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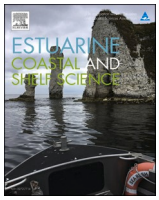

Temperature history determines the adult size and maturation rates in seasonal cohorts of *Loligo forbesii* squid

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ABSTRACT

We hypothesised that the large variation observed in squid life-cycle traits, such as growth rate and size and age at maturity, is a consequence of extended breeding throughout the year. Using data from Scotland and Ireland, we tested whether hatching date, specifically exposure to a cooling (October to April) or warming (May to September) temperature period could be associated with these traits in *Loligo forbesii*, a commercially fished squid species. In agreement with predictions, squid hatched in the warming temperature period matured at smaller size and age and grew more slowly than those from the cooling temperature period, in both sexes. Squid hatched in the cooling temperature period were further sub-divided into those which hatched in October – December and matured at large size/age, and those which hatched in January - April and were mature over a broad range of sizes and ages, although both groups were significantly larger/older than the warming temperature group. All three hatching groups also varied in their timing in the fisheries catches: small/young mature squid were caught from January until May, large/older mature animals were caught in late October to December and the mature animals with variable sizes/ages were captured over a longer period, from October to the end of April. This agreed with a Length-at-Maturity (LM_{50}) time series from Scotland, which showed highest LM_{50} in squid caught in November, and lowest values in squid caught in February/March. Hatching during warming temperatures (May - September) was mostly absent in Ireland.

1. Introduction

The life-cycles of many squid species are short, approximately annual, but with extended periods of reproduction and recruitment, a variable life-cycle in terms of timing (phenology) and a lack of synchrony in annual cohorts (Boyle et al., 1995; Collins et al., 1999; Pierce et al., 2005; Arkhipkin et al., 2015). This is presumably driven by some combination of intrinsic (genotypic) and environmentally driven (phenotypic) variation (Arkhipkin et al., 2015). Extended breeding, sometimes throughout the year, perpetuates flexibility and variability in the life-cycle, which makes assessment of the biomass production and escapement very challenging in fished species.

The veined squid, *Loligo forbesii*, is an important commercial species in the NE Atlantic (ICES, 2024). *Loligo forbesii* is described as an intermittent terminal spawner, i.e. it is semelparous and spawns only once, however population spawning can take place over an extended period (Rocha et al., 2001). It has an approximately annual life span, though animals of up to 18 months old have been reported in northern Spain (Rocha and Guerra, 1999). Its life-cycle has been well studied, particularly in the Atlantic waters of Scotland, Ireland, France and the Iberian Peninsula, where it is most commonly found, and where it is commercially fished (Jereb et al., 2015; ICES, 2024).

Extended spawning takes place in *L. forbesii* in the seas around the UK and Ireland (Lum-Kong et al., 1992; Boyle et al., 1995; Laptikhovsky

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et al., 2022), with potential for more-or-less 'continuous recruitment' in Scottish waters (Lum-Kong et al., 1992). However, studies show great variability in timing, for instance the occurrence, duration and abundance of summer breeding in Scotland, which ranged from no summer spawning at all in some years (Lum-Kong et al., 1992), to a high proportion of summer spawning in others (Pierce et al., 2005). Still more studies have shown that spawning mostly took place at other times of year, i.e. in winter and spring in both Scotland and Ireland, with a relatively small amount also taking place in summer (Collins et al. 1995a, 1997; Bellido et al., 2001; Pierce and Boyle, 2003). As for recruitment, which is usually defined by the presence of small immature squid in landings, one peak was seen in autumn in Scotland and Ireland, with an additional peak in spring (April) in Scotland (Lum-Kong et al., 1992; Pierce et al., 1994; Boyle et al., 1995; Collins et al., 1997). However, consistent with a general theme of variability, recruitment was routinely reported at other times, e.g. 'mainly occurring' in summer with occasional winter (December) recruitment in Ireland (Collins et al., 1995a).

It is plausible that all this variability in timing links to an important issue in squid fisheries management, that is the question of intra-annual cohorts, sometimes termed "micro-cohorts", which we are going to define as animals from the same breeding year and geographic region but with different life history traits, including size- and age-at-maturity and growth and, crucially, often with different phenologies. One of the first studies into flexible life histories in *L. forbesii* was by Boyle et al. (1995), who showed maturity at two size modes in both sexes and suggested alternative life-history strategies in this species. Collins et al. (1999) used size modes to identify recruitment pulses in *L. forbesii* fisheries and showed that these happened in April and again in November in western Scottish waters, but that both groups greatly differed in size (April recruits were larger at maturity). These authors asked how a single (extended) breeding period inside an annual life-cycle could lead to two size modes in *L. forbesii*; also, how two recruitment pulses per year were produced (Collins et al., 1999)? Explanations suggested included delayed hatching of some of the spawned eggs due to cold water temperatures, or migration of squid spawned in warmer areas to Scottish waters, amongst other possible reasons (Boyle et al., 1995; Collins et al., 1999).

The present study seeks to link the variability in size-at-maturity to the extended breeding period: since female maturity and spawning is extended over the year, this exposes hatchlings and young squid to seasonally contrasting growth conditions, driven by temperature and food availability at crucial moments in their ontogeny. Our hypothesis is that variation in hatch date leads to distinct intra-annual cohorts in *L. forbesii* that can best be described as 'seasonal' cohorts, due to their link to the temperature regime. Specifically, we test the hypothesis that individuals hatched in the warming temperature period have a different growth, maturity, and age profile from those hatched in the cooling temperature period. We also propose that the abundance of groups with distinct life history traits in any one location will be determined by the amount of hatching that takes place in seasonal temperature regimes at that location. To examine the latter, we compare the situation in two locations with important *L. forbesii* fisheries, Scotland and Ireland. The results of this study have implications for adult stock timing, biomass, female reproductive output and the potential of immature life stages to escape from fisheries.

2. Methods

2.1. Biological sampling, maturity and ageing

Sampling of hatch timing was carried out in Ireland from 1991 to 1993 inclusive. Fishery-caught *Loligo forbesii* were obtained from ports in the west, south-east and east of Ireland. For all individuals, sex was determined based on examination of the reproductive system (and the presence of a hectocotylus in mature males), the dorsal mantle length (DML, mm) was measured, and maturity was assigned using a five-stage scale (Lipiński, 1979). Juveniles were defined as small individuals which could not reliably be sexed (see Collins et al., 1995b for more details on sampling in Ireland). Squid were obtained from ports in Scotland during 1990, 1993, 1994, 1997, 2007, 2008 and 2009, comprising a minimum of 1 box of squid per month with no apparent size sorting having taken place in the fisheries landings prior to sampling. Sampling intensity aimed at sampling a minimum of 30 males and 30 females per month across the size range present (more details on sampling in Scotland are available in Pierce et al., 1994). Length was measured (DML), and maturity was categorised using a five-stage scale adapted from the Lipiński scale (Boyle and Ngoile, 1993; Pierce et al., 1994). Following maturity staging, maturity status was defined for all samples (Ireland and Scotland) as 'immature' or 'mature' based primarily on the presence of eggs in the oviducts or spermatophores in the Needham's sac (Pierce et al., 2005; see also Supplementary Table S1).

Ageing was performed in a subsample of squid by counting daily growth rings from statoliths using the procedures described in Collins et al. (1995b) for the Irish samples and by Arkhipkin and Shcherbich (2012) and Wangvoralak (2012) for Scottish samples. Briefly, Irish statoliths were prepared by mounting in Polarbed 812 resin (Fison's Scientific Equipment, Loughborough, UK) or Crystalbond 509 thermoplastic cement (Amber Aremco Products, Inc., USA) and Scottish samples were mounted with Crystalbond 509. Polishing of statoliths was carried out using wet graded sandpaper (600 grit followed by 1000 or 2000 grit) and dry sections were then embedded in a mounting medium, such as Canada balsam, that filled any tiny scratches on the statolith surface and made them invisible; Eukitt mounting medium (Sigma-Aldrich, UK) was also used for this purpose in some Scottish samples. Then the section was covered with thin cover glass for extra protection. The statolith microstructure was analysed under transmitted light of the compound microscope Olympus BX 51 at x200 or x400 magnification and increment counting was conducted by author MAC (Irish samples, see Collins et al., 1995b) and authors SW/AA (Scotland samples, Arkhipkin and Shcherbich, 2012; Wangvoralak, 2012). Counting began at the natal ring, which was the first particularly prominent increment outside the nucleus and age readings were completed along the lateral dome (Irish samples) or along the lateral dome and rostrum (Scottish samples); for the latter, increments were read from the natal ring until the first stress mark in the lateral dome, and then the rest of the rings were counted in the rostrum. Growth increments within the statolith microstructure were assumed to be daily in *L. forbesii* (Hanlon et al., 1989; Rocha and Guerra, 1999, see also Collins et al., 1995b). Scottish statolith readings were accompanied by four-point quality index based on the condition of the statolith (from 1- poor to 4 – very good) which was used to filter out statoliths with a 'poor' age reading prior to further analysis.

Following ageing, analysis proceeded with 398 males, 399 females and 34 juveniles from Scotland. The Irish samples included 139 males, 135 females and 42 juveniles. Hatch date was calculated by subtracting the number of daily increments from the catch date. Individuals were then placed in a 'cooling' or 'warming' temperature period, by hatch date (see section 2.2).

To examine the timing of size at maturity patterns in the fisheries catch, samples obtained from Scotland (above), were supplemented with additional port and market sampling from 1990 to 2001 inclusive, as outlined in Pierce et al. (2005). These samples were categorised for maturity using identical methods but note that these samples were not aged. This resulted in at least 200 individuals per month for a total dataset of $n = 14{,}752$ females and $n = 12{,}572$ males. Length at 50% maturity (LM_{50}) was calculated by month in individual years as well as for pooled months across the time series (see section 2.3).

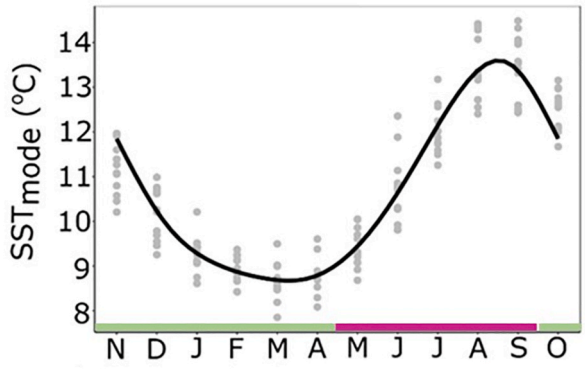

Fig. 1. Monthly modal SST (°C) in ICES Area 6a showing oceanographic 'cooling' (green, October-April) and 'warming' (purple, May-September) seasonal temperature periods for comparing squid hatching groups. Grey circles indicate individual monthly values by year (1980-2018). The trendline was plotted using smoothers from a GAM (using month as a smoother with a cubic spline). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Hatching seasonality

For animals which had been aged, hatching seasonality was determined after assigning hatch date and squid were then placed into one of two hatching temperature periods, based on whether their hatch date fell into a cooling or warming temperature regime. To assign squid to one of these groups, daily sea surface temperature data were acquired at 1 km × 1 km grid resolution from the NOAA SST-AVHRR database between 1980 and 2018 (www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/access/avhrr-only/; date accessed 17/07/2019) and monthly modal SST was calculated for ICES Area 6a, which is north of Ireland and west of Scotland and therefore representative of general seasonal water temperatures in both Irish and Scottish datasets. Following inspection of these data, oceanographic seasons, and hence hatching temperature groups, were defined as: cooling temperatures between October – April inclusive and warming temperatures from May – September inclusive (Fig. 1). In this case, April was included as a cold month as SST mode values in April were more similar to March values than to May values (Fig. 1). The same rationale applied in September but, this time, the SST modal values were more similar to warm months.

2.3. Data analysis

Hatch dates versus catch dates were plotted for each individual after first converting calendar dates into fractions of a year using the YEARFRAC function in excel. This calculated the number of days elapsed between 1st January and a given hatch (or catch) date each year and divided this by the total number of days in that year to obtain a fraction. Timing of these phenomena in the different temperature groups could then be inspected and compared.

Differences between hatching temperature groups in median squid age, size and lifetime growth (individual DML divided by individual's age in days) were tested separately in males and females using Moods median test for independent samples, which does not assume normally distributed data or homogeneous variances between groups, and it is less sensitive than other tests to unequal sample sizes and outliers (Mosteller et al., 1948). Tests were carried out in IBM SPSS Statistics for Windows, version 28.0 (IBM Corp., Armonk, N.Y., USA).

To define the 'maturity cycle' in the Scottish maturity data series, a monthly LM_{50} was calculated through the 1990 - 2001 time series, starting in November, which is considered the start of the biological year for *L. forbesii* in both Scotland and Ireland (Collins et al., 1995a; Pierce et al., 2005). Monthly LM_{50} was calculated separately in males and females using a logistic regression to model the expected probability of being mature, *P(m)*, as a function of dorsal mantle length (DML) using a binomial Generalised Linear Model (GLM) with a logit link function (Ogle, 2019; R Core Team, 2019), as shown in Equation (1).

$$P(m) = \frac{e^{\alpha+\beta.\ DML}}{1 + e^{\alpha+\beta.DML}} \quad \text{(Equation 1)}$$

Equation (1) includes the dorsal mantle length (*DML*), the intercept of the model α and the slope of the dorsal mantle length variable β. The modelled regression curves were used to extract the expected DML when the probability of being mature was a half ($P(m) = 0.5$), i.e. DML at which half the population in a given month was mature (=LM_{50}). LM_{50} calculations from models were filtered to exclude calculations with a sample size of <50 individuals per month, as were those from poorly performing models (R^2 value < 0.15 and explanatory variable p-values >0.05). The latter occurred in months when samples were dominated by either immature or mature individuals, resulting in a poor fit to the logistic model. Monthly LM_{50} was also calculated using the same methods but including data for all years in a given month (i.e. 13 years of data for each month).

3. Results

3.1. Age profiles

The sampled age range in *Loligo forbesii* from Ireland (1991-1993) was 173-359 days old (d) in females (n = 135) and 156-376 d in males (n = 139). Only five individuals exceeded 365 d, all of them males. The sampled age profile for adult females and males was evenly spread, apart from very young (<178 d) males, which were less represented (Supplementary Fig. S1). Juveniles (n = 42), which were defined as animals which could not reliably be sexed, spanned 112-186 d, most of which were older juveniles (142-186 d); only 13/42 juveniles were younger than 142 d.

In Scotland (1990-2009), the age profile of adult squid was somewhat broader than in Ireland, males (n = 398) ranged from 128 to 432 d, females (n = 399) from 133 to 408 d and juveniles (n = 34) from 141 to 217 d. Both males and females in Scotland were mostly of intermediate age groups (~230-330 d) but with some representation (>10 statoliths) of all age categories, apart from the oldest category of >383 d in females or >425 d in males (Supplementary Fig. S2).

3.2. Hatching seasonality in mature individuals

Capture months were evenly represented across calendar months in both locations, therefore, we would not expect any important bias to arise in the analysis of hatching dates as all possibilities should be represented (although fisheries catches themselves vary between months) (Supplementary Fig. S3). For animals that were mature at capture, hatching took place over a longer period in Scotland compared with Ireland, with high frequencies of hatching in both warming and cooling temperature periods in Scotland (Fig. 2). In Ireland, very few mature animals hatched in the warm period, totalling only n = 9/135 females and n = 8/139 males (Fig. 2), with the rest hatching in cold months. In Ireland, mature animals mostly hatched from December (males) or January (females) to May, whereas, in Scotland, hatching in mature animals mainly took place over a longer period, from November/December to July. The corresponding hatching periods for immature animals are shown in Supplementary Fig. S4, where an extended hatching period in Scotland compared with Ireland can also be seen.

3.2.1. Size-at-age and growth in mature individuals

Mature *L. forbesii* hatched during warming temperatures (May – September) were of smaller size and younger age in both sexes than their counterparts hatched during cooling temperatures (October – April), particularly in Scotland (Fig. 3). Statistical comparisons of both

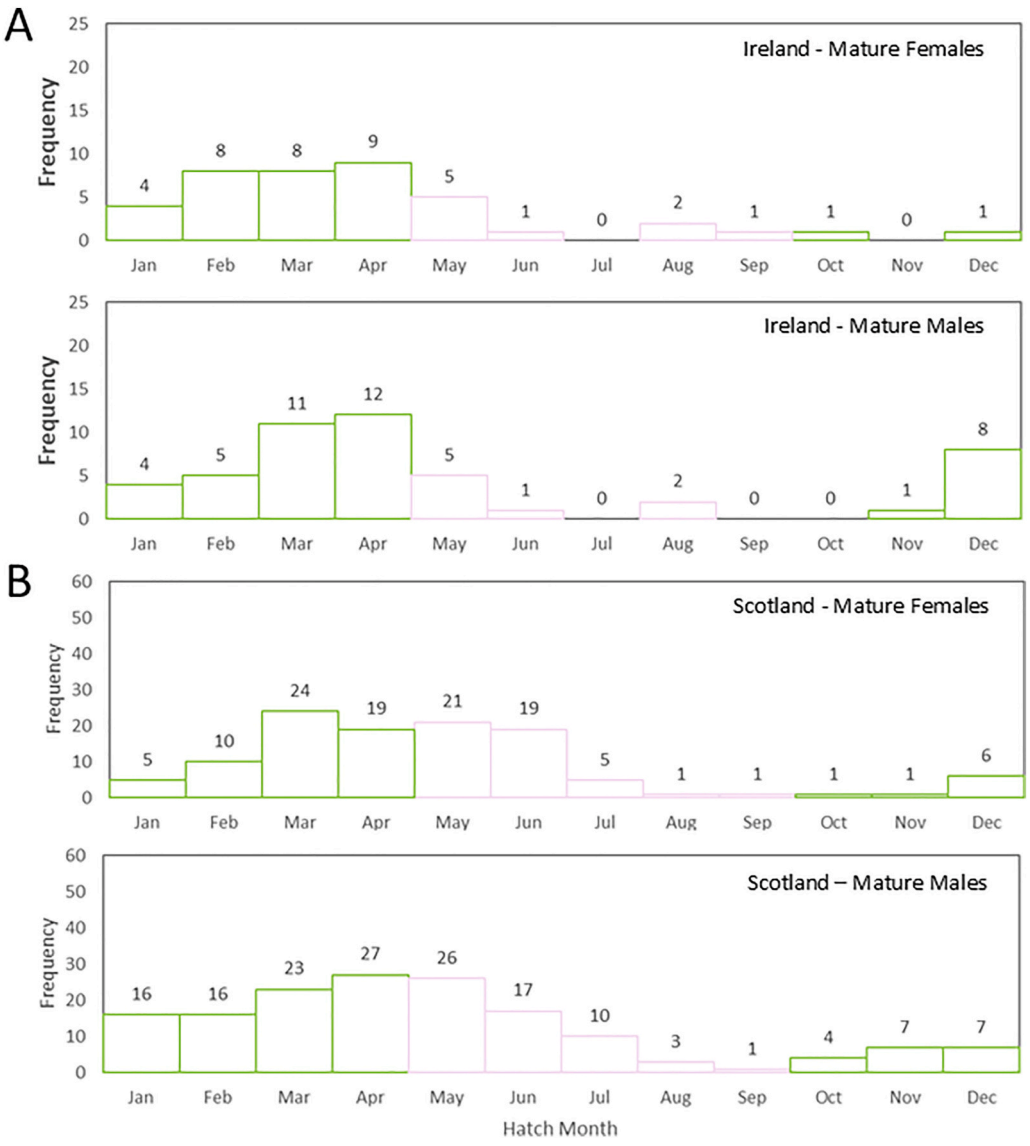

Fig. 2. Hatch month frequency by group in mature *Loligo forbesii*: A) Ireland, B) Scotland, y-axes vary. Histogram colours indicate warming (purple) and cooling (green) temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

temperature groups were possible in Scotland as both hatching periods were well-represented there (Supplementary Table S2). As well as being younger and smaller in size, these squid grew more slowly than the other temperature group. By contrast, the mature squid hatched during cooling temperatures were highly variable, spanning a broad range of sizes and ages in both sexes and locations (Fig. 3; Supplementary Table S2).

To interrogate variability during cool temperatures, a further subdivision was made for mature squid: those that hatched from October – December (when values are steeply declining, Fig. 1) and those that hatched from January – April (the period of temperature minima on Fig. 1), with each of these being compared to squid hatched in warming temperatures. The results show that October – December hatching gave rise to the largest and oldest mature *L. forbesii* in both sexes, whereas January – April was associated with highly variable sizes/ages in mature animals (Fig. 4; Table 1).

Thus, overall three seasonal cohorts were identified based on hatching period: small/young mature animals that hatched in May – September, large and old mature animals that hatched in October – December, and highly variable mature squid that hatched from January – April, though the latter group was still larger and older, on average, compared with the warming temperatures group (Table 1).

3.2.2. *Timing in mature individuals*

To examine trends in when each of these three groups was captured in fisheries, the hatch dates and catch dates were plotted as fractions of a year, for mature animals (Fig. 5). This revealed several patterns, the first of which was that no mature animals were available in the fisheries catch for two and a half months between the beginning of September to mid-November in the sampled population (Fig. 5), although immature animals were caught throughout this period (Fig. S6). A second pattern was that each hatching cohort had a distinctive period when it appeared in fishery catches: small/young mature animals were almost always captured early in the year, from January to April when they were less than nine months old. Large/old mature animals were only captured late in the year (late October onwards to December) when they were about one year old, and the mature animals with variable sizes/ages were captured over a long period, from October in males and November in females to the end of April (Fig. 5).

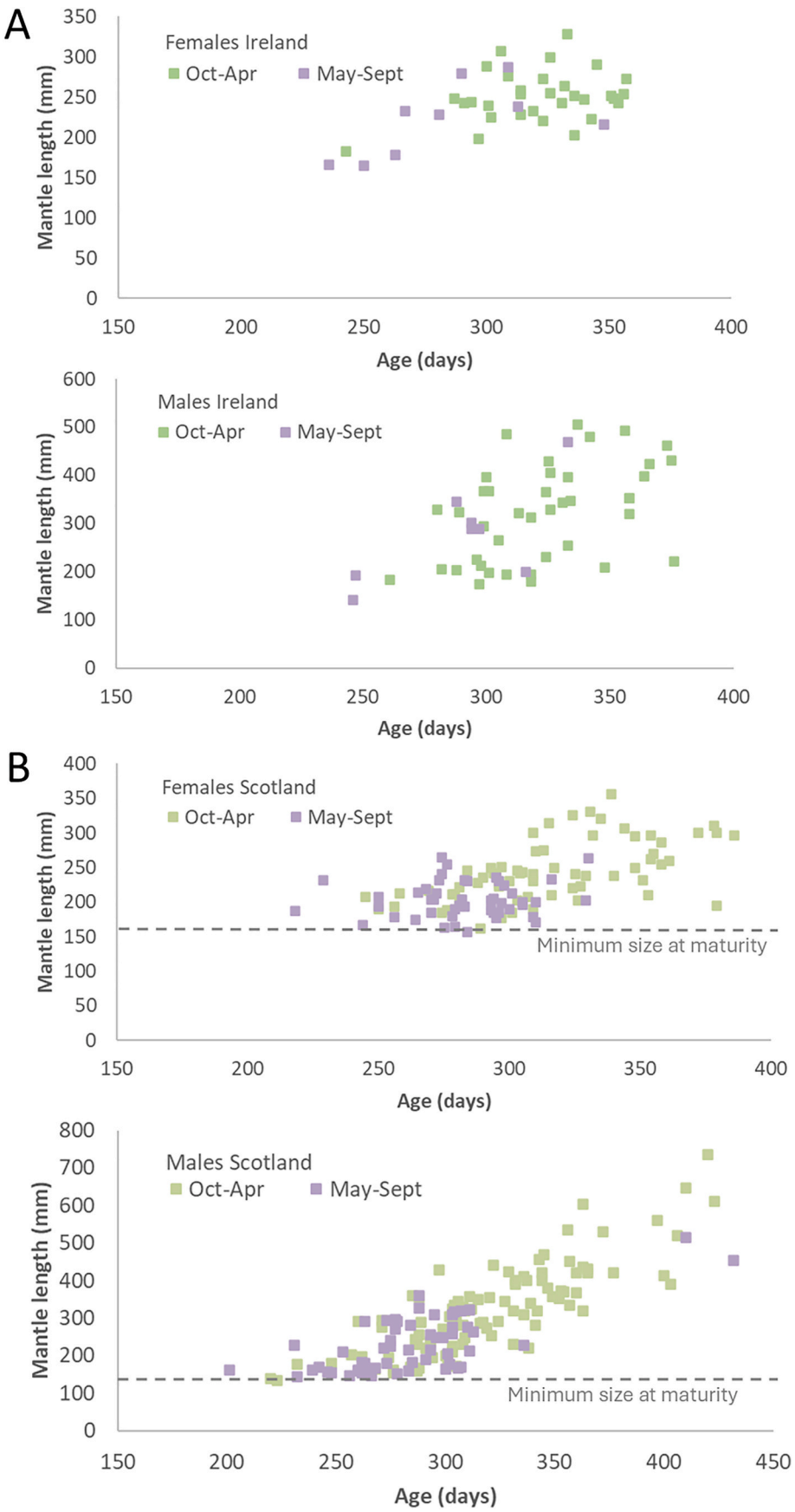

Fig. 3. Size-at-age in mature *Loligo forbesii* females and males: A) Ireland, B) Scotland, y-axes vary. Data are organised by hatching date, green boxes: October-April, purple boxes: May-September. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

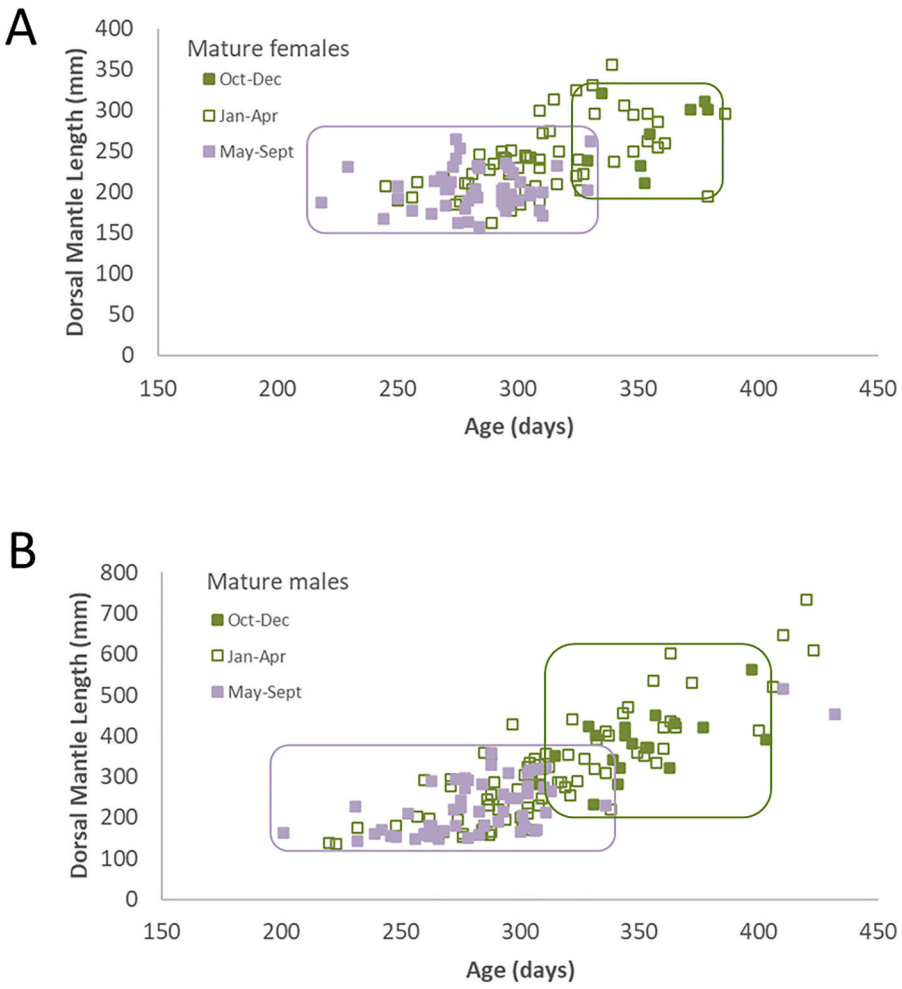

Fig. 4. Hatching cohort detail for mature *Loligo forbesii* in Scotland: A) females, B) males, y-axes vary. Colours indicate three different hatching groups, from warming temperatures (May-September, small at maturity, shown in purple), cooling temperatures (October-December, large at maturity, in green), and a second cooling temperature cohort (January-April, variable in size at maturity, in white with green outline). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Median values (with range) of age, size and lifetime growth for mature *Loligo forbesii* that hatched in different temperature regimes in Scotland. Statistical comparison of medians show the warming temperature group versus two cooling temperature groups using Mood's median test statistic (*M*), $^{**}p < 0.01$, $^{***}p < 0.001$.

Mature animals	Female Hatching Dates			Male Hatching Dates		
	Warming temperatures (May-Sept)	Cooling temperatures (Oct-Dec)	Cooling temperatures (Jan-Apr)	Warming temperatures (May-Sept)	Cooling temperatures (Oct-Dec)	Cooling temperatures (Jan-Apr)
Age (days)	283 (218-330)	354 (329-379)	306 (245-386)	283 (201-432)	344 (308-403)	305 (220-423)
M		10.44***	15.27***		24.32***	12.61***
Size (mm)	200 (157-265)	285 (210-320)	236 (162-356)	214 (144-515)	385 (231-560)	290 (135-735)
M		10.44***	16.27***		19.28***	8.19**
Lifetime growth (mm/day)	0.70 (0.55-1.01)	0.78 (0.59-0.96)	0.77 (0.51-1.05)	0.76 (0.54-1.26)	1.10 (0.70-1.41)	0.94 (0.55-1.75)
M		2.52^{NS}	8.16**		14.83***	8.19**
Overall trend	Small & young at maturity, slower growing	Large & old at maturity	Variable but larger/older, on average	Small & young at maturity, slower growing	Large & old at maturity	Variable but larger/older, on average

3.3. Size-at-age in immature individuals

Immature squid hatched during the warming temperature period appeared to be smaller in size-at-age compared to those from the cooling temperature period, especially in females; therefore the immature animals exhibited the same trend as mature squid (Supplementary Fig. S5). This pattern was only detectable in Scotland because no immature females were found that hatched in the warming temperature regime in Ireland and there were only three immature males found in Ireland for this group. In Scotland, no gap was seen in fisheries catches for immature squid (Supplementary Fig. S6), unlike the gap observed in mature animals (Fig. 5).

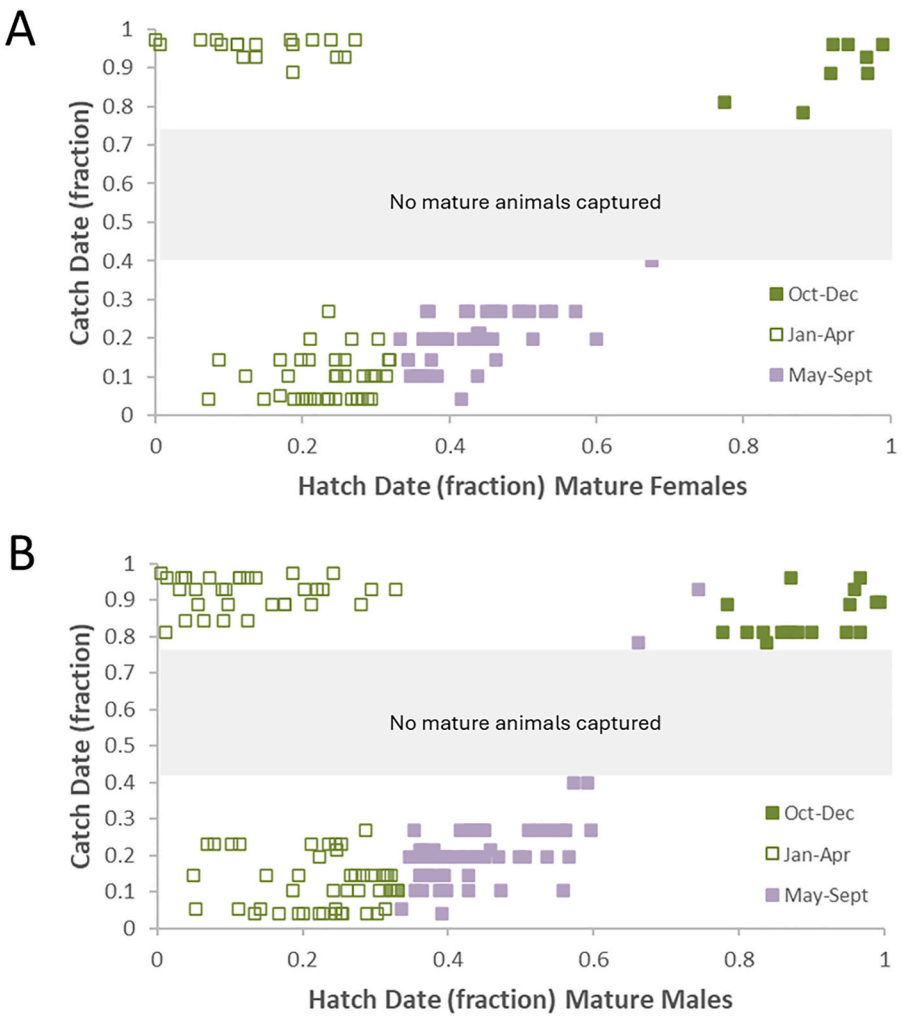

Fig. 5. Hatching and capture date (both expressed in fraction of a year) for mature *Loligo forbesii* in Scotland: A) females, B) males. Colours indicate the hatching cohorts (from Fig. 4) corresponding to warming temperatures (small at maturity, shown in purple), cooling temperatures (large at maturity, in green) and a second cooling temperature cohort (variable in size at maturity, in white with green outline). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Maturity cycle and length at maturity (LM_{50}) time-series

Fig. 6 shows a monthly length at maturity (LM_{50}) time-series from Scotland - note that these animals were not aged so this data analysis is organised by capture date rather than hatch date. 53 months across the time-series had sufficient data quality for LM_{50} to be calculated in females, and this showed an apparently consistent annual cycle over the 13-year time series. Monthly LM_{50}s in females were largest at ~280 mm DML in squid captured in November (occasionally October) each year and smallest in squid captured in February and March each year (LM_{50}s of ~163 mm), shown as black dots on Fig. 6A; see also Table 2. From February/March to June each year female LM_{50} remained low at ~142-199 mm DML (Table 2). Pooling monthly data across years we can see that LM_{50} dropped by about 117 mm within the 3–4-month period from November to February, staying low over subsequent months until June (Table 2).

Hence LM_{50} maxima in October/November and minima in February/March from the fisheries catch time-series matched the hatching groups seen in Fig. 5. Specifically, large/old mature animals were captured late in the year (late October onwards to December) and small/young mature animals were captured early in the year (y-axis on Fig. 5). Mature squid with variable size-at-age were captured in both periods (y-axis on Fig. 5).

Compared with LM_{50} trends, the proportion of mature females showed the opposite monthly pattern: December to March each year coincided with a rapid increase in the proportion of mature females. Hence, when length at maturity was minimal, the proportion of mature squid was maximal, and vice-versa (compare Tables 2 and 3).

In males it was not always possible to calculate monthly LM_{50} values; only n = 33 months met the data quality and quantity criteria needed to calculate this metric (see Methods). But although it was difficult to determine a cycle due to missing monthly values, males still showed a key similarity to females with the same decreasing trend in mantle length of mature males from October/November to January/February (see green versus orange data points in Fig. 6B). Following this decline, male length at maturity increased again from March to May i.e. earlier than females, staying high until at least July.

4. Discussion

Several works have posed a question in relation to *Loligo forbesii*, which is, how are two size-at-maturity modes produced from a single breeding period in a ~1 year life-cycle? (Boyle et al., 1995; Collins et al., 1999). The present study shows that this is associated with a very extended hatching period, which takes place during different temperature conditions (and indeed a post-hatching lifespan which can

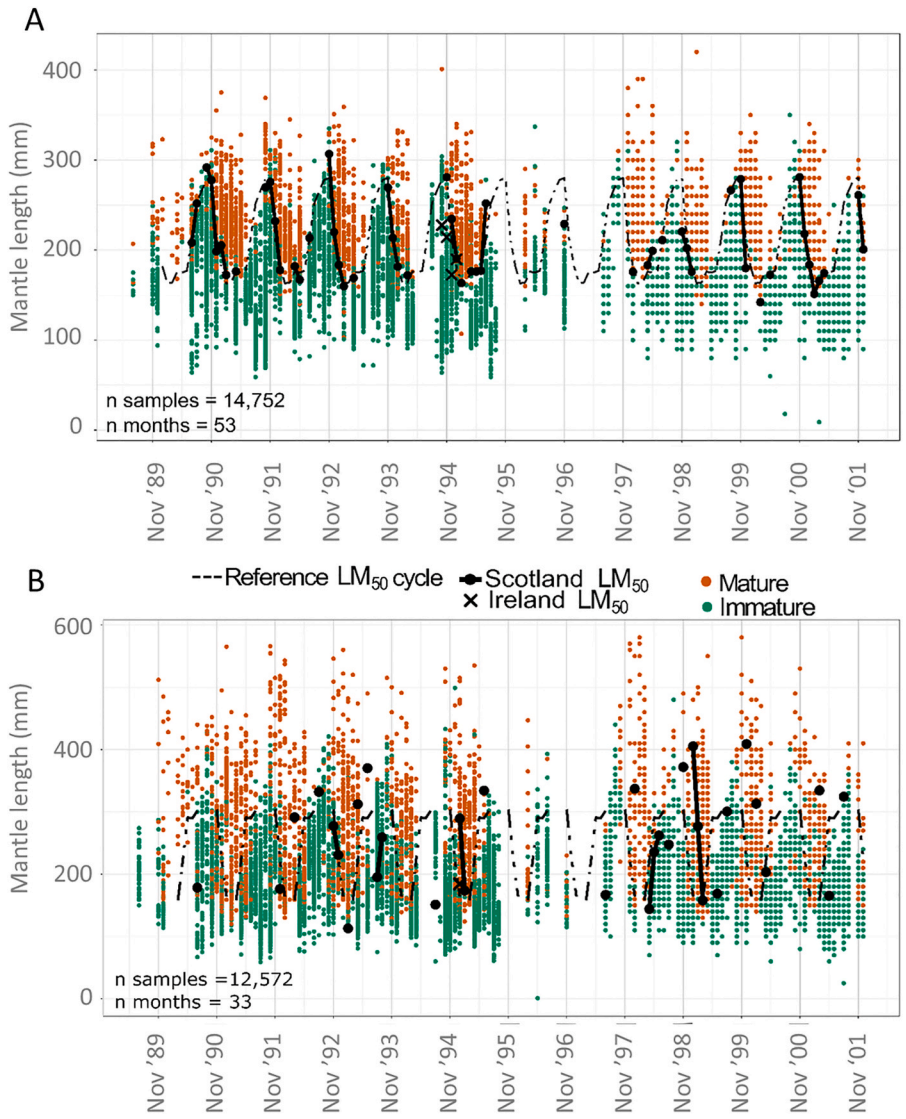

Fig. 6. Monthly LM_{50} (length at 50% maturity) in *Loligo forbesii* from Scotland: A) females, B) males, y-axes vary; note that months shown represent the capture date (not hatch date). Vertical lines indicate November each year when LM_{50} was maximal (main line). Individual squid that are mature (orange circles) and immature (green circles) are also shown. Black dots represent monthly LM_{50} in Scotland and crosses (x) show the LM_{50} in Ireland in 1994/95. The black dashed line shows LM_{50} calculated from the global data, i.e. size-at-maturity for data pooled per month across 13 years, which was repeated through the series for comparison. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

considerably exceed one year). The size of mature squid depended on the time of year when hatching took place, i.e. hatching during a period of warming temperatures led to mature squid of smaller sizes and younger ages, whereas hatching during cooling temperatures led to larger/older mature squid, although squid hatched in one part of the cooling period, from January – April, were highly variable. Hatch date also revealed which cohort(s) were found in each study location and, because hatching was more extended across the year in Scotland than it was in Ireland, Scotland possessed three seasonal cohorts of different sizes and ages at maturity, whereas one of these cohorts (i.e. maturity at small size and young age) was largely absent in Ireland. There were no months when hatching was absent in Scotland, demonstrating how extensive the hatching period is throughout the year in this location, and also showing that low temperatures did not prevent hatching (and indeed subsequent successful development) taking place there in any month. Finally, each of the three hatching periods was associated with mature adults of different sizes appearing during distinct periods in fisheries catches (Fig. 7).

Squid hatched in the warming season were mostly mature at small size and young age in both sexes, whereas squid hatched during the cooling season were mature over a broad range of sizes and ages in Ireland and Scotland (Fig. 3). Despite overlaps, there were statistically significant differences between both cohorts in terms of size, age and in lifetime growth (see results of Moods median tests, Supplementary Table S2). Larger sample sizes in Scotland permitted two hatching cohorts to be identified inside the cooling season – hatching in the early part of this period, from October to December, when temperatures were decreasing, was associated with large mature squid of about one year old in both sexes, whereas hatching during temperature minima in January to April was linked to mature squid of variable sizes and ages (Fig. 4). Both of the cooling season cohorts differed significantly from the warming season cohort, being larger, older and with a faster lifetime growth rate in both sexes, apart from one female growth comparison (lifetime growth in females hatching in May-September versus October-December were not significantly different, Table 1).

The warming season cohort showed characteristics of precocious

Table 2
Monthly length at maturity (LM_{50}, mm) cycle in female *Loligo forbesii* from Scotland by capture month (i.e. not hatching month). Cell colour indicates months with maximum (green cells) and minimum (orange cells) length at maturity values. Empty cells are months with no data or when quality criteria to calculate LM_{50} were not met. Monthly LM_{50} was also calculated for data pooled across all years together.

	1990-91	1991-92	1992-93	1993-94	1994-95	1998-99	1999-2000	2000-2001	Pooled Years
Nov	278	276	307	270	281	221	279	281	280
Dec	199	232	220	214	234	202	180	218	212
Jan		205	178	183	182	176	176		182
Feb		172		160					163
Mar					172			142	164
Apr		176	182	168		183			176
May			167			199		173	175
Jun									177
Jul	208		213			211			213
Aug	252								252
Sep							266		266
Oct	292	270							278

Table 3
Monthly proportion of maturity in female *Loligo forbesii* from Scotland by capture month (not hatching month). Note that months with maximum values (orange cells) correspond to months with minimum monthly LM_{50}s (Table 2). Proportion of maturity was also calculated for data pooled across all years together.

	1990-91	1991-92	1992-93	1993-94	1994-95	1997-98	1998-99	1999-2000	2000-2001	Pooled Years
Nov	0.22	0.25	0.11	0.06	0.03		0.07	0.10	0.16	0.10
Dec	0.46	0.38	0.40	0.85	0.19	0.65	0.52	0.79	0.43	0.55
Jan	0.91	0.61	0.94	0.65	0.45	0.78	0.25	0.99	0.76	0.63
Feb	0.82	1.00	0.76	0.86	0.82	1.00	0.89	0.97	0.92	0.87
Mar	1.00	1.00	1.00	0.54	0.98	0.92	0.94	0.93	0.36	0.80
Apr	0.39	0.06	0.24	0.02	0.26	0.07	0.96	0.00	0.12	0.21
May	0.97	0.73	0.75		0.08	0.35	0.01	0.15	0.01	0.32
Jun	0.03	0.50	0.06		0.58	0.01	0.00	0.01	0.03	0.06
Jul	0.01	0.02			0.01	0.14	0.00	0.00	0.00	0.02
Aug	0.01	0.02	0.01	0.00	0.00	0.03	0.02	0.00	0.00	0.01
Sep	0.00	0.00	0.01	0.00	0.04	0.00	0.02	0.01	0.01	0.01
Oct	0.07	0.00	0.04	0.01		0.00	0.02	0.02		0.03

maturity as these individuals were mature at small size (200/214 mm DML in females/males respectively) and at the relatively young age of ~283 days old, on average, in both males and females (Table 1). These squid were caught in fisheries from January – May but mostly before April (Fig. 5). Precocious maturity in the fisheries catches during Spring months was also consistently seen in a 13-year time-series in Scotland (Fig. 6), noting that the proportion of mature animals in the catch also increased rapidly in the Spring months (compare orange cells in Tables 2 and 3). These squid also grew slower than those in the other temperature groups (Table 1), but they matured early, despite lower growth. The linked timing of both smaller sizes at maturity, and high proportions of the catch being mature, suggests individuals that were running out of time to complete the annual lifecycle.

Hatching during the cool season (October to April) produced squid that matured over a broad range of sizes and ages in both sexes and locations but there was a pattern within this variability. Hatching during the first part of this period, from October to December, was associated with large mature animals, 385 mm DML median size in males and 285 mm DML in females, which were almost one year old (median age of 354 days in females, 344 days in males, Table 1). This group also showed the highest lifetime growth (0.78 mm/day in females and 1.10 mm/day in males, Table 1). A second sub-division of the cool season, hatching from January to April, was more variable and included both large and small mature animals, however, this group was still statistically larger and older at maturity than the precocious group (Table 1) and this was also the dominant mode in both locations, especially in Ireland (Fig. 2).

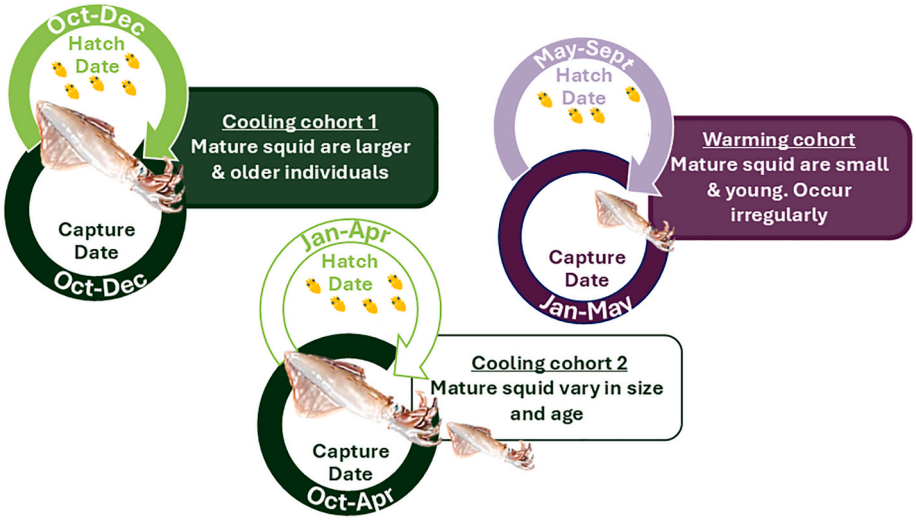

Fig. 7. Schematic of seasonal cohorts in *Loligo forbesii* from Scotland showing their hatch timing as well as their timing as mature adults in fisheries catches.

In Ireland, mature squid mostly hatched in January to April, although this may vary year-to-year and sample sizes in Ireland were also low. In Scotland, substantial numbers of squid hatched during the warming season and more precocious maturation was seen there, but the two cold cohorts were still dominant.

As well as having distinct size and age-at-maturity profiles, the three hatching cohorts had different timings in the fisheries catches: precociously mature individuals were captured in early Spring. The two cold season cohorts also had distinctive fisheries catch profiles, squid with the largest size-at-maturity (i.e. hatched in October to December) were only captured in a discrete period from late October to December in the following year, when they were about one year old. Catch dates for the second cold cohort were more widespread, from October in males (November in females) to the end of April. The catch timings for all individuals with known hatching dates matched the 13-year time-series in Scotland, showing maximum values in size-at-maturity (LM_{50}) from fisheries catches in November each year but minimum values in Spring (Fig. 6). Overall, a catch date late in the year only captured the two cold-season cohorts, whereas a catch date early in the year captured the warm-season (precocious) cohort, along with the variable cold-season cohort. Meanwhile, catch dates in the middle of the year were associated with immature squid (Fig. 5).

Length-frequency analysis has previously described three size-at-maturity strategies in *L. forbesii* males (Collins et al., 1999). A 'summer breeding cohort', which we assume to be synonymous with the warm cohort in the present study, has been shown to appear only in certain years in Scotland (Pierce et al., 2005), which we now assume to depend on the amount of hatching taking place in Spring/Summer months. Intra-annual cohorts in *L. forbesii* life-cycles have also been described outside of the current study area (e.g. Rocha and Guerra, 1999; Hanlon et al., 2002; Moreno et al., 2007). These also occur in other species of loliginid (Hatfield, 2000; Arkhipkin et al., 2013) and ommastrephid squid (Arkhipkin et al. 2000, 2015), with explanations for their occurrence suggested to be temperature influences during hatching and growth. An open question is whether these cohorts may be associated with alternative reproductive tactics (ARTs) in loliginid squid because of the existence of 'consort' males which mature at larger sizes and 'sneaker' males which mature at smaller sizes (Iwata et al., 2011; Filice and Dukas, 2019; Apostólico and Marian, 2020). Consorts and sneakers have recently been suggested to arise from different hatch dates in a loliginid species, *Heterololigo bleekeri*, where sneakers hatched later in the annual cycle compared with consorts, giving rise to a "Birth Date Hypothesis" for ARTs (Hosono et al., 2024), although hatching during only a short part of the year was considered in that study. The hatch date of cohorts in the present study might also link to ARTs, with the important *proviso* that the existence of sneaker and consort tactics and evidence of spermatophoric complex differences associated with ARTs (see Iwata et al., 2011; Filice and Dukas, 2019) have not yet been demonstrated in *L. forbesii*. Secondly, what we see from studying the full annual hatching life cycle of *L. forbesii* is that small mature males hatch in *both* temperature periods (i.e. these animals' hatch dates come from across the year from January to September) whereas large mature males occur only in the cooling season (October to April, Fig. 4). This would need to be reconciled with ART timings (if these exist) in *L. forbesii*. Multiple paternity of *L. forbesii* egg capsules (Shaw and Boyle, 1997), hence polygamy in females, provides suitable conditions for sperm competition via ARTs or other means.

Temperature seems to be an important driver of size-at-maturity variation (Forsythe and Hanlon, 1989; Forsythe, 2004; Pecl et al., 2004; Arkhipkin et al., 2015), though whether this is a proximate and/or ultimate causal factor is not known. Even though males have received far more attention (Mather, 2024), we can see from the present study that precocious maturity does not only affect males. Females also had two cohorts and an enormous range in size-at-maturity. Nevertheless, the smallest mature individuals in the sampled population were always males, and females' size and age minima at maturity were slightly higher than males in equivalent temperature groups (comparing range minima in Table 1). Tactics in males and females are likely to have different selective pressures, e.g. in terrestrial snails, phenotypic plasticity in size (and age) at maturity showed different reaction norms under different experimentally-controlled food deprivation treatments. Males matured once a minimum age was reached, despite small size in low growth conditions, because the ability to access a female was not size-related (this also seems to be the case in squid). However, because reproductive output was size-related in females, low food treatments resulted in much longer times to maturity (Tamburi and Martín, 2009). These authors speculated that in unproductive habitats where food was limited, most females would have to overwinter before attaining sexual maturity. Such lifecycle extension on account of poor growth is not possible in *L. forbesii* since biannual life-cycles do not occur in this species (Boyle et al., 1995) and only a few individuals exceeded 365 days old in the present study (Supplementary Fig. S1 and S2). Indeed, this constraint probably explains why precocious maturation takes place, since the proportion of mature animals suddenly increases in concert with precocity (Table 3). Nevertheless, female squid may probably delay maturation to some degree since maturity occurred

across such a wide spread of ages (Fig. 3). In addition, different egg size modes in the ovary suggest that spawning itself may be stretched over several months in *L. forbesii* (Boyle et al., 1995; Rocha and Guerra, 1996). Indeed, the ability to fertilise egg capsules over a period of time using stored sperm from different males may permit females to maximise reproductive fitness (Hanlon et al., 2002). While females may store sperm and extend the spawning period, laying eggs fertilised from a few different males, male *L. forbesii* seem to disappear earlier than females from fished populations after spawning (Coelho et al., 1994; Collins et al., 1999).

The presence of seasonal cohorts, with different sizes-at-maturity, growth rates and appearance timings in fisheries catches, has consequences for stock biomass and also has important management implications. All three seasonal cohorts apparently only occur in some years and locations, which we suggest links to the relevant hatching periods, with small mature animals notably rare in some years (Scotland) and locations (Ireland). Predictive modelling could add further details on how the amplitude in length at maturity changes over the year, as well as adding details about its timing, and specifically, the influence of hatching time on both. Which seasonal hatching cohort(s) are dominant will also influence female reproductive output (smaller mature females are expected to spawn fewer eggs) as well as fisheries escapement of immature squid. For instance, we observed that mature squid were absent in fisheries catches between September-mid November (Fig. 5), although immature animals were caught throughout this period, some of which were very large-bodied (Supplementary Fig. S5 and S6). Fisheries active during this period were therefore likely to capture immature animals, that were difficult to identify due to their large size. Predictive modelling to understand the drivers of timing in large immature squid, including the influence of hatching time, would also be useful for management.

CRediT authorship contribution statement

A.M. Power: Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. **M.A. Collins:** Formal analysis, Investigation, Methodology, Writing – review & editing. **A. Arkhipkin:** Formal analysis, Investigation, Methodology, Writing – review & editing. **S. Wangvoralak:** Formal analysis, Investigation, Methodology, Writing – review & editing. **M. Petroni:** Formal analysis, Investigation, Methodology. **G.J. Pierce:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Anne Marie Power reports financial support was provided by Interreg Atlantic Area Programme. Graham J. Pierce reports financial support was provided by Interreg Atlantic Area Programme and EU CEC FAR, CEC AIR, and CEC FAIR programmes. Michael Petroni reports financial support was provided by Interreg Atlantic Area Programme. S. Wangvoralak was in receipt of a Royal Thai government Science and Technology Scholarship. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2026.109999.

Data availability

Data will be made available on request.

References

Apostólico, L.H., Marian, J.E.A.R., 2020. Cephalopod mating systems as models for the study of sexual selection and alternative reproductive tactics: a review. Bull. Mar. Sci. 96 (2), 375–398. https://www.ingentaconnect.com/content/umrsmas/bullmar/2020/00000096/00000002/art00010.

Arkhipkin, A., Argüelles, J., Shcherbich, Z., Yamashiro, C., 2015. Ambient temperature influences adult size and life span in jumbo squid (*Dosidicus gigas*). Can. J. Fish. Aquat. Sci. 72 (3), 400–409. https://doi.org/10.1139/cjfas-2014-0386.

Arkhipkin, A., Jereb, P., Ragonese, S., 2000. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57, 31–41. https://doi.org/10.1006/jmsc.1999.0488.

Arkhipkin, A.I., Hatfield, E.M.C., Rodhouse, P.G.K., 2013. *Doryteuthis gahi*, Patagonian long-finned squid. In: Rosa, R., O'Dor, R., Pierce, G. (Eds.), Advances in Squid Biology, Ecology and Fisheries. Part, vol. 1. Nova Science Publisher, Inc., New York, USA, pp. 123–157, 978-1-62808-331-6.

Arkhipkin, A.I., Shcherbich, Z., 2012. Thirty years' progress in age determination of squid using statoliths. J. Mar. Biol. Assoc. U. K. 92, 1389–1398. https://doi.org/10.1017/S0025315411001585.

Bellido, J.M., Pierce, G.J., Wang, J., 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fish. Res. 52, 23–39. https://doi.org/10.1016/S0165-7836(01)00228-4.

Boyle, P.R., Pierce, G.J., Hastie, L.C., 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. Mar. Biol. 121, 501–508. https://doi.org/10.1007/BF00349459.

Boyle, P.R., Ngoile, M.A.K., 1993. Assessment of maturity state and seasonality of reproduction of *Loligo forbesi* (Cephalopoda: loliginidae) from Scottish waters. In: Okutani, T., O'Dor, R., Kubodera, T. (Eds.), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo, pp. 37–48. https://oceanrep.geomar.de/id/eprint/50933.

Coelho, M.L., Quintela, J., Bettencourt, V., Olavo, G., Villa, H., 1994. Population structure, maturation patterns and fecundity of the squid *Loligo vulgaris* from southern Portugal. Fish. Res. 21, 87–102. https://doi.org/10.1016/0165-7836(94)90097-3.

Collins, M.A., Boyle, P.R., Pierce, G.J., Key, L.N., Hughes, S.E., Murphy, J., 1999. Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 56, 500–509. https://doi.org/10.1006/jmsc.1999.0485.

Collins, M.A., Burnell, G.M., Rodhouse, P.G., 1995a. Recruitment, maturation, and spawning of *Loligo forbesi* Steenstrup (Cephalopoda: loliginidae) in Irish waters. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 52, 127–137. https://doi.org/10.1016/1054-3139(95)80021-2.

Collins, M.A., Burnell, G.M., Rodhouse, P.G., 1995b. Age and growth of the squid *Loligo forbesi* (Cephalopoda: loliginidae) in Irish waters. J. Mar. Biol. Assoc. U. K. 75, 605–620. https://doi.org/10.1017/S0025315400039047.

Collins, M.A., Pierce, G.J., Boyle, P.R., 1997. Population indices of reproduction and recruitment in *Loligo forbesi* (Cephalopoda: loliginidae) in Scottish and Irish waters. J. Appl. Ecol. 34, 778–786. https://doi.org/10.2307/2404922.

Filice, D.C., Dukas, R., 2019. Winners have higher pre-copulatory mating success but losers have better post-copulatory outcomes. Proceedings of the Royal Society B 286 (1900), 20182838. https://doi.org/10.1098/rspb.2018.2838.

Forsythe, J.W., 2004. Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. Mar. Freshw. Res. 55, 331–339. https://doi.org/10.1071/MF03146.

Forsythe, J.W., Hanlon, R.T., 1989. Growth of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). Aquacult. Fish. Manag. 20, 1–14. https://doi.org/10.1111/j.1365-2109.1989.tb00437.x.

Hanlon, R.T., Smale, M.J., Sauer, W.H., 2002. The mating system of the *squid Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: fighting, guarding, sneaking, mating and egg laying behavior. Bull. Mar. Sci. 71 (1), 331–345. https://www.ingentaconnect.com/content/umrsmas/bullmar/2002/00000071/00000001/art00025.

Hanlon, R.T., Yang, W.T., Turk, P.E., Lee, P.G., Hixon, R.F., 1989. Laboratory culture and estimated life span of the eastern Atlantic squid, *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda). Aquac. Res. 20, 15–34. https://doi.org/10.1111/j.1365-2109.1989.tb00438.x.

Hatfield, E.M., 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: loliginidae). Fish. Res. 47, 27–40. https://doi.org/10.1016/S0165-7836(99)00127-7.

Hosono, S., Masuda, Y., Tokioka, S., Kawamura, T., Iwata, Y., 2024. Squid male alternative reproductive tactics are determined by birth date. Proceedings of the Royal Society B 291, 20240156. https://doi.org/10.1098/rspb.2024.0156.

ICES, 2024. Working Group on Cephalopod Fisheries and Life History (WGCEPH; outputs from 2023 meeting). ICES Scientific Reports 6 (62), 69. https://doi.org/10.17895/ices.pub.26048101.

Iwata, Y., Shaw, P., Fujiwara, E., Shiba, K., Kakiuchi, Y., Hirohashi, N., 2011. Why small males have big sperm: dimorphic squid sperm linked to alternative mating behaviours. BMC Evol. Biol. 11, 1–9. https://doi.org/10.1186/1471-2148-11-236.

Jereb, P., Allcock, A.L., Lefkaditou, E., Piatkowski, U., Hastie, L.C., Pierce, G.J. (Eds.) 2015. Cephalopod biology and fisheries in Europe: II. Species Accounts. ICES Cooperative Research Report No. 325. 360 pp. https://doi.org/10.17895/ices.pub.5493.

Laptikhovsky, V., Allcock, A.L., Barnwall, L., Barrett, C., Cooke, G., Drerup, C., Firmin, C., Lozach, S., MacLeod, E., Oesterwind, D., Petroni, M., Robin, J.-P., Sheerin, E., Power, A.M., Pierce, G.J., 2022. Spatial and temporal variability of spawning and nursery grounds of *Loligo forbesii* and *Loligo vulgaris* squids in ecoregions of Celtic Seas and Greater North Sea. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79 (6), 1918–1930. https://doi.org/10.1093/icesjms/fsac128.

Lipiński, M.R., 1979. Universal maturity scale for the commercially important species. The results of maturity classification of Illex illecebrosus (LeSueur, 1821) population for years 1973–1977. International Commission for Northwest Atlantic Fisheries (ICNAF), Research Document 79/II/38 40. Serial No. 5364.

Lum-Kong, A., Pierce, G.J., Yau, C., 1992. Timing of spawning and recruitment in *Loligo forbesi* (Cephalopoda: loliginidae) in Scottish waters. J. Mar. Biol. Assoc. U. K. 72, 301–311. https://doi.org/10.1017/S0025315400037711.

Mather, J., 2024. Half the picture: sex bias in the study of squid reproductive strategies. Mar. Biol. 171 (9), 175. https://doi.org/10.1007/s00227-024-04490-7.

Moreno, A., Azevedo, M., Pereira, J., Pierce, G.J., 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. Mar. Biol. Res. 3, 49–59. https://doi.org/10.1080/17451000601129115.

Mosteller, F., Brown, G.W., Mood, A.M., Minville, E., Aroian, L.A., Hamilton, C.H., 1948. Questions and answers. Am. Statistician 2 (3), 22–23. https://doi.org/10.2307/2682087.

Ogle, D., 2019. Recruit maturity analysis. IFAR. Retrieved from. http://derekogle.com/IFAR/supplements/maturity/index.html.

Pecl, G.T.A., Steer, M.A.A., Hodgson, K.E.A., 2004. The role of hatchling size in generating the intrinsic size-at-age variability of cephalopods: extending the Forsythe Hypothesis. Mar. Freshw. Res. 55, 387–394. https://doi.org/10.1071/MF03153.

Pierce, G.J., Boyle, P.R., Hastie, L.C., Key, L., 1994. The life history of *Loligo forbesii* (Cephalopoda: loligindae) in Scottish waters. Fish. Res. 21, 17–41. https://doi.org/10.1016/0165-7836(94)90094-9.

Pierce, G.J., Zuur, A.F., Smith, J.M., Santos, M.B., Bailey, N., Chen, C.-S., Boyle, P.R., 2005. Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters. Aquat. Living Resour. 18, 327–340. https://doi.org/10.1051/alr:2005037.

Pierce, G.J., Boyle, P.R., 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. Fish. Res. 59, 305–326. https://doi.org/10.1016/S0165-7836(02)00028-0.

R Core Team, 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rocha, F., Guerra, Á., González, Á.F., 2001. A review of reproductive strategies in cephalopods. Biol. Rev. Camb. Phil. Soc. 76, 291–304. https://doi.org/10.1017/S1464793101005681.

Rocha, F., Guerra, A., 1996. Signs of an extended and intermittent terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: loliginidae). J. Exp. Mar. Biol. Ecol. 207, 177–189. https://www.sciencedirect.com/science/article/abs/pii/S0022098196026317.

Rocha, F., Guerra, A., 1999. Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain). J. Mar. Biol. Assoc. U. K. 79, 697–707. https://doi.org/10.1017/S002531549800085X.

Shaw, P.W., Boyle, P.R., 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: loliginidae), demonstrated with microsatellite DNA markers. Mar. Ecol. Prog. Ser. 160, 279–282. https://doi.org/10.3354/meps.

Tamburi, N.E., Martín, P.R., 2009. Reaction norms of size and age at maturity of *Pomacea canaliculata* (Gastropoda: ampullariidae) under a gradient of food deprivation. J. Molluscan Stud. 75, 19–26. https://doi.org/10.1093/mollus/eyn031.

Wangvoralak, S., 2012. Life History and Ecological Importance of Veined Squid *Loligo forbesii* in Scottish Waters. University of Aberdeen, p. 227. PhD thesis.