

Importance of trophic mismatch in a winter-hatching species: evidence from lesser sandeel

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ABSTRACT: Understanding the mechanisms responsible for variability in fish recruitment can improve our ability to predict the response of marine species to environmental change. The synchrony between fish hatching and zooplankton productivity is widely considered to be a major driver in recruitment failure, but studies considering variability in the phenology of both predator and prey are scarce. Using otolith microstructure and a time series of predator and prey abundance, we studied the influence of the mismatch between fish hatching and the timing of egg production in 2 copepod prey species on recruitment variability in lesser sandeel *Ammodytes marinus*, a key trophic link in the North Sea. We found that year-class strength is established during early larval development in sandeel, and depends on the degree of synchrony between hatching and *Calanus helgolandicus* egg production. Therefore, this study identifies the critical life stage at which year-class strength is established and provides empirical support for the mismatch hypothesis in a key forage fish.

KEY WORDS: Recruitment · Match–mismatch · Phenology · *Ammodytes marinus* · *Calanus* · Year-class strength

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INTRODUCTION

Understanding the mechanisms responsible for recruitment variation has been a major topic in both fisheries science and marine ecology for over a century. Since Hjort (1914) first proposed that food limitation at the time of first feeding determined recruitment success, much research has focussed on the importance of hatching at a suitable time of year, relative to seasonal cycles in prey, predators and sea circulation (Houde 2008). Popular amongst such explanations of recruitment variation is the match–mismatch hypothesis (Cushing 1969, 1975, 1990), which proposes that the synchrony or match between hatching and an appropriate phase of the prey production cycle is an important selective influence on growth and mortality. Central to this hypothesis is the need for sufficient food at the right time to sustain high growth rates for larvae to minimise size-dependent predation (Ware

1975, Shepherd & Cushing 1980, Pope et al. 1994). Climate change has led to different levels of phenological response throughout the marine pelagic community, leading to a greater mismatch between trophic levels (Edwards & Richardson 2004, Richardson 2008).

Though zooplankton–larval fish interactions correspond to the most studied system with regard to the match–mismatch hypothesis, often only zooplankton phenology is considered, assuming the seasonality of fish larvae hatching is fixed (Durant et al. 2005). However, spawning and hatching times are typically variable among years, even in some total spawning species (Wright & Trippel 2009), and there is evidence for mismatch from differences in both the timing of larval hatching and zooplankton production (Wright & Bailey 1996, Huwer et al. 2014). While zooplankton form one of the most important resources for larval fish (Simonsen et al. 2006, Danielsen et al.

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2016), only copepod eggs and early naupliar stages may be suitable prey at first feeding due to limits on gape size and swimming speed (Simonsen et al. 2006, Jackson & Lenz 2016). As there is rarely time-series information on these early copepod stages, later stages are often used to infer fish larval prey availability.

While starvation mortality may be an important consequence of mismatch, sub-optimal feeding conditions may often cause poor growth, affecting larval vulnerability to predation mortality (Houde 2008). Size-dependent mortality might favour individuals that hatch when prey are abundant and can sustain high growth, as the larger individuals at a given age will have a lower probability of mortality than smaller individuals of the same age (i.e. a 'bigger is better' mechanism; Leggett & Deblois 1994). In addition, if the probability of mortality is a decreasing function of size, faster-growing larvae will have a lower probability of mortality compared to slower-growing larvae (i.e. a 'fast growth' mechanism; see Ware 1975, Shepherd & Cushing 1980). Even if mortality rates are size- and growth rate-independent for a given stage, small percentage changes in instantaneous growth rate can have orders of magnitude consequences for the number of survivors reaching a particular developmental stage, and so individuals that reach the stage at younger ages could have a lower probability of mortality (i.e. 'stage duration' mechanism; Houde 1987).

The lesser sandeel *Ammodytes marinus* (Raitt 1934) is an important link between secondary production and higher trophic levels (Wanless et al. 2004). This species shows limited dispersal (Christensen et al. 2008, Gibb et al. 2017), spawns in December and January (Gauld & Hutcheon 1990), and the larvae hatch between February and May and settle in sandy areas between late May and June (Wright & Bailey 1996). All winter-hatching sandeel species have larvae that are able to begin feeding prior to resorbing their large yolk sacs (Yamashita & Aoyama 1986) and can go without food for relatively long periods (around 15 d in *A. marinus*, Winslade 1971). These traits help them to cope with low prey densities which are important as they hatch around the onset of the spring bloom (Wright & Bailey 1996).

If the mechanism responsible for variations in sandeel recruitment is a mismatch with larval prey, **year-class strength (YCS)** is expected to be established at an early stage of development. Consistent with this view, Lynam et al. (2013) found that the abundance of *A. marinus* larvae was correlated with that of later life stages. However, estimates of *A. mar-*

inus biomass in June off the Firth of Forth (east coast of Scotland), derived by combining data from both sediment and water column samples, indicated differences in relative YCS between age 0 and older ages (Greenstreet et al. 2010). This led Heath et al. (2012) to propose that YCS was established between June and the successive year. Nevertheless, estimates of YCS in June might be influenced by movements, as Wright (1996) found that juvenile *A. marinus* continued to enter Shetland grounds until late July.

Copepods are the major prey of sandeel larvae (Ryland 1964, Simonsen et al. 2006), with *A. marinus* **exhibiting an increasing selectivity towards *Calanus finmarchicus* by the late larval stage** in the northern North Sea (Economou 1991). However, in much of the North Sea, ***C. helgolandicus* is the most dominant large calanoid copepod** (Barnard et al. 2004, Hinder et al. 2014), and while egg production culminates in summer and autumn, an initial seasonal increase is observed as early as February in the central western North Sea (Bonnet et al. 2005). Low prey availability at the time of hatching has been linked to a high mortality of first feeding in winter-hatching sandeel larvae (Gilbert et al. 1992) and reduced growth rate (Fortier et al. 1995). Using otolith microstructure, Wright & Bailey (1996) found that low survival in an early hatched cohort of *A. marinus* from around Shetland in 1992 was associated with low prey density. Moreover, they found that the fastest-growing and most abundant year-class arose from the long-term median hatching month. Using simulations of trophic interactions, Gurkan et al. (2012, 2013) also predicted that mismatch may be an important source of recruitment variation in *A. marinus*.

Off the east coast of Scotland, sandeel in the local ICES sandeel Stock Area 4 (ICES 2010), corresponding to the central western North Sea, are recognised to be relatively slow-growing and late-maturing (Boulcott et al. 2007, Rindorf et al. 2016). Since the mid-1980s, a net decline in age-0 length has been observed in June survey catches (Wanless et al. 2004), and inter-annual variation in recruitment is very high (ICES 2015). Using otolith microstructure analysis to consider variations in sandeel phenology may help resolve why such variations occur. The otoliths of sandeel exhibit clearly discernible daily increments from hatching, as well as secondary growth centres formed at settlement (Wright 1993), although comparatively few studies have used otolith microstructure to study the early life history.

In this study, **otolith microstructure was used to estimate hatch date frequency, size and age at settlement of post-settled fish (survivors) from 7 year-**

classes of differing strengths, collected in the Firth of Forth in Stock Area 4 (ICES 2010). In addition, the abundance of newly hatched and juvenile *A. marinus* was used to assess larval loss rate in 5 of these 7 years. By these means, we aimed to (1) identify the life stage at which YCS is determined and (2) assess the effect of these early life history traits on recruitment success. Further, by comparing these traits with weekly sea temperature and zooplankton samples from a monitoring station within the stock area, we evaluated the importance of temporal mismatch between copepod and sandeel phenologies as a driver of recruitment in this key forage fish.

MATERIALS AND METHODS

Sandeel data

June surveys

Post-settled sandeel *Ammodytes marinus* were sampled from the Firth of Forth region in the western North Sea (Fig. 1) in June, using an International Young Gadoid Pelagic Trawl (PT154), fitted with a 6 mm codend, during Marine Scotland Science (MSS) surveys from 1999–2003, 2009 and 2013.

Age (in years) at length was assessed from a subsample of individuals to generate age–length keys for each year, and a multinomial logistic model (Gerriksen et al. 2006) was used to estimate age composition, based on size distribution. These models provide an appropriate way to deal with potentially underrepresented size classes in the size distribution. Post-settled survivor abundances were then calculated as the average density of age-0 *A. marinus* among the different hauls from a given year.

Stonehaven samples

Newly hatched *A. marinus* larval abundances (<8 mm total length, corresponding to fish hatched in the 10 d preceding the capture date; T. Régner unpubl. data) were obtained in 5 years (2000–2003 and 2009) from the MSS Stonehaven coastal ecosystem monitoring site (Fig. 1) which is situated in the middle of ICES sandeel Stock Area 4 (ICES 2010, Fig. 1) and has shown to be representative of adjacent coastal waters (Falkenhaus et al. 2013). For 2013, data for newly hatched larvae were collected in earlier dedicated ichthyoplankton surveys in the Firth of Forth (April and May).

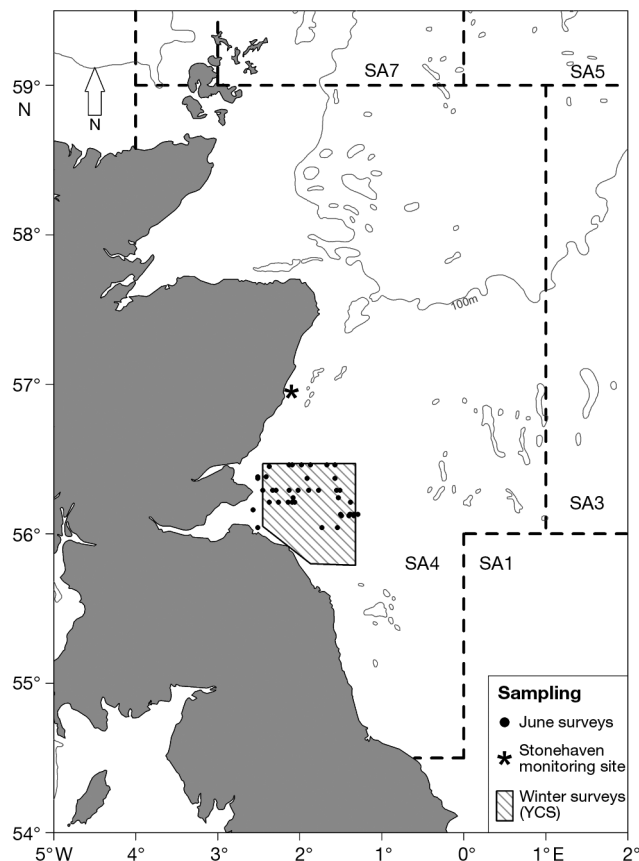


Fig. 1. The central western North Sea, showing ICES Sandeel Areas (SA), the sampling sites for the June surveys providing *Ammodytes marinus* juvenile abundances, the Stonehaven coastal ecosystem monitoring site providing temperature and zooplankton time series (and *A. marinus* larval abundances for the years 2000–2003 and 2009), and the sampling area for the winter surveys providing *A. marinus* year class strength (YCS) estimates

Winter surveys

Age-based catch per unit effort for sandeel Stock Area 4 was taken from the MSS sandeel winter dredge survey (ICES 2010) for the Firth of Forth survey area (Fig. 1) and for the whole assessment area (SA4). The abundance index of age-0 *A. marinus* for the years 1999–2003, 2009 and 2013 is hereafter referred to as YCS. Length and age frequency distributions from the winter dredge surveys for the years 1998–2002, 2008 and 2012 were used to produce an estimate of egg production in the parental generation and how it relates to juvenile abundances.

Hatch date determination through otolith analysis

Sagittal otoliths from *A. marinus* post-settled survivors were cleaned with water and mounted on the

Table 1. Sample sizes (no. of fish) for the variables measured in sandeel *Ammodytes marinus* at the individual level

Variable	1999	2000	2001	2002	2003	2009	2013
Hatch date	70	72	47	45	68	59	73
Age and size at settlement	74	79	41	36	70	47	49

sagittal plane to glass slides with Loctite® Glass Bond. They were polished to the level of the primordium with a range of diamond lapping films (0.5–9 µm), cleaned with ethanol and cleared with immersion oil. Microstructure was analysed using a Zeiss Axioskop 2 Plus light microscope linked to a PC with image analysis software (Image Pro Insight, Media Cybernetics UK). An estimate of age at capture (in days) was made for each otolith by counting the number of increments between the hatch check and otolith edge (Table 1; Wright 1993). Counts were repeated by another independent reader on a subset of otoliths; average percentage error was 3.6 ± 2.2 (SD)% and average coefficient of variation (CV) was 4.66 ± 2.69 %. Ages at capture in 2013 were estimated from lapillae rather than sagittae, but a comparison study between counts from sagittae and lapillae from the same fish showed no significant difference in age between the 2 methods (slope = 1.1; 95% CI = 0.99–1.2, N = 469). Hatch dates were then calculated by subtracting age at capture from the calendar date of capture. Otolith measurements (± 0.01 µm) were made from primordium to edge along the post-rostral axis and along the same axis, from primordium to the start of the secondary growth centre, which is indicative of larval metamorphosis to the juvenile stage (Wright 1993), and used as a proxy for settlement. Counts of increments from hatch check to the start of this secondary growth centre were also made (Table 1).

Sea temperature and zooplankton data

Data on weekly monitoring of sea temperature and zooplankton for the period between 1999 and 2013 were taken from the MSS Stonehaven coastal ecosystem monitoring site (Fig. 1). A 1 m ring net fitted with a 350 µm mesh size net was towed obliquely from a depth within 3 m of the seabed (45 m) to the surface. Zooplankton data comprised the densities ($n\ m^{-3}$) of *Calanus finmarchicus* and *C. helgolandicus*.

Data analyses

Stock recruitment

In order to analyse the influence of egg production on juvenile abundances, egg production was estimated in the parental generation from size frequency distributions obtained from the winter surveys, and calculated as:

$$\text{Eggprod}_{\text{Year}} = \sum_{(j=1)}^n \text{Density}_{(j,\text{Year})} \times \text{SR} \times \text{Mature}_j \times \text{Fecundity}_j \quad (1)$$

where $\text{Eggprod}_{\text{Year}}$ is the density of eggs ($n\ m^{-3}$) produced in a given year, $\text{Density}_{j,\text{Year}}$ is the number of fish m^{-3} for size class j in a given year, SR is the sex ratio (assumed to be 0.5), Mature_j is the proportion of fish of size class j being mature, and Fecundity_j is the average number of eggs produced by mature females of class j . Maturity and fecundity were derived from data obtained in the area off the Firth of Forth in 1999 and 2004 (Boulcott et al. 2007, Boulcott & Wright 2011). Two classical stock-recruitment models were then fitted to YCS as a function of egg production. A Ricker and a Beverton-Holt model were fitted with a non-linear least square method, and goodness of fit was assessed by comparing the residual sum of squares to that of a model with only the mean.

Sandeel hatch date distribution

For every year, hatch dates were grouped into 10 d age classes. Age at length data were then used to produce an age-length key for each year, and a multinomial logistic model was used to estimate 10 d cohort composition, based on length–frequency distributions calculated for each June survey. Cohort abundances for each year were then obtained by averaging abundances of a given cohort obtained from the different subsamples. To compensate for cumulative mortality between early and late hatched cohorts, a daily mortality rate of 0.042 was used, derived from a field measure of the decrease in age-0 abundance between April and June 2013 in the Firth of Forth (T. Régner unpubl. data). For the years 2000–2003 and 2009, hatch date distributions were compared to time series of <8 mm larvae abundance recorded at the Stonehaven monitoring station. Each record of <8 mm larvae was assigned to the 10 d cohort corresponding to the sampling date. For the year 2013, as Stonehaven records were not available,

the abundance of <8 mm larvae corresponding to 2 cohorts was measured from 2 surveys in the Firth of Forth in April and May.

Inter-annual differences in early life history traits

Inter-annual differences in age and size of post-settled survivors were tested using analysis of variance with year as the explanatory factor, and the significance of pairwise differences was estimated with Tukey's honestly significant difference test. Otolith radius at settlement was Box-Cox transformed to satisfy normality of residuals and homogeneity of variances.

Establishment of YCS

In order to assess if YCS is established by settlement, the relationship between YCS (winter) and post-settled survivor abundance (June) was analysed using a linear regression. In addition, an **index of loss rate (incorporating both mortality and advection out of the studied area)** between hatching and June was calculated for the different 10 d cohorts using cohort abundances in Stonehaven (2000–2003, 2009) and Firth of Forth (April and May 2013) and abundances for the corresponding cohorts measured in June:

$$\text{Loss rate}_i = \frac{(\log(\text{Larval abd})_i - \log(\text{post-settled survivor abd})_i)}{\text{time}_i} \quad (2)$$

where time_i corresponds to the number of days between the measure of larval and post-settled survivor abundances (abd) for the i^{th} cohort. **Loss rate is considered as a relative index, as the pelagic and demersal gears used to determine larval and post-settled survivor abundance are expected to differ in terms of catchability.** The effect of this relative index, and early life-history traits such as average size or age at settlement on log-transformed YCS was investigated using linear regression.

Sea temperature time series

A generalized additive model with a thin plate smoothing term on the date and a high basis dimension (90) was fitted to weekly sea temperature time series between January 1998 and December 2013, as it provided an excellent fit ($R^2 = 0.98$) to the temperature data and allowed reasonably reliable extrapolation

for the few weeks when temperature data were not available.

Seasonality of zooplankton egg production

As discrimination at the species level is unreliable prior to Copepodite stage 5 (CV) and earlier stages may be underrepresented in the sample due to mesh size, we relied on CVI stage abundances recorded at the Stonehaven monitoring station for the following estimations of the seasonality of egg production (due to aberrant records in 2001 for *C. finmarchicus*, copepodite stage CV was used for this year instead). From the CVI abundances, we back-calculated the date corresponding to the egg stage using temperature-dependent development times as described by Kvile et al. (2017). As early stage abundances were not available, estimates of mortality during copepod development could not be calculated; thus the back-calculated population-level egg productions were directly estimated from the abundance of the CVI stages and should be considered as a relative measure of abundance for inter-annual comparisons, assuming similar mortalities among years. Therefore, the models are meant to resolve seasonality of zooplankton egg production rather than absolute abundances.

Records of *C. finmarchicus* and *C. helgolandicus* CVI abundances between January and June were considered in order to avoid the summer or autumn peaks present in some species. For the 2 species considered, **egg production was back-calculated** using the following formulae (Cook et al. 2007):

$$\text{Timing}(\text{peak egg production}) = \text{Timing}(\text{CVI peak abundance}) - DT \quad (3)$$

$$\text{and} \quad DT = \frac{1}{b_i(T + T_0)^{2.05}} \quad (4)$$

where DT is development time between the egg and CVI stage, T is temperature (average temperature in the 50 d preceding each CVI record), T_0 is a species-specific temperature parameter for the considered species (*C. finmarchicus*: 9.75°C, *C. helgolandicus*: 6.01°C; Cook et al. 2007), b_i is a stage-specific coefficient (*C. finmarchicus*: 6.186×10^{-5} , *C. helgolandicus*: 8.106×10^{-5} ; Cook et al. 2007), and the exponent (2.05) characterises the temperature response of a large range of copepod species (Corkett et al. 1986). Available published data on both *C. finmarchicus* (Diel & Klein Breteler 1986, Hygum et al. 2000, Campbell et al. 2001) and *C. helgolandicus* (Corkett

1972, Thompson 1982, Diel & Klein Breteler 1986) development at different temperatures were compiled, and the validity of the relationship reported by Cook et al. (2007) was assessed for the observed range of temperatures in Stonehaven (see the Supplement at www.int-res.com/articles/suppl/m567p185_supp.pdf).

A 6-parameter Weibull-type function was then fitted to the smoothed seasonal time series of abundances for each species and life stage (Rolinski et al. 2007). Curve fitting was performed with the 'cardi-dates' package (Rolinski et al. 2007) of the statistical data analysis system R (R Development Core Team 2015). This method provided estimates of the date of maximum spring production for CVI and peak egg production for the species and years considered.

Trophic mismatch

The mismatch index between sandeel hatching and their potential prey was calculated as follows:

$$\text{Mismatch index} = \text{Date of 50 \% sandeel hatching} - \text{Date of maximum CVI OR Egg production} \quad (5)$$

Therefore, a negative mismatch index indicates that sandeel hatched before the peak of zooplankton production, and a positive mismatch index indicates that sandeel hatching occurred after the peak of zooplankton. The relationships between temporal mismatch (for the 2 copepod species and 2 life stages: egg and CVI stages) and YCS were investigated using linear regressions. The mismatch indices are hereafter referred to as $M_{A,Cf}$ and $M_{A,Ch}$ for the mismatch with the date of maximum adult abundances for *C. finmarchicus* and *C. helgolandicus*, respectively, and $M_{E,Cf}$ and $M_{E,Ch}$ for the respective back-calculated dates of maximum egg production. The relationship between larval loss rate and mismatch index is expected to take a parabolic shape with loss rate minimised when sandeel hatching matches the phenology of their prey. Accordingly, the relationship between cohort loss rate and cohort mismatch index was investigated using a mixed effect polynomial regression of the second order to account for year effects, with:

$$\text{Loss rate}_{iy} = \alpha + \beta_1(\text{mismatch}_{iy}) + \beta_2(\text{mismatch}_{iy})^2 + u_y + \varepsilon_{iy} \quad (6)$$

where Loss rate_{iy} is the loss rate for cohort i in year y . α , β_1 and β_2 are the parameters for the fixed effects on the linear and quadratic terms, u_y represents the random effects, and ε_{iy} represents the error term. Model selection was based on Akaike's information crite-

rion (AIC). The relationship between annual loss rate and annual mismatch was investigated with linear regression.

Relative zooplankton egg abundance during sandeel hatching was calculated as the area under the curve of back-calculated egg production (Eq. 1) using the linear trapezoidal rule during a period of 30 d centred on median sandeel hatching date. The relationship between YCS and zooplankton egg abundance during sandeel hatching was investigated using linear regressions. All statistical analyses were performed with the open source software R 3.2.2 (R Development Core Team 2015).

RESULTS

Stock recruitment

There was no clear relationship between YCS and estimated egg production, as both Beverton-Holt and Ricker stock-recruitment models provided a poor fit to the data considering that ratios of residual sum of squares on total sum of squares (defined by a model with only the mean) were 1 or above (Beverton-Holt: 1, Ricker: 1.5).

Sandeel hatch date distribution

All hatch date distributions estimated from larval abundances in Stonehaven overlapped with hatch date distributions back-calculated from post-settled survivors captured in June surveys (Table 2). These survivor hatch date distributions differed among years (Table 2), with median hatching dates being as early as the first week of March in 2001 (Days 60–69), and as late as the first week of April in 2013 (Days 90–99, Fig. 2). Length of the hatching period, measured as the number of days between the centres of the 10 d periods when 5% and 95% of sandeel had hatched, was variable (Table 2). In 1999 and 2013, the hatching period was short and lasted 20 d, while in 2001, 2003 and 2009 hatching lasted 40 d (Fig. 2).

Inter-annual differences in early life history traits

Age at settlement varied among years ($F_{6,389} = 12.61$, $p < 0.001$); however, the extent of inter-annual variation was low, with average settlement age ranging from 53 to 59 d old (Table 2). Size (distance between otolith core and secondary growth centre along

Table 2. Calendar days of the year (DOY) of 5, 50 and 95 % of the cumulated hatching distributions of sandeel *Ammodytes marinus* for the studied years. Length of the hatching period (number of days between 5 and 95 % hatching) is also indicated. Numbers within brackets correspond to hatch date distributions estimated from abundances of newly hatched larvae (<8 mm total length) recorded at Stonehaven. Average traits of post-settled juveniles are indicated with standard deviation within brackets. Otolith radius at settlement is used as a proxy for size at settlement

Year	Central DOY of the 10 d interval			Traits at settlement		
	5 %	50 %	95 %	Hatching period	Age (d)	Otolith radius (μm)
1999	65	75	85	20	59.2 (4.7)	118.6 (14.1)
2000	65 (75)	85 (85)	95 (85)	30 (10)	52.7 (4.8)	107.0 (11.6)
2001	45 (55)	65 (75)	85 (105)	40 (50)	57.2 (3.8)	118.9 (14.2)
2002	65 (65)	75 (85)	95 (95)	30 (30)	54.2 (4.0)	116.1 (11.6)
2003	45 (55)	75 (75)	85 (95)	40 (40)	55.3 (4.2)	118.8 (12.9)
2009	55 (55)	75 (75)	95 (85)	40 (30)	53.1 (4.6)	124.0 (21.6)
2013	75	95	95	20	57.3 (4.9)	124.7 (14.3)

the post-rostral radius) at settlement was also variable among years ($F_{6,389} = 18.06$, $p < 0.001$) and was statistically smaller in 2000 than in any other year (Table 2). YCS was unrelated to both average age ($F_{1,5} = 0.024$, $p = 0.96$) and average size at settlement (using otolith radius at settlement as a proxy, $F_{1,5} = 1.23$, $p = 0.32$).

Establishment of YCS

There was a strong positive relationship between YCS in winter and post-settled survivor abundance in the preceding June survey (Fig. 3a), indicating that sandeel year class strength was established before June. In addition, YCS was negatively related to loss rate between hatching and June (Fig. 3b; calculated for the years 2000–2003 and 2009, $F_{1,3} = 25.38$, $r^2 = 0.89$, $p = 0.01$).

Back-calculation of egg production

Measured dates of spring maximum zooplankton abundances were variable among years for the 2 copepod species considered, ranging from mid-April (Day 110) in 2003 to early June (Day 154) in 2001 for *C. finmarchicus*, and from early May (Day 121) in 2001 to mid-May (Day 138) in 2013 for *C. helgolandicus* (Table 3). Accordingly, back-calculated dates of peak egg production were also vari-

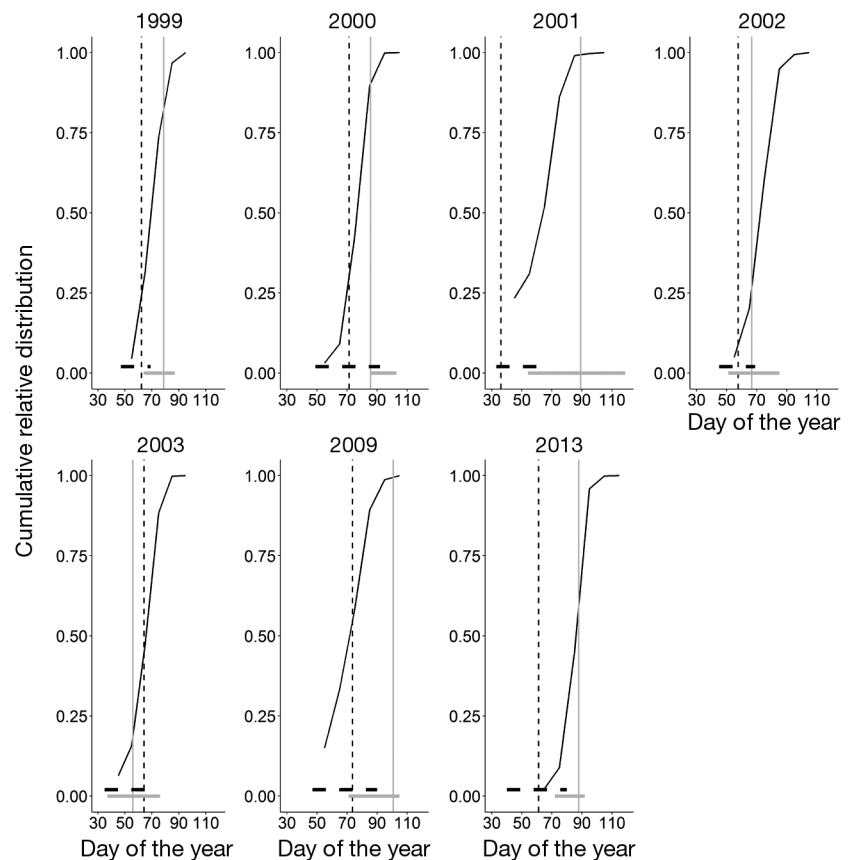


Fig. 2. Cumulative sandeel *Ammodytes marinus* hatch date (day of the year) distribution for the different years studied. Estimated dates of peak egg production are indicated by a vertical line (grey: *Calanus finmarchicus*; black dashed: *C. helgolandicus*) and horizontal lines indicate the length of egg production for *C. finmarchicus* (grey) and *C. helgolandicus* (black dashed)

able, ranging from the end of February (Day 56) in 2003 to mid-April (Day 101) in 2009 for *C. finmarchicus* and from early February (Day 36) in 2001 to mid-March (Day 74) in 2009 for *C. helgolandicus* (Table 3).

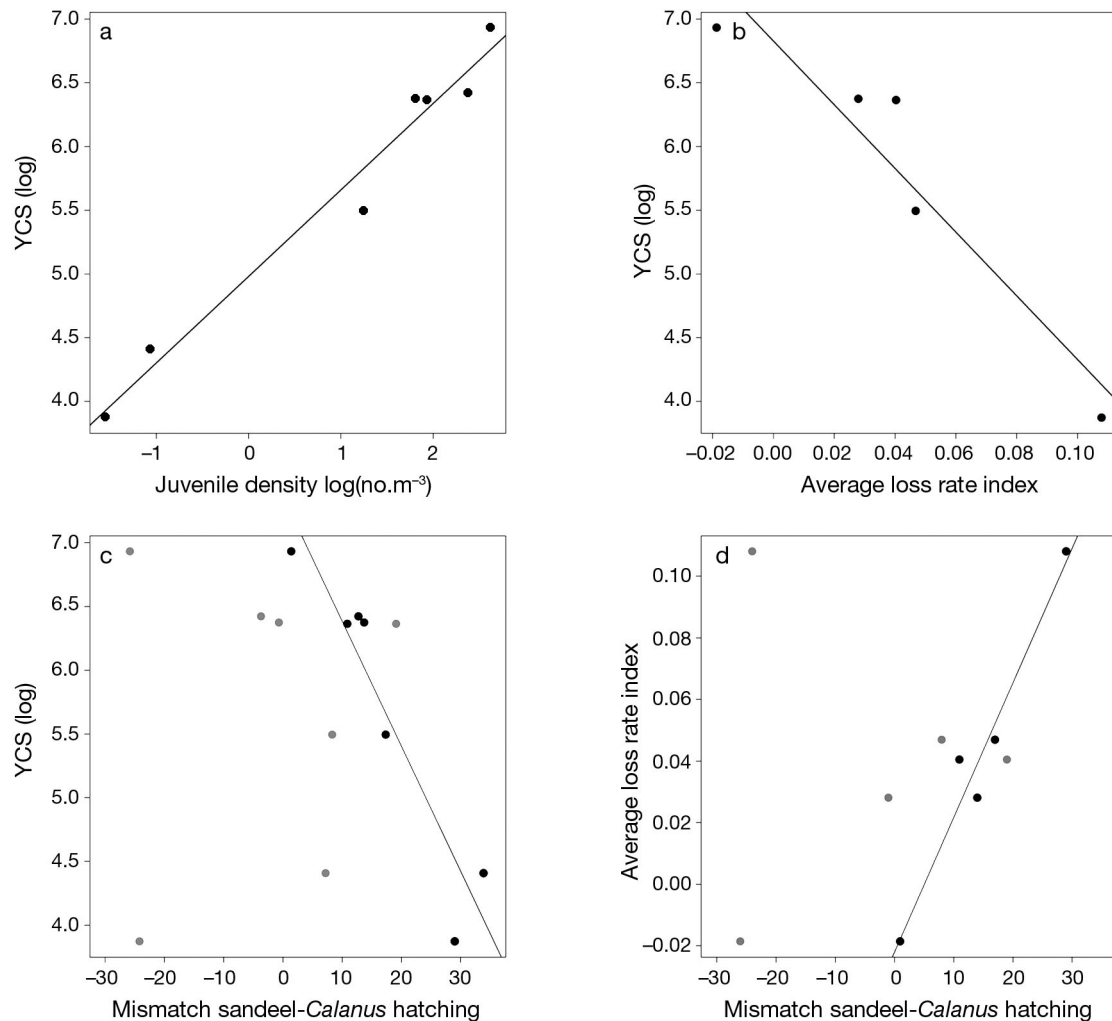


Fig. 3. Relationships between: (a) year-class strength (YCS) and juvenile densities of sandeel *Ammodytes marinus* estimated from length–frequency distributions in June ($F_{1,5} = 169.1$, $r^2 = 0.97$, $p < 0.001$); (b) YCS and annual loss rate index calculated between hatching and June ($F_{1,3} = 26.5$, $r^2 = 0.89$, $p = 0.01$); (c) YCS and the mismatch between sandeel median hatching date and *Calanus* egg production; and (d) annual loss rate in sandeel between hatching and June and the mismatch with dates of maximum egg production for *C. finmarchicus* ($M_{E,Cf}$, grey dots) and *C. helgolandicus* ($M_{E,Ch}$, black dots, solid line)

Trophic mismatch

No relationship was found between *Ammodytes marinus* YCS in winter and $M_{A,Cf}$ ($F_{1,5} = 0.96$, $p = 0.37$) and $M_{A,Ch}$ ($F_{1,5} = 1.325$, $p = 0.3$). YCS was also unrelated to $M_{E,Cf}$ ($F_{1,5} = 0.04$, $p = 0.84$). However, a highly significant relationship was found between YCS and $M_{E,Ch}$ ($F_{1,5} = 39.9$, $r^2 = 0.89$, $p = 0.001$, Fig. 3c). For the 5 years with available data of sandeel hatching in Stonehaven, a highly significant relationship was also found between YCS and $M_{E,Ch}$ ($F_{1,3} = 47.6$, $r^2 = 0.94$, $p = 0.006$). The average larval loss rate calculated between hatching and June was related to $M_{E,Ch}$ ($F_{1,3} = 63.4$, $r^2 = 0.95$, $p = 0.004$, Fig. 3d).

It is important to note that for the year characterised by the highest YCS (i.e. 2009), the $M_{E,Ch}$ was slightly over 1 d, corresponding to a synchronous hatching of sandeel and *C. helgolandicus*. Accordingly, the YCS index was related to the estimated relative abundance of *C. helgolandicus* eggs during a period of 30 d centred on sandeel median hatching date ($F_{1,5} = 10.1$, $r^2 = 0.67$, $p = 0.02$), but not to that of *C. finmarchicus* ($F_{1,5} = 5.6$, $p = 0.06$). At the cohort level, loss rate was found to vary with $M_{E,Ch}$ through a quadratic relationship (Table 4) showing minimum loss rates when sandeel hatched within 10 d following the peak of *C. helgolandicus* egg production (Fig. 4).

Table 3. Cardinal dates (day of year, DOY) of January to June zooplankton abundances, estimated for the adult stages (Copepodite vI, CVI) of *Calanus finmarchicus* and *C. helgolandicus* and back-calculated DOY of maximum egg abundance. Max.: maximum

Year	Peak start–end	DOY of max. abundance	Abundance at peak (n m ⁻³)	DOY of max. egg abundance
<i>Calanus finmarchicus</i>				
1999	95–148	125	12.86	79
2000	96–161	127	3.43	86
2001	121–176 ^a	154 ^a	6.57 ^a	89 ^a
2002	90–141	122	5.57	67
2003	88–129	110	4.18	56
2009	120–151	145	93.98	101
2013	125–147	138	26.27	88
<i>Calanus helgolandicus</i>				
1999	109–146	131	7.88	62
2000	106–165	136	3.88	71
2001	101–138	121	3.56	36
2002	105–134	122	17.94	58
2003	100–132	127	10.59	64
2009	115–150	136	10.7	74
2013	113–154	138	16.9	61

^aDenotes measures and estimates based on CV stage

Table 4. Output of the mixed effect polynomial regression of sandeel *Ammodytes marinus* cohort loss rate on cohort mismatch: $\text{Loss rate}_{iy} = \alpha + \beta_1(\text{mismatch}_{iy}) + \beta_2(\text{mismatch}_{iy})^2 + u_y + \varepsilon_{iy}$ (Eq. 6), where Loss rate_{iy} is the loss rate for cohort i in year y . α , β_1 and β_2 are the parameters for the fixed effects on the linear and quadratic terms, u_y represents the random effects, and ε_{iy} represents the error term

Fixed factor	df	Loss rate χ^2	p
β_1	1	29.9	<0.001
β_2	1	24.3	<0.001
Random factor	Variance		
u_y		0.00054	
Residual (ε_{iy})		0.00027	

DISCUSSION

The degree of synchrony between sandeel larvae hatching and estimated egg production of their copepod prey provided the most parsimonious explanation for the observed variation in YCS in *Ammodytes marinus*. Few other studies have provided such clear empirical support for the mismatch hypothesis (Fortier & Cagne 1990, Fortier et al. 1995, Theilacker et al. 1996). Mismatch arose both from differences in

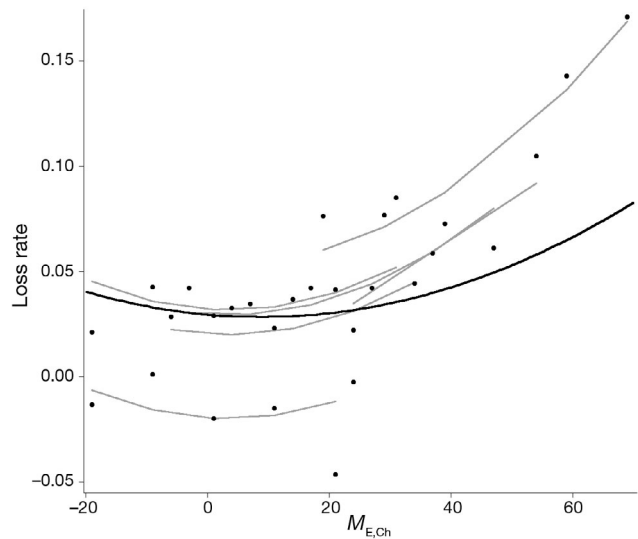


Fig. 4. Relationship between sandeel *Ammodytes marinus* cohort loss rate index and the mismatch with dates of maximum egg production for *Calanus helgolandicus* ($M_{E,Ch}$). Cohorts refer to individual sandeels hatched within each 10 d interval for the years 2000 (5 cohorts), 2001 (5 cohorts), 2002 (6 cohorts), 2003 (6 cohorts), 2009 (5 cohorts) and 2013 (2 cohorts). Average relationships are shown in black; grey shows annual variations associated with random effects on the intercept and the linear term of the quadratic regression

the timing of copepod production and sandeel hatch date. Hence, contrary to the original mismatch hypothesis of Cushing (1969, 1975), variation in the timing of fish hatching as well as plankton prey was important. Inter-annual variation in sandeel hatch date composition has previously been reported both for this species (Wright & Bailey 1996) and others including *A. personatus* (Kimura et al. 1992). However, no other empirical study has accounted for inter-annual variability in both the predator and prey phenologies or considered the appropriate prey life-stage relevant to newly hatched fish.

Sandeel YCS measured in winter was related to juvenile densities estimated from pelagic trawls in June, but not to estimated egg production in the parental generation. In addition, YCS was related to the loss rates estimated between hatching (in Stonehaven) and settlement (June), indicating that year class strength in *A. marinus* is established between these life stages. These results are thus in accordance with evidence from trawl surveys around Shetland in June and July (Wright 1996) and the correlation with larval survey abundance reported by Lynam et al. (2013), but are contrary to the proposal of Heath et al. (2012) who, based on a composite index of sandeel age-0 abundance (derived from different fishing

gears; Greenstreet et al. 2010), suggested that variations in abundance were determined between the first summer and the following spring. As juvenile sandeel form pelagic feeding schools in June (Winslade 1971, Wright 1996), pelagic gears appear to be the most relevant sampler available to provide an index of age-0 sandeel abundance in early summer. Juvenile abundance in June and loss rate indices may result from 2 combined processes, namely mortality (direct through starvation or indirect through a longer exposure to predation related to reduced growth) and dispersal out of the study area (Peck et al. 2012).

YCS was not related to variations in either age or size at settlement, indicating no support for the 'bigger is better' mechanism (Leggett & Deblois 1994), or that a shorter duration of the 'vulnerable' larval stage (Chambers & Leggett 1987, Houde 1987) affected recruitment. Insufficient longitudinal data precluded the study of inter-annual and inter-cohort variation in growth rate, their dependence on zooplankton phenology and their consequences to sandeel recruitment. Consequently, we cannot say whether differences in loss rate were related to growth rate during the larval phase and so have no direct test of the 'fast growth' mechanism (Shepherd & Cushing 1980). However, while the relative contributions of direct and indirect mortality cannot be determined in the present study, biophysical models do predict high retention off the Scottish east coast (Proctor et al. 1998, Christensen et al. 2008), suggesting that advection is not the main driver of variations in *A. marinus* recruitment.

The results of our study highlight the need to consider both prey and predator phenologies when studying the match–mismatch hypothesis, as both the timing of *A. marinus* hatching and the seasonal increase in zooplankton were variable over the period considered in this study. Analysis of otolith microstructure revealed up to 1 mo difference in the dates when 50% of *A. marinus* had hatched, and 2-fold differences in the duration of the hatching periods. These results are similar to those obtained by Wright & Bailey (1996) in Shetland between 1990 and 1992, with up to 40 d differences in median hatching dates and hatching periods lasting between 31 and 53 d. Although no other study has considered early survival from otolith microstructure in our study area, Frederiksen et al. (2011) applied growth models to length data from larvae extracted from the Continuous Plankton Recorder and age-0 sandeel caught by puffins in June and July. From these estimated growth rates, they inferred that a decline in sandeel size in June

was initially related to later hatch dates, followed by slower growth rates. In comparison, our results based on aged individuals did not show any trend in hatch dates for the years overlapping with their study, although there was a large inter-annual variation. YCS was not solely related to *A. marinus* hatching date, nor was it linked to the temporal mismatch between sandeel hatching and the peak of maximum abundance of *Calanus finmarchicus* ($M_{A,Cf}$) or *C. helgolandicus* adult stages ($M_{A,Ch}$).

As gape size limitation makes copepod eggs and first naupliar stages the only suitable prey for newly hatched *A. marinus* (Economou 1991, Simonsen et al. 2006), early survival is expected to depend on the *Calanus* species producing eggs at the time of sandeel hatching. In accordance, the degree of mismatch between *A. marinus* hatching and the back-calculated timing of *C. helgolandicus* egg production ($M_{E,Ch}$) was tightly related to recruitment success (Fig. 3c). The year characterised by the highest recruitment corresponded to synchronous hatching of sandeel and egg production of *C. helgolandicus*. When loss rate index and $M_{E,Ch}$ were considered at the cohort level, high mismatch corresponded to high loss rates during the larval period (Fig. 3d). Surprisingly, no relationship was found between sandeel recruitment and the mismatch with the timing of *C. finmarchicus* egg production ($M_{E,Cf}$). These results are opposite to the association between *A. marinus* recruitment and *C. finmarchicus* abundances and the lack of association with *C. helgolandicus* found in a previous correlative study (van Deurs et al. 2009), although they only considered late *Calanus* copepodite stage abundances in February. While *C. helgolandicus* is a coastal species presenting a seasonal low abundance in May in the North Sea (Planque & Fromentin 1996, Jónasdóttir et al. 2005), *C. finmarchicus* invade the North Sea from the overwintering stock situated in the Northeast Atlantic (Backhaus et al. 1994, Heath et al. 1999). Therefore, the spring abundance maximum used to back-calculate egg production in *C. finmarchicus* in this study might be composed in large part of these immigrating overwintering individuals, which might explain the lack of relationship found between *A. marinus* recruitment and $M_{E,Cf}$. Instead, *A. marinus* larvae appear to rely on egg production by *C. helgolandicus*, for which reproduction at these dates and temperatures has been reported (Corkett 1972, Thompson 1982, Laabir et al. 1995, Irigoien et al. 2000, Bonnet et al. 2005). In accordance, YCS was positively related to the estimated relative abundances of *C. helgolandicus* eggs during *A. marinus* hatching. Due to the

back-calculation of egg production and lack of mortality estimates, these relative abundances mirror the adult spring abundances and need to be considered with caution, as inter-annual variations in *Calanus* mortality might alter these results. Nonetheless, as *C. helgolandicus* is around 10 times more abundant than *C. finmarchicus* in the study area (Falkenhaus et al. 2013), its apparent relevance to *A. marinus* is perhaps not surprising.

Our results indicate that recruitment in *A. marinus* is maximised when hatching is synchronous with *C. helgolandicus* egg production. As a 2°C change in water temperature is predicted to lead to a 2 to 3 wk change in the seasonality of *Calanus* peak abundance (Maar et al. 2013), it is relevant to consider how such a change may affect mismatch. According to development time measured in *A. americanus* (Smigielski et al. 1984), a 1 wk change in embryonic development is expected under a similar scenario. Therefore, provided that *A. marinus* embryonic response to temperature is similar to that of *A. americanus*, and that spawning dates remain the same, rising temperatures would lead to a greater mismatch between sandeel hatching and *Calanus* egg production. Sandeel larvae hatch with a yolk-sac, providing a 'buffer' period of around 15 d allowing them to survive at low food abundance (Winslade 1971, Buckley et al. 1984). However, the rate at which fish larvae deplete their yolk and therefore are able to resist starvation is inversely related to temperature (Winslade 1971, Laurel et al. 2011). In addition, due to the rapid growth of *Calanus* copepods (Cook et al. 2007), the favourable time window when suitable prey are abundant is relatively narrow. As a consequence, rising temperature might narrow the favourable window for first feeding and increase the cost of mismatch resulting in poor recruitment in this key forage fish, with consequences carrying over multiple trophic levels (Engelhard et al. 2008).

CONCLUSION

The match–mismatch hypothesis has been frequently invoked as a driver of recruitment in fish over the last decades. Most support for this hypothesis comes from correlations between stock level recruitment and indices of prey abundance (Arnott & Ruxton 2002, Beaugrand et al. 2003, Durant et al. 2005, van Deurs et al. 2009), but very little direct empirical evidence is available. In this study, otolith microstructure analysis and information on prey hatching have been combined to challenge the

match–mismatch hypothesis. Recruitment success of a key forage fish, *Ammodytes marinus*, was linked to the availability of young stages of *Calanus helgolandicus* at the time of hatching. With *A. marinus* being the target of numerous marine predators and the largest industrial fishery in the North Sea, our results support the need for careful management of sandeel in the present context of rising sea temperatures. Further research is now needed to understand the causes of variations in sandeel hatch date in order to anticipate the potential consequences of this mismatch at the scale of the North Sea ecosystem.

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