered (5 to 120 mm TL) but could be described by separate linear regressions for the larval phase (5 to 39 mm TL) and small (40 to 59 mm TL) and large (60 to 120 mm TL) juvenile phases (Fig. 2). These regressions were used to back-calculate length-at-age from a representative sample from each cohort. Back-calculation was limited to comparing radii of a 14 to 20 increment sequence because of the uncertainties involved in the otolith back-calculation method (see Campana and Jones 1992).

Seasonal variation in environmental conditions

Data on the densities of microzooplankton were collected at all Shetland stations in the 1992 cruises. A pumped seawater supply was used to collect microzooplankton samples from 10 m depth. Fifteen litres of water were filtered through a disc of 40 μm-mesh netting, and the entire catch of plankton was preserved in a vial of 4% neutral buffered formaldehyde solution. In the laboratory, samples were sorted by species, stage and size and the number of prey items was estimated using the relationship between prey width and larval length for sandeels derived by McGurk et al. (1992) and information on larval diet (Ryland 1964; Economou 1991). Data on sandeel-prey densities were also collected from the same area during surveys in May and June 1991, and were used to consider temporal changes in prey availability for sandeel larvae.

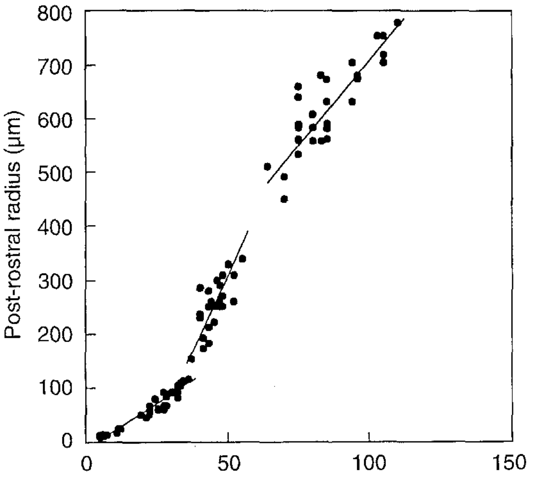

Fig. 2 *Ammodytes marinus*. Relationship between sagitta post-rostral radius and total length in sandeels from Shetland. Linear regressions were fitted on basis of different radius-length stanzas: 5 to 39 mm TL PRR = − 6.49 + 3.1644TL; $r^2 = 0.96$; $N = 56$; $P < 0.001$; 40 to 59 mm TL PRR = − 104.1 + 8TL; $r^2 = 0.535$; $N = 27$; $P < 0.01$; 60 to 120 mm TL PRR = − 134.5 + 5.74L; $r^2 = 0.73$; $N = 31$; $P < 0.001$ (where TL = total length and PRR = post-rostral radius)

Information on salinity and temperature was collected at all stations in 1992 using a remote conductivity–temperature–depth probe (SensorData SD-200). Wind speed and direction for the period of larval hatching were obtained from the Meterological Office's Sumburgh Head Meterological Station, Shetland.

Results

Inter-annual variability in hatching date

There were significant inter-annual differences between the hatch-date distributions of survivors of *Ammodytes marnus* from the three years studied (Kolmogorov–Smirnov test; $P < 0.001$). Indeed, there was little overlap in the range of hatch dates between 1991 and the other two years. In 1990, the hatching period extended from 22 January to 16 March 1990, but 50% of the 0-group survivors hatched before 24 February 1990. In contrast, the hatch-date range for 0-group survivors in 1991 was from 5 March to 21 April 1991 (Fig. 3). The hatching period of the 1992 year-class, determined from juvenile age compositions, ranged from 18 February to 20 March 1992, i.e. it was slightly later than in 1990 but earlier than the 1991 survivors. In 1990 and 1991, actual hatching periods, as indicated by the presence of yolk-sac larvae from the continuous plankton-recorder, broadly corresponded with the range of survivor hatch-dates, i.e. larvae were only present in February and in March samples in 1990 and March and April samples in 1991. The range in back-calculated hatch-date distribution for 1992 survivors was 19 February to 22 March, and covered a similar range to that actually observed (see last subsection of "Results").

Based on daily increment counts between the primordia and yolk-absorption zones in larvae from all years, the duration of the yolk-sac phase ranged from

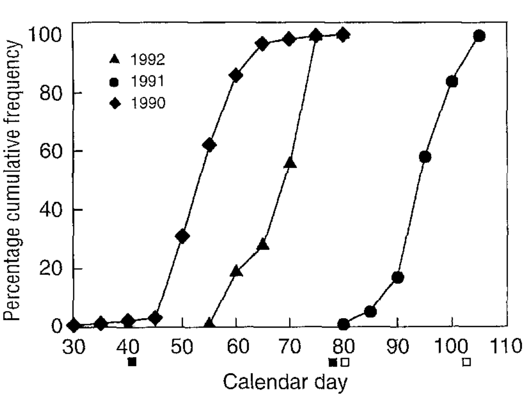

Fig. 3 *Ammodytes marinus*. Percentage cumulative hatch-date frequency distributions of 0-group from 1990 to 1992 based on sample-weighted and combined age-composition data in June [■ *(1990) and* □ *(1991) on abscissa* indicate presence of < 6 mm TL sandeel larvae in monthly continuous plankton recorder surveys for the two years]

Table 2 *Ammodytes marinus.* Timing of occurrence (+) of newly hatched larvae. Data based on presence of larvae of < 6 mm total length in monthly plankton surveys from Sir Alister Hardy Foundation (*SAHF*)and Marine Laboratory, Aberdeen(*MLA*)

Year	February	March	April	Source
1909		+		Bowman (1914)
1910		+		
1911		+		
1912		+		
1952		+		SAHF
1953		+		
1958		+	+	
1960		+		
1961	+	+		
1963		+		
1966		+		
1967		+		
1976		+	+	
1978		+	+	
1980				
1989	+			MLA
1990	+			SAHF
1991			+	SAHF
1992	+			MLA

8 to 16 d. Consequently, larvae would have had to begin to feed exogenously between early February and late March in 1990, late March and early May in 1991, and early March and early April in 1992. Continuous plankton-records for the northwest North Sea, north of 59°N, indicated that the seasonal increase in copepod standing stock from < 200 to > 1000 m^{-3} occurred between April and May in the three years studied (Sir Alister Hardy Foundation unpublished data). Therefore, larvae hatching in 1990 and during the early part of the 1992 hatching period would have begun feeding at least a month prior to the onset of the spring bloom in production of copepod nauplii, the main prey of *Ammodytes marinus* larvae (Ryland 1964; Economou 1991). Historical information on the appearance of newly hatched (< 6 mm TL) sandeel larvae in continuous plankton-recorder surveys and (Marine Laboratory, Aberdeen) plankton surveys indicates that March is the main month of hatching in the Shetland region (Table 2). Newly hatched larvae were present in March in all years for which records exist. In contrast, larvae were only recorded in 4 and 6 out of 19 yr during February and April, respectively.

Inter-annual variation in growth rates

Fig. 4 shows growth of juvenile sandeels in 1990 to 1992, based on length-at-age data. The growth trajectories of juveniles in all three years could be described by a linear regression, although there was considerable variation in length-at-age of individuals from the 1991 year-class. Statistical comparison of the growth rates using analysis of covariance (ANCOVA) and Scheffé multiple-comparison tests indicated that there were significant differences in the age–length relationships of juvenile sandeels between year-classes (for juveniles > 55 mm TL $F_{2,292} = 6.47$; $P < 0.002$). The Scheffé multiple-comparison test showed that were significant growth differences between all year-classes, with juveniles from the 1991 year-class having the highest growth rates whilst individuals from the 1990 year-class had the lowest growth rates ($P < 0.10$).

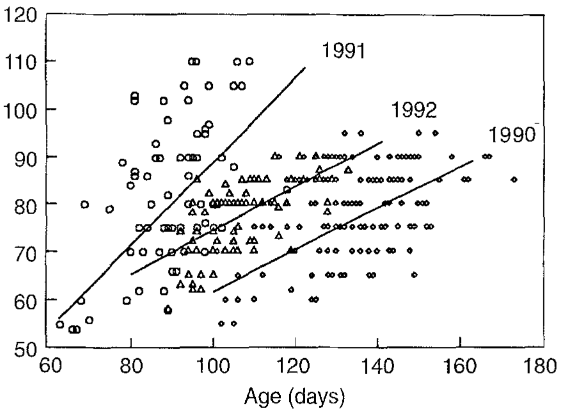

Fig. 4 *Ammodytes marinus.* Relationship between age and length for 0-group caught in June 1990 to 1992. Linear regressions were fitted for each year-class: 1990 TL (mm) = 16.72 + 0.457 age; r^2 = 0.66; $N = 151$; $P < 0.01$; 1991 TL (mm) = 3.31 + 0.879 age; $r^2 = 0.65$; $N = 95$; $P < 0.01$; 1992 TL (mm) = 29.8 + 0.443 age; $r^2 = 0.41$; $N = 93$; $P < 0.01$

Fig. 5 presents back-calculated growth trajectories for the larval phase of survivors from the three year-classes, based on otolith radii measurements. Linear regressions provided acceptable fits to the combined growth trajectories of individuals within a year-class ($P < 0.001$). As with age-at-length data, there were significant differences in the back-calculated length-at-age among year-classes (ANCOVA, $F_{4,203} = 9.94$; $P < 0.0005$). Similarly, a Scheffé test showed that growth rates of individuals from the 1991 year-class were significantly greater than those from 1990 and 1992, even within the first 40 d following hatching.

The length of larvae at metamorphosis ranged from 40 to 55 mm TL. Estimates of the date at metamorphosis from otolith microstructure indicated that 95% of *Ammodytes marinus* caught in June had metamorphosed between 14 May and 7 June in the three years studied. The median date of larval metamorphosis was estimated to be Calendar Day 141 in 1990 and 1991 and Calender Day 147 in 1992. Owing to the relatively short window of metamorphosis, the duration of the larval phase varied in relation to hatching date, ranging from 76 to 110 d in 1990, 42 to 55 d in 1991, and 82 to 102 d in 1992.

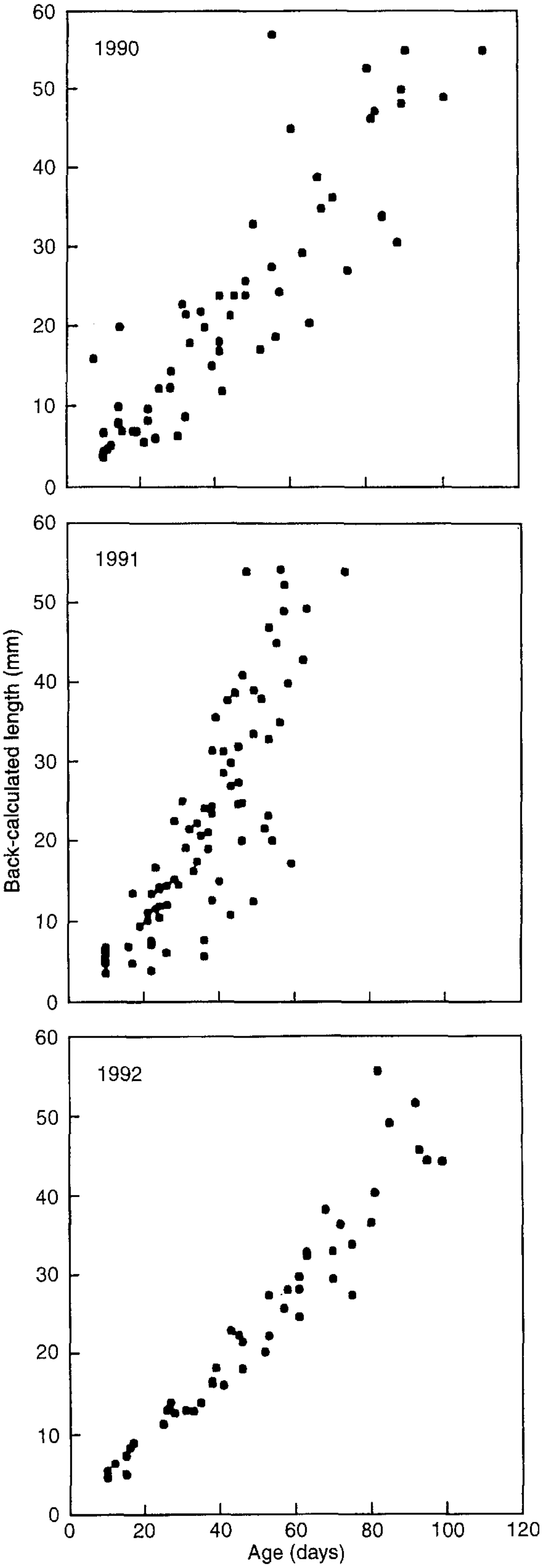

Fig. 5 *Ammodytes marinus.* Estimated length-at-age of individual survivors inferred from otolith back-calculation for 1990 to 1992

Intra-seasonal variation in hatch date, survivorship and growth rate in 1992

A geographically discrete concentration of *Ammodytes marinus* larvae was present in the south Shetland study area during all four surveys. A survey of this region in May 1991 also recorded a geographically discrete patch of late larvae, suggesting that larvae may be retained close to the Shetland coast (Wright and Bailey unpublished data). Other areas of relatively high larval abundance (> 100 m^{-2} of the water column) were found to the west, off Foula, and to the south in the vicinity of the Fair Isle channel. Larval ages from the Shetland stations ranged from 2 to 10 d during the first cruise, and 5 to 22 d during the second cruise. Age ranges of larvae at stations other than the Shetland grid were 2 to 10 d during the first cruise, and 3 to 29 d during the second cruise.

An analysis of the larval hatch-date frequency composition indicated the presence of two larval cohorts, whose mean hatch dates were Calender Days 56 and 73. These two cohorts were also evident within the hatch-date frequency composition of survivors (whose mean hatch dates were Calender Days 57 and 71, respectively). However, the hatch-date distributions of larvae and survivors differed significantly (Kolmogorov–Smirnov test; $P < 0.001$; Fig. 6a). This was due to the differences in the relative contribution made by the two cohorts to the larval and survivor hatch-date distributions. Based on a MIX analysis of hatch-date frequency distributions, the late-hatched cohort (LC) comprised 64% of the juveniles compared with only 35% of the larvae. These differences in hatch-date composition provide evidence for selective mortality, with the later-hatched cohort apparently experiencing a lower rate of mortality. The specific growth rates of individual survivors from the later-hatched cohort was also generally higher than that of the early-hatched cohort (EC), and mean growth rates differed significantly [mean (range) specific growth-rate LC = 0.027 (0.024 to 0.031); EC = 0.023 (0.021 to 0.024); $t_{94} = 10.87$; $P < 0.001$].

Information on environmental conditions during the larval hatching period indicated that the two larval cohorts were subject to quite different conditions at hatching and first-feeding. Chlorophyll *a* concentrations increased significantly between the first and second cruise (Mann–Whitney U-test: $U_{66} = 80$; $P = 0.001$), and became more evenly distributed between the formation of the two cohorts (variance:mean ratio for Cruise 1 = 0.23, for Cruise 2 = 0.06). Further, chlorophyll *a* concentrations were below those associated with the onset of the spring phytoplankton bloom (1 mg m^{-3}) during late February and early March. The density of microzooplankton differed significantly between surveys (Kruskal–Wallis: nauplii$_{90,3}$ = 14.66, $P = 0.002$; copepodites$_{90,3}$ = 21.61, $P = 0.005$; Fig. 6b), with prey densities increasing from a mean of

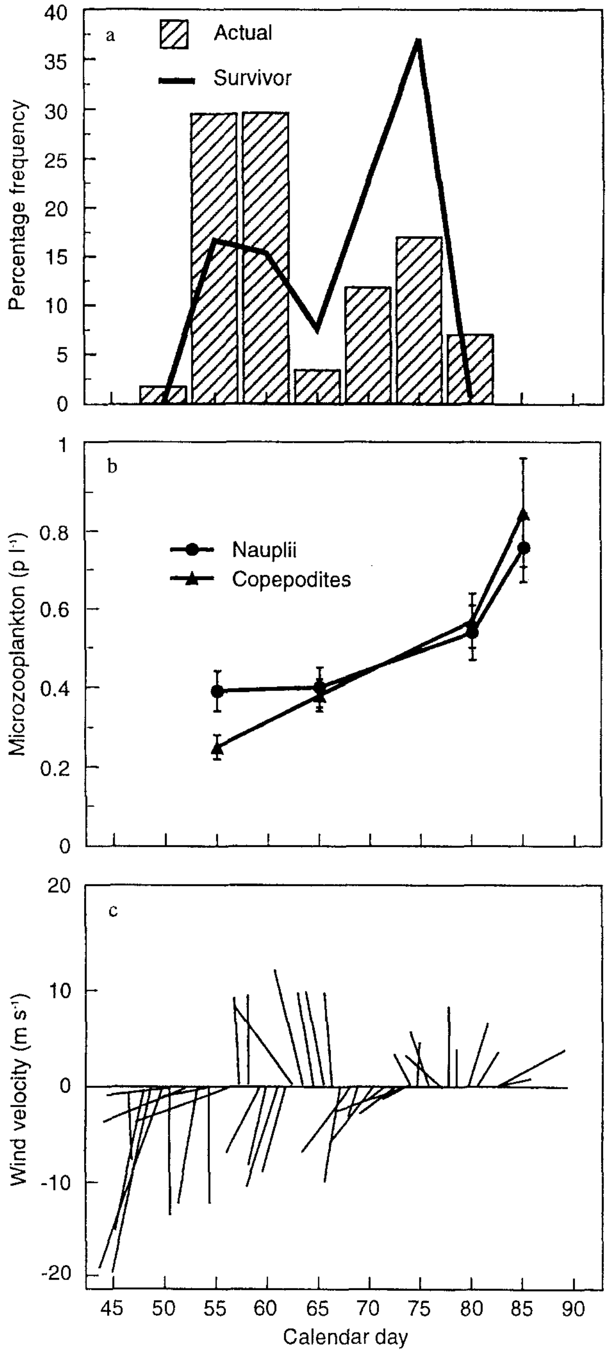

Fig. 6 *Ammodytes marinus.* Comparison between hatch-day distribution of larvae (*Actual*) and juveniles (*Survivor*) (**a**), temporal trends in densities of copepod nauplii and copepodites (mean ± SE plankters per litre) (**b**) and wind velocity and direction (**c**) during 1992 hatching period

0.6 plankters l^{-1} on 25 February 1992 to 1.5 plankters l^{-1} on 24 March 1992.

There was little difference in sea temperature between sample times, with bottom temperature declining by 0.2C° during the study period. However, there were marked differences in the wind speed and direction during the formation of the two cohorts. Mean daily wind velocity was in excess of 10 m s^{-1} for $> 70\%$ of the time when the larvae from the first cohort were hatching. Further, winds were predominantly from a direction associated with high southerly inflow between Shetland and Norway (median wind direction = 220°; range = 80 to 350° cf. Turrell 1992). In contrast, wind velocity rarely exceeded 10 ms^{-1} during the formation of the second cohort, and winds were frequently from a direction that would be expected to lead to a low southerly flow both east of Shetland and in the Fair Isle current. Based on the salinity characteristics (35.15‰ isohaline), the northern boundary of the Fair Isle current appeared to remain between Fair Isle and Orkney throughout the sampling programme.

Discussion

Evidence from the temporal incidence of larvae indicates that the median hatch date of *Ammodytes marinus* within the Shetland–Orkney region is in March (Bowman 1914; Langham 1971; Hart 1974; Coombes 1980; and present Table 2). Consequently, peak hatching during the present study appears to have been early in 1990 and close to the median date in 1991. Annual differences in hatch date coincided with marked differences in the growth rate of survivors, with the later-hatching year-class exhibiting the highest mean growth rate. A similar coincidence between hatch date and growth rate was also observed from a comparison of cohorts in 1992. This association between hatch date and growth rate suggests that *A. marinus* larvae were subject to a similar seasonal cycle of growth opportunity during the three years of study. Although temperature and food intake are both important factors governing the growth of fish larvae (Houde 1989a), the decrease in sea temperature between February and March in the Shetland region (Turrell and Slesser unpublished data; see also present Fig. 6b) means that the observed differences in growth rate could only have resulted from varying food intake.

Monthly monitoring of chlorophyll *a* concentration in the inshore waters around Shetland suggests that the spring phytoplankton bloom (based on > 1 mg m^{-3}) generally begins by April, although it may be as late as May (Turrell and Slesser unpublished data). Consequently, first-feeding larvae (12 d post hatch) that hatch close to the median peak hatch-date would tend to coincide with the onset of the spring bloom in primary production, as in the case of the late-hatching 1992 cohort. This coupling between the appearance of first-feeding larvae and the onset of plankton production appears to be common to winter-hatching *Ammodytes* species, as it has also been reported for sandeel larvae from the western North Atlantic (Sherman et al. 1984; Monteleone and Peterson 1986) and Japanese waters (Inoue et al. 1967). Whilst no data is available on inter-annual variability in the production rates of copepods and other sandeel prey, data on adult copepod standing stocks from continuous plankton records suggests there would have been little difference in the onset of prey production between 1990 and 1992. Indeed, seasonal changes in copepod standing-stock during the study period were similar to the 40 yr average (Fransz et al. 1991). Consequently, variability in the match between first-feeding larvae and the onset of the spring bloom may explain the seasonal differences in growth observed in the present study. However, without information on larval feeding success and prey availability at a scale relevant to larvae, this explanation cannot be tested.

The relevance of seasonal changes in prey density to fish larval growth has been widely questioned, since other factors such as the foraging ability of larvae, encounter rates with prey, and the physical factors influencing them are known to influence food intake (Sundby and Fossum 1990). Starving larvae have also been found in association with prey densities that are much higher than those determined to be limiting in food-ration experiments, as for example McGurk et al. (1992) recently demonstrated in a study of *Ammodytes hexapterus* larvae. Nevertheless, there is evidence that the growth and survival of some marine fish larvae may be influenced by seasonal changes in food availability (e.g. Canino et al. 1991; Fossum and Moksness 1993). Clearly, this potential for seasonally food-limited growth is highest in those species whose larvae initiate feeding months before the maximum abundance of their prey (Fortier et al. 1995).

An indication of the potential for seasonal prey limitation on sandeel larval growth can be obtained by fitting values of prey density determined in the present study to a growth:ration relationship for another winter-hatching sandeel species, *Ammodytes americanus* (Buckley et al. 1987). Based on the relationship of Buckley et al. it is clear that potential growth of the two cohorts in 1992 would be expected to have differed, with zero growth being predicted for larvae hatching in February (Table 3). Similarly, using estimates of nauplii densities determined from 1991 and 1992, the magnitude of observed differences in growth rate between the beginning of April and the end of February in all years studied can be explained. Prey patchiness (MacKenzie et al. 1990) and inter-annual differences in the timing of secondary production can make estimates of growth based on comparisons of food-ration experiments and field estimates of prey availability misleading. Nevertheless, the density of microzooplankton at all stations in February and March 1992 were far lower than those shown to have a serious effect on sandeel larval growth and survival in laboratory experiments (Buckley et al. 1984). Clearly, the degree of synchrony between the seasonal increase in secondary production and hatching will not be the only factor influencing the growth of *A. marinus* larvae. For example, in 1992 the higher incidence of storms during the formation of the first cohort could have greatly disrupted prey patches and consequently could have led to initially low growth rates. However, storm-induced turbulence cannot explain the protracted low growth rates of survivors in 1992 inferred from otolith back-calculation.

Table 3 *Ammodytes marinus*. Back-calculated and predicted growth rates ($Gw = \%$ weight d^{-1}) of larvae in relation to hatch date. Actual growth rates of first-feeding larvae for hatch dates shown are based on data from Fig. 5 for larvae from 1992 (Hatch Days 50 and 70) and 1991 (Hatch Day 90). Predicted growth rate is based on growth-ration equation for *A. americanus* derived by Buckley et al. (1987) from data on microzooplankton densities in Shetland study area

First feeding day	Actual Gw	Predicted Gw
50	2.9	0
70	6.1	1.2
90	9.8	7

The present study provides circumstantial support for a link between growth rate and survival. This can be seen from the higher growth rate and survival of the late-hatched cohort in 1992. Further, given that survivors from all years appeared to be representative of their respective hatching periods, the markedly high growth rates of survivors from the large 1991 year-class suggests that inter-annual variability in growth rates may have contributed to the observed differences in year-class size (see Wright 1996). Although changes in the abundance of a cohort are an immediate consequence of mortality, the processes governing mortality are closely tied to growth as a consequence of the size-selective nature of many mortality processes, in particular predation (Houde 1989b; Pepin 1991). In principle, this linkage between growth and mortality means that temporal variability in growth rate alone has the ability to generate fluctuations in the survival of a cohort. By simple modelling, Houde (1989b) demonstrated that small percentage changes in the daily instantaneous growth rate over the whole pre-recruit period may have order-of-magnitude consequences for the number of survivors reaching a particular development stage. This is in contrast to the effect of high-mortality episodes in the early life since, in general, $> 80\%$ loss is required before an episode will have a significant effect on the number surviving. Estimates of mortality rates in larval and early juvenile stages of another winter-hatching sandeel species, *Ammodytes personatus*, highlights the potential significance of size-selective growth and mortality. Mortality rates range from $0.07\ d^{-1}$ in yolk-sac larvae to $0.12\ mo^{-1}$ in late larvae (Kimura et al. 1992). Given this variability in stage- and size-related mortality, the marked differences in growth rate between year-classes found in the present study would be expected to have led to large inter-annual differences in cumulative mortality.

Consequently, growth variability may account for a high proportion of the inter-annual variation in year-class strength observed.

Clearly, factors other than growth rates may explain the difference in relative survival of the two 1992 cohorts. For example, no information was collected on the temporal variation in predation pressure during the study. Advective losses could also have acted as an important source of local mortality. Indeed, from investigations of wind-induced sea circulation in this region (Turrell et al. 1991), it would seem likely that the early-hatched cohort in 1992 would have been subject to a higher rate of offshore advection than that experienced by the later-hatched cohort. However, whilst larval advection from south Shetland may have varied over the hatching period and could have led to the apparent variable local survival rates, there is no certainty that displaced larvae would have been lost to the region. Moreover, advective losses cannot explain the higher growth rate of the late-hatching cohort.

The link between growth opportunity and the phase of plankton production suggested by the present study lends support to the idea that seasonal variation in food availability is important to early survivorship. This view is central to the match/mismatch hypothesis, which proposes that reproductive strategies of fishes reflect the seasonal pattern of plankton of the area, and that variation in the timing of seasonal plankton blooms are a major determinant of inter-annual variability in larval survival (Cushing 1975, 1990). However, in contrast to predictions by the match/mismatch hypothesis, hatching of *Ammodytes marinus* larvae generally precedes the maximum annual availability of prey. It has been proposed that selection for such a strategy may be related to the need to avoid predators during early development or to synchronise larval metamorphosis with the peak abundance of zooplankton (Sinclair and Tremblay 1984; Bollens et al. 1992). The latter could explain why *A. marinus* has both a relatively well synchronised metamorphosis period and exhibits an increasing dietary selectivity towards adult *Calanus finmarchicus* coinciding with the peak in standing stock of these copepods (Economou 1991; Fransz et al. 1991; Hay et al. 1991).

A second assumption central to the match/mismatch hypothesis, that only the timing and intensity of prey production varies, is also clearly not applicable to *Ammodytes marinus*. The population spawning period of *A. marinus* in the Shetland region is known to range from early December to late January (Gauld and Hutcheon 1990), but, as the present this study shows, the hatching period can be more protracted. The reason for the differences in the hatching periods observed in the present study is unknown, but could be related to either the peak timing of spawning and/or the duration of embryological development. Experimental studies of embryonic development in *Ammodytes marinus* have shown that development times can range from 1 to 3 mo depending on prevailing temperature and oxygen concentration (Winslade 1971). However, based on sea-temperature records for the inshore waters around Shetland (Marine Laboratory, Aberdeen, unpublished data) and temperature-development relationships for *A. marinus* (see review by McGurk and Warburton 1992), the observed variation in monthly bottom temperatures recorded during recent years of early hatching is not sufficient to explain the observed variation in hatch dates. Unfortunately, there is no information on oxygen concentrations near the egg beds or inter-annual variability in spawning times. Clearly, further research is needed to investigate the proximal causes that lead to early spawning or hatching in this species.

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