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North Sea herring (*Clupea harengus* L.) recruitment failure may be indicative of poor feeding success

Susan Mærsk Lusseau[1]*, Alejandro Gallego[1], Jens Rasmussen[1], Emma M. C. Hatfield[1], and Mike Heath[1,2]

[1]*Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK*
[2]*Present address: Department of Mathematics and Statistics, University of Strathclyde, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH, UK*

*Corresponding author: tel: +44 1224 876544; fax: 44 1225 295511; e-mail: s.lusseau@marlab.ac.uk

Recruitment of the 2002–2012 year classes to the North Sea herring stock has been below expectations given the spawning biomass, due to exceptionally low overwinter survival of larvae. Here, we investigate whether changes in survival of larvae in the northwestern North Sea could be attributed to changes in parasite prevalence or feeding conditions. We used a method that combined particle tracking models and survey data to estimate survival, and microscopic examination of gut contents of archived samples of larvae collected in February each year between 1995 and 2007 to investigate parasite prevalence and feeding. We deduced that we can use the incidence of tetraphyllidean parasites as an index of the cumulative feeding history of the larval population. We found that the prevalence of larvae of a tetraphyllidean cestode in the gut contents varied significantly between years and was positively correlated with feeding success. High feeding success, indicated by high prevalence of tetraphyllideans, influenced survival by offsetting the effect of a second parasite type, a digenean trematode. We suggest that variability in cumulative food intake over the lifespan up to February is a significant determinant of variability in survival.

Keywords: feeding success, fish larvae, North Sea herring, overwintering, parasites, recruitment, survival.

Introduction

The North Sea herring stock has experienced a sustained and unprecedented period of low productivity since 2002 (Payne *et al.*, 2009). Although the spawning-stock biomass has been consistently high and well above the level where impaired recruitment is expected to set in, the number of recruits produced per spawner continues to be at the lowest levels recorded (ICES, 2013).

In the northwestern North Sea, herring spawn along the east coast of Scotland and around the Orkney and Shetland Islands, with spawning commencing in the north around August–September and progressing south into the early winter (Heath and Richardson, 1989). The larvae develop over winter and metamorphose in early spring the following year. During this period, the developing larvae are fully planktonic and disperse with the prevailing currents to a potential North Sea-wide distribution. It is over this period that the strength of the recruiting year-class in North Sea herring is determined (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009).

The International Council for the Exploration of the Seas (ICES) coordinates two surveys of North Sea herring larvae. The first one is carried out in autumn and produces an index of abundance of newly hatched larvae on the spawning grounds. The second survey is

carried out towards the end of winter and measures abundance of the late stage larvae that have survived winter development period. Despite a consistently high larval production measured in autumn surveys, the abundance of late stage larvae just before metamorphosis is at an all-time low (ICES, 2013). The poor recruitment, it is concluded, is linked to increased mortality rates during this overwinter larval development period (Payne *et al.*, 2009; Fässler *et al.*, 2011). The causes of the increased mortality remain under investigation and several explanatory hypotheses have been proposed (ICES, 2007).

Corten (2013) argued that cannibalism by adult herring could explain the change in survival. Hufnagl and Peck (2011) used a physiological individual-based model of the foraging and growth of herring larvae to demonstrate a possible link with temperature and prey composition and concentrations, with the timing around first feeding being particularly sensitive. Increased temperatures, particularly in the northern North Sea, were also linked to increased mortality rates in the northern components of herring larvae by Fässler *et al.* (2011). Payne *et al.* (2009) and ICES (2007) suggested a link between the poor herring larvae survival and changes in the North Sea physical and biological environment. Edwards *et al.* (2007) documented a shift in the North Sea plankton community

towards a more diverse warmer-water community around 2000, just before the onset of the period of poor herring recruitment (Payne *et al.*, 2009). A similar regime shift in the North Sea in the late 1980s has been linked to reduced survival of larvae of Atlantic cod (*Gadus morhua* L.) in the North Sea through changes in the availability and suitability of prey (Beaugrand *et al.*, 2003). The increased temperature in the North Sea has also been linked to changes in the distribution of many fish species, with the potential for increased predation on herring larvae (Payne *et al.*, 2009). Coincidences between changes in herring larvae survival and, for example, shifts in the zooplankton community composition or changes in the temperature regime experienced only provide clues about the processes that may be involved in the decline in recruitment. Both of these factors have the potential to affect survival rates of fish larvae either directly or indirectly by affecting growth rates (Leggett and DeBlois, 1994, Houde 2002). Such a link between the growth rates of herring larvae in the North Sea and their survival was recently demonstrated by Payne *et al.* (2013). However, without direct evidence of a change in diet composition or food intake, it is not clear exactly how or whether these changes in the plankton community might have been involved in the changes in recruitment.

Heath and Nicoll (1991) investigated the relationship between helminth parasite infection and feeding incidence in herring larvae from the 1987 year class in the North Sea. They found significantly lower feeding incidence in herring larvae infected with larvae of tetraphyllidean cestodes (*Scolex pleuronectes*) and suggested that the survival of herring larvae could be impacted as a consequence. However, the year class they investigated did not suffer from low survival and they suggested that population level effects could possibly be observed at very high prevalence.

The potential for parasites to act as major regulators of animal populations has been well described (May, 1983; Minchella and Scott, 1991). They can affect their host organism in many ways, including altering their behaviour (Lafferty and Morris, 1996) and competing with them for nutrients. Additionally, their presence and activities can lead to physical damage to the host (Rosenthal, 1967; Ivanchenko and Grozdilova, 1985). All these effects can lead to lower survival through decreased growth rates, severe physical damage, or by exposing the host to increased predation risk.

Herring larvae are infected with tetraphyllidean cestode larvae through the ingestion of infected copepods (Rosenthal, 1967; Marcogliese, 1995). The adult cestodes are generally restricted to elasmobranch fish and herring larvae are only one of many intermediate hosts for this parasite (Marcogliese, 1995). Both Heath and Nicoll (1991) and Rosenthal (1967) reported an increase in the intensity of parasite infection with increasing size of herring larvae indicating that the infection accumulates over time. Rosenthal (1967) did not observe any obvious detrimental effects on the herring larvae at relatively low intensities of infection in an aquarium experiment, but did notice that one herring larvae with a heavy infection (8 parasites) was impeded in its swimming ability.

Parasites such as tetraphyllidean cestode larvae, which are acquired through the diet and are relatively benign, accumulate in host populations and individuals and can therefore provide an index of cumulative feeding history (Campbell *et al.*, 1980; Williams *et al.*, 1992). High prevalence of infection is acquired, therefore, either through a generally higher intake of food in high prevalence years or a proportionally higher intake of infected prey.

Digenean trematodes are also commonly found in herring larvae (*Brachyphallus crenatus*, Ivanchenko and Grozdilova, 1985; *Lecithaster gibbosus*, Tolonen and Karlsbakk, 2003; *Hemiurus* sp.,

Karlsbakk *et al.*, 2003 and Heath and Nicoll, 1991, *Derogenes varicus*, Karlsbakk *et al.*, 2003). The primary host of digeneans is a mollusc from which free swimming cercaria are released to infect intermediate hosts, typically calanoid or harpacticoid copepods (Køie, 1979, 1989, 1990, 1992), which are the main prey of herring larvae (Checkley, 1982; Cohen and Lough, 1983; Munk, 1992). Some digenean trematodes such as *D. varicus* grow and feed inside herring larvae but do not typically reach maturity in this host, whereas others such as *Hemiurus* sp. can grow to maturity and reproduce in herring larvae (K. Mackenzie, unpublished data). Heath and Nicoll (1991) rarely found an intensity of digeneans exceeding one and observed no increase with the length of larvae and therefore no accumulation of parasites over time. Their conclusion was that herring larvae were only exposed to the infective stages of the digeneans for a brief period. However, a similar pattern would be observed if the accumulation of parasites in the herring larvae was detrimental and larvae with heavier infection were removed from the population. Such a scenario is supported by Ivanchenko and Grozdilova (1985). They reported detrimental effects on White Sea herring larvae from the digenean trematodes *L. gibbosus* and *B. crenatus*. The parasites damaged the mucous membranes of the herring intestines, causing embolisms which ultimately inhibited the passage of food, resulting in cessation of feeding and death.

Given the different patterns of infection and pathogenicity of tetraphyllidean cestode and digenean trematodes in larval herring, it is likely that their incidence provides different information on the feeding ecology of the host. Digeneans would be expected to have a negative effect on feeding success and therefore potentially on survival. In contrast, tetraphyllidean cestode larvae should have less direct impacts on survival and instead provide insights into feeding conditions experienced over the lifespan of the herring larvae.

The aim of this study was to investigate some of the mechanisms related to food consumption by which survival of herring larvae may have changed over 12 years, spanning periods of both good and poor recruitment. Key to our approach was the fact that larvae feeding in the wild coincidentally acquire gastroenteric parasites. The different behaviours and pathogenicity of parasite species means that their incidence can potentially be used to infer patterns of food intake and survival. If helminth parasite infection plays a role in the recent poor recruitment of North Sea herring, through a reduction in feeding incidence as suggested in Heath and Nicoll (1991), we would expect to see a difference in the pattern of parasite infection between years of high and low overwinter survival of herring larvae.

Material and methods
Selection of herring larvae specimens

Since 1977, late stage herring larvae in the North Sea have been surveyed as part of the ICES coordinated International Bottom Trawl Survey (IBTS, ICES, 2006). The synoptic survey is carried out by research vessels from participating institutes during late January and February, and measures abundance of herring larvae using a 2 m ringnet, the Methot–Isaacs–Kidd net (ICES, 2006). This component of the IBTS survey is commonly referred to as the MIK survey in reference to the net used.

Archived specimens of formaldehyde preserved herring larvae caught during the Marine Scotland Science (MSS) contributions to the ICES MIK surveys in February were available to this investigation. The samples were collected in the northwestern North Sea (Figure 1) and provided an opportunity to investigate stomach

contents and infection with intestinal parasites over a succession of years with varying levels of overwinter survival. We chose to focus our study on herring larvae collected during the period 1995–2007 (1994–2006 year classes) to cover both the most recent period of poor survival (2002–2007) and a period before this with "normal" survival in the North Sea as a whole (1995–2001, Payne *et al.*, 2009).

The key feature of our study was the analysis of diet composition and gastroenteric parasite incidence between different years. However, parasite infection and feeding by herring larvae has been shown to vary geographically and with body size (Heath *et al.*, 1989; Heath and Nicoll, 1991; Munk, 1992; Busch, 1996). Hence, to avoid confounding our results with these factors, it was necessary to restrict our analysis to larvae from a standardized geographical area and size range.

A geographical subset of the available samples was defined such that in every year, there were >100 specimens of larvae available for analysis from a common set of ICES statistical rectangles. The area within which these samples were collected was referred to as the "study area". Within this geographical subset, the abundance in 1 mm length classes was extracted from the MIK survey database for the Scottish component and the median and quantiles calculated for each year. We selected a common length interval for examination that was contained within the 5th and 95th quantiles in every year and spanned the median of the length distribution for the majority of years.

The formaldehyde-preserved specimens of larvae from the geographical subset were rinsed thoroughly in water and measured to the nearest millimetre. Only larvae within the chosen length range were subsequently dissected. The entire digestive tract was removed under a dissecting microscope with needles and placed in a drop of a
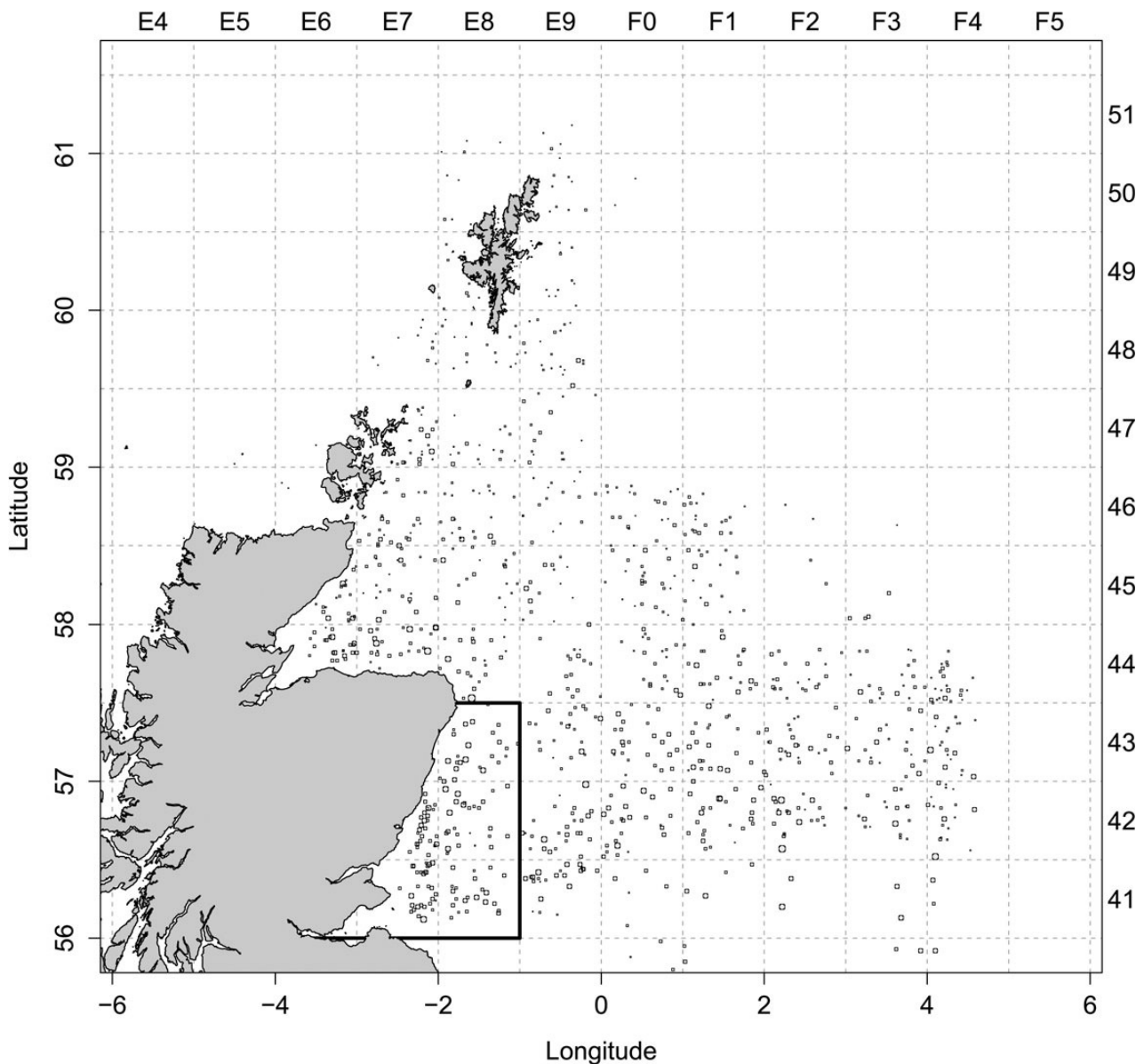
Figure 1. Location of study area in the northwestern North Sea off north-eastern Scotland and position of all hauls taken during the MSS component of the MIK survey in January–February between 1995 and 2007. Bubble radius is proportional to the number of larvae caught in each haul with the largest size corresponding to 510 larvae.

mixture of water and glycerine (50/50 mixture) for easier handling. Only digestive tracts that were found to still be intact after extraction were examined further.

Prey items and parasites were extracted, identified, and measured as they were encountered. All parasites were photographed and identification of type specimens was confirmed by an independent expert (K. MacKenzie, University of Aberdeen, pers. comm.).

Herring larvae survival

Two internationally coordinated surveys provide global indices of abundance of herring larvae in the North Sea both before and after the winter period.

The ICES International Herring Larvae Survey (IHLS) is carried out in autumn (September–October) and winter (December–January) each year and samples larvae with a fine-mesh plankton net (250 μm mesh) at predetermined stations covering the main spawning areas: Orkney-Shetland, Buchan, Central North Sea, and Downs (Figure 2, Heath, 1993). The herring larvae caught in each haul are counted and measured to the nearest millimetre below, and the data are processed to estimate the abundance (number m^{-2}) of newly hatched larvae (<10 mm length) for each ICES statistical rectangle (1° longitude × 0.5° latitude). For each of the four sampling units (Figure 2), a larval abundance index (LAI) is calculated by summing the larval abundances for all
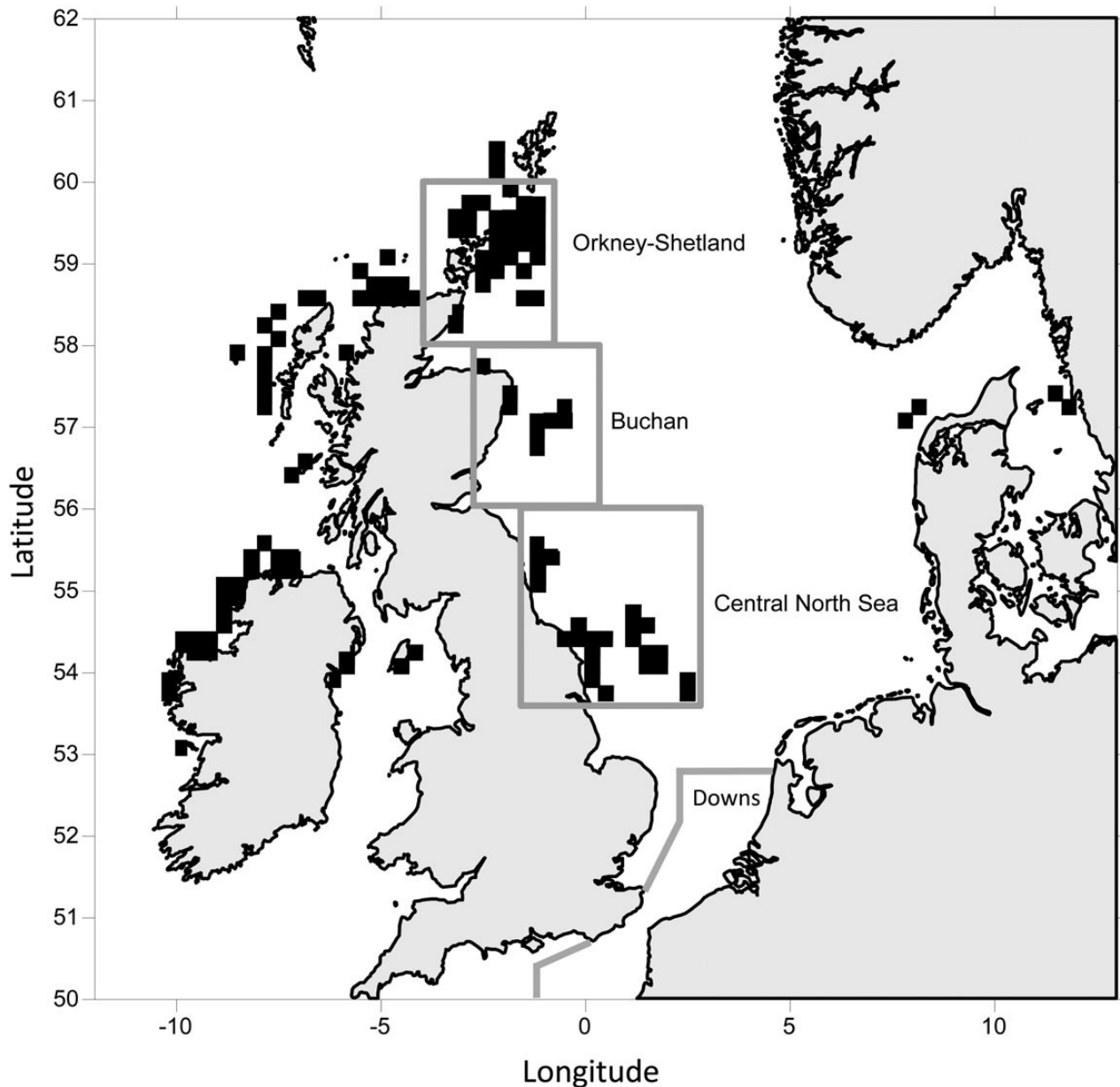
Figure 2. Locations of North Sea herring spawning distribution in autumn (August to September in Orkney-Shetland, Buchan, and Central North Sea) and winter (December – January in Downs) determined from catches of yolk-sac herring larvae, ripe fish, and haddock with herring eggs in the stomach (Based on Heath and Richardson, 1989). In the particle simulations, particles were released from all areas marked in black corresponding to known autumn spawning locations. Grey rectangles shows the delineation of North Sea herring spawning components as defined in the International Herring Larvae Survey. No particles were released within the Downs component area.

rectangles contained in the unit. Difficulties in interpreting this time-series due to missing observations, high sampling noise, and differences in the spawning intensity between surveys (ICES, 2013) have led to the development of the spawning component abundance index (SCAI, Payne, 2010). The SCAI is a statistical model designed to analyse the LAI's from the IHLS and provides an index of abundance of newly hatched larvae for each of these spawning components. The SCAI has been shown to be robust to the challenges posed by the LAI time-series and the index has been used in the assessment of North Sea herring since 2012 (ICES, 2013).

Over the winter period, the developing herring larvae disperse with the prevailing currents to a potential North Sea-wide distribution. In the late winter, a second survey of these surviving herring larvae is carried out. This is the MIK survey mentioned above and it covers the whole of the North Sea during late January and February. The abundance index resulting from this survey—the IBTS0 index—is expressed as total abundance of late stage herring larvae in the North Sea and is used as a recruitment index in the assessment of North Sea herring (ICES, 2013).

These two surveys cover the entirety of the known distribution of both newly hatched and late stage larvae of North Sea herring. Abundance of late stage larvae in late winter at any point in the North Sea is a function of larval production in spawning areas in autumn, dispersal of the larvae, and mortality during the intervening period. The proportional relationship between the SCAI for all spawning components and the IBTS0 index therefore provides an index of survival of herring larvae over the winter period on a North Sea-wide scale. We calculated a North Sea-wide survival index for the study period (1995–2007) as a straight ratio between the sum of SCAI for all four spawning components (from Payne, 2013) and the IBTS0 index (from ICES, 2013, Table 2.3.3.1).

Local survival index

The North Sea-wide survival index however does not automatically apply to our local study area. Because the study area covered only a fraction of the total distribution of both early and late stage larvae, and because distribution of early and late larvae is not uniform throughout the North Sea (ICES, 2008), it was necessary to calculate a local index of survival that took account of dispersal patterns.

The dispersal of larvae was accounted for using a particle tracking model to estimate the proportional contribution of the different spawning components to the abundance of larvae in the study area in February. The SCAI for each of these individual spawning components provided the magnitude of larval production in these spawning areas and it was then possible to calculate an index of expected abundance in the study area in February if no mortality was experienced along the advection paths. The actual abundance of larvae in the study area in February was calculated from the MIK survey hauls from the study area for each year. The proportional relationship between the observed actual and the modelled expected abundance was taken as an index of survival. The index was not considered to be an absolute estimate of the mortality rate each year, but was used to compare relative local survival among years.

The Buchan spawning area was not surveyed in 1994 and 1995 and the level of uncertainty for the Buchan component of SCAI for these 2 years is almost double of that for the remaining series as a consequence (Payne, 2010). We felt unjustified to use these modelled values without any underlying observations for those 2 years in the Buchan component SCAI. It was thus not possible

to estimate the survival of herring larvae in the study area for 1994 and 1995.

Particle tracking

The particle tracking model was based on methods described by Heath and Gallego (1998). The basis of the model was that year-specific daily horizontal flowfields were produced by the SNAC model (Logemann *et al.*, 2004), forced with atmospheric pressure data extracted from the ECMWF Operational Analysis dataset (ECMWF 2006–2008). The horizontal resolution of the model was 0.125° latitude by 0.250° longitude, which corresponds to a distance of 13.9 km in latitude and ∼13.5–15.5 km in longitude over the domain of interest. The model was run for the period mid-September (day 258, or 15 September) to the end of February (168 days duration) in each of the start-years 1994–2006.

Particles were released from all "wet" (i.e. water depth >0 m) start positions on a 5×5 km grid covering all the known autumn spawning areas of herring identified in Heath and Richardson (1989) in both the North Sea and to the west of Scotland (Figure 2). No particles were released in the Downs area as the timing (December/January) and the location of spawning of this component makes it unlikely that larvae with this origin should be present in our study area as demonstrated by hydrographic modelling in Dickey-Collas *et al.* (2009).

Twenty-five particles were released from each start location, each of which had the potential to follow a unique trajectory due to the effects of horizontal diffusion which was parameterized as a stochastic process in the model. A total of 148 625 particles were released over all areas. Although 25 particles per release location was the maximum we could use within the constraints of our computing hardware, exploratory sensitivity analyses suggested that an adequate number of particles was $n < 50$ (see Gallego, 2011). In addition, we carried out a number of identical simulations (using 1994 flowfields) and estimated that, for that number of particles, the coefficient of variation resulting from stochastic processes was ∼8%.

The tracking time-step was 1 h and particle positions were stored daily. All particles migrated with a sinusoidal diel vertical migration pattern between 5 and 45 m depth. The number and origin of particles reaching the study area within the month of February were extracted from the dataset of daily tracks of all simulated particles (Figure 3). To account for differences in abundance of larvae between different years and spawning areas, particles were weighted with the year- and area-specific SCAI at their origin. Interannual differences in the (unweighted) number of particles reaching the target area were the result of interannual differences in transport patterns from each spawning area, while interannual differences in the (weighted) simulated larvae abundance index were the result of the combination of interannual differences in transport patterns from each spawning area and annual differences in their respective SCAI-derived weighting. The total number of expected arrivals could not be calculated for 1994 and 1995 due to the lack of surveying in the Buchan area as mentioned above.

Observed abundance of late stage larvae in February

An annual abundance index for late stage herring larvae in the study area was calculated based on samples of herring larvae taken within the limits of the study area during the ICES MIK survey in February, including only samples with the mean larval length of 20 mm or more. This follows the procedure used to produce the IBTS0 abundance index of late stage herring larvae for the North Sea, based on
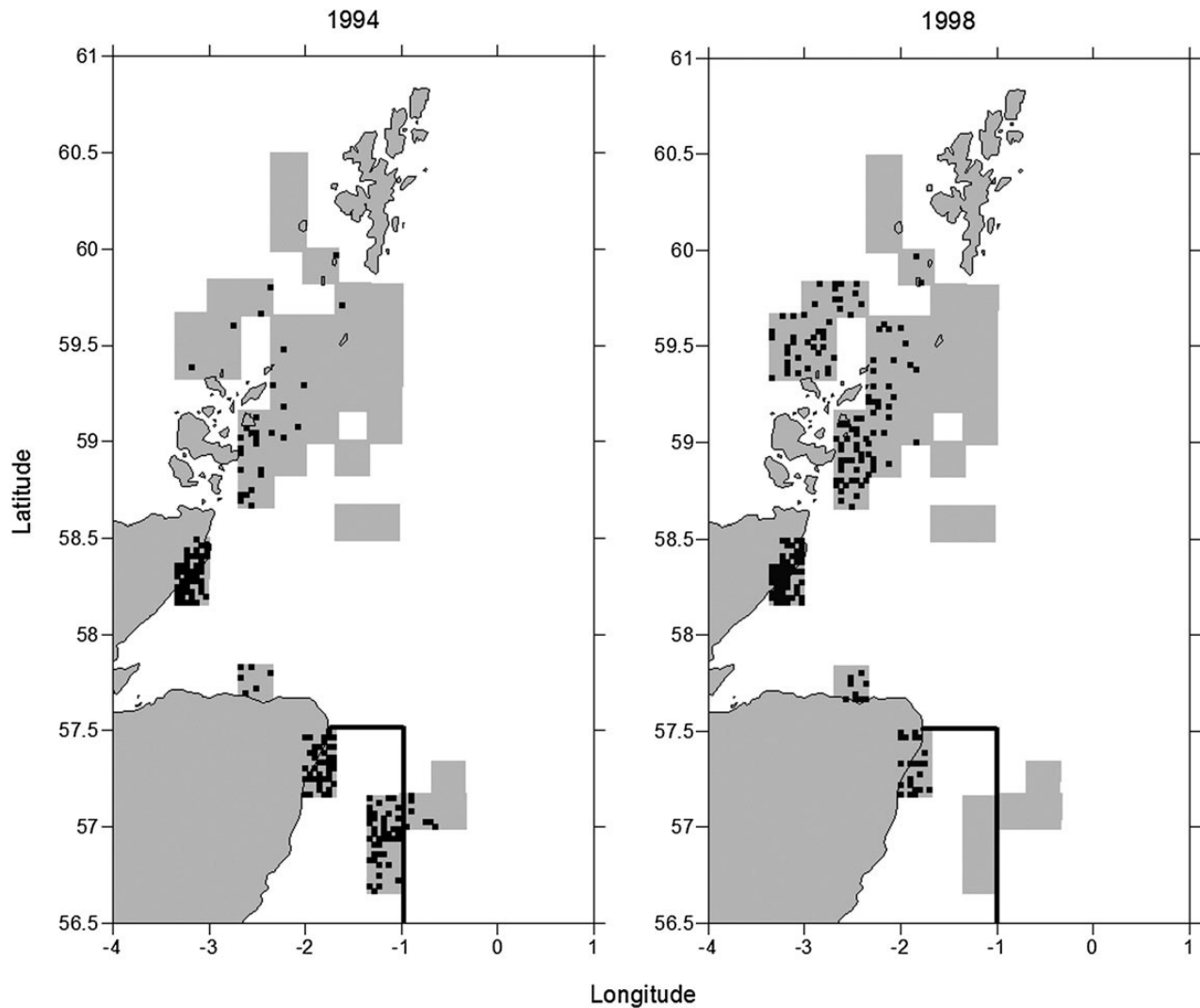
Figure 3. Results from particle tracking simulations for particles released on 15 September from known herring spawning grounds in the North Sea between 1994 and 2006. Example of two contrasting years (left: 1994 spawning; right: 1998 spawning) when particles recorded within our study area at any time during February originated from quite different source locations. Spawning grounds (particle release areas) are represented by grey shading on the maps. Black dots represent the origin of the particles that subsequently reached our study area (outlined in black).

these same surveys (ICES, 1996). The mean abundance per square metre was calculated for each sampled ICES rectangle within the study area and this number was raised by the "wet" surface area of the corresponding rectangle to obtain a total number of larvae per rectangle. The total number of larvae was summed over all rectangles surveyed and divided by the number of rectangles surveyed to obtain the mean number of larvae per surveyed ICES rectangle. The total number of larvae in the study area was obtained by multiplying the mean number of larvae per surveyed ICES rectangle with the number of ICES rectangles in the study area ($n = 5$).

## Data analysis
Survival and parasites
We tested whether the survival of herring larvae was influenced by the prevalence of tetraphyllidean and digenean parasites by fitting a general linear model (lm function in R version 3.0.1) to the data with log-transformed survival modelled as a response and tetraphyllidean and digenean prevalence as independent variables. Survival was log-transformed to satisfy the assumption of normality of residuals and diagnostics plots confirmed constant variance with the mean after transformation. The best fitting model was selected by comparing the Akaike information criteria corrected for sample size (AIC_c) and the adjusted R^2-values for the models.

Feeding incidence
We tested the hypothesis that feeding incidence of herring larvae in the study area was similar for larvae with and without parasites. Feeding incidence was measured by the presence or absence of prey items in the herring larvae and larvae were characterized as having either no parasites, digenean trematodes, or tetraphyllidean cestode larvae present in the intestine. To take into account the anticipated effect of time of day of capture on feeding incidence, we included this parameter in the model as time-lag from sunset to capture time.

Given the sampling structure of this study and the patchy distribution of both larvae and prey in the environment, larvae captured
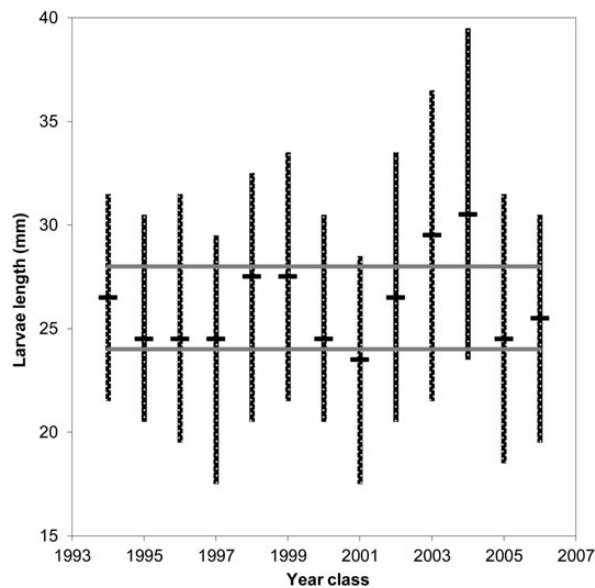
Figure 4. Yearly length distribution of herring larvae caught in the study area on the MSS component of MIK surveys between 1995 and 2007 (year classes 1994–2006). Median length is represented by the short horizontal bars and the error bars extend from the 5th to the 95th quantile. The long horizontal bars at 24 and 28 mm represent the minimum and maximum length of larvae selected for use in this investigation.

in the same haul would potentially have been subject to more similar feeding conditions than larvae coming from different hauls. Larvae captured from the same haul were therefore considered pseudo-replicates of that haul. To account for this, we used a generalized linear mixed-effects model (binomial distribution, logit link function, lme4 package in R version 3.0.1, Bates *et al.*, 2013) with haul included as a random effect to assess how the parasite state of the larvae influenced the likelihood that the larvae had been feeding (GLMM-parasite).

The model was validated following the guidelines provided by Bolker *et al.* (2009).

Results

Study area and length ranges of larvae

When aggregated over all years in the period 1995–2007, the MSS component of MIK surveys in February showed that herring larvae were concentrated in the coastal strip (25–35 km wide) along the northeast of Scotland and in a band stretching eastwards across the North Sea between 56 and 57°N. However, there was considerable interannual variability in this pattern, and when this was taken into account the area where larvae were most consistently caught was between 56 and 57.5°N, between the coast and 1°W (Figure 1). This area (the study area) defined the geographical subset of samples used in the project.

Within the study area, the length distribution of larvae in February varied between years (Figure 4), with larvae from the 2003 and 2004 year classes being particularly large, and those in 1997 and 2001 year classes being particularly small. These differences imply differences in growth rate between years, or differences in age at capture, or a combination of the two. Differences in growth rate and age at capture could reflect variations in the hatching origin of larvae. A length interval of 24–28 mm met the criteria for

defining a subset of lengths to be examined for gut contents (i.e. spanned the median in all but 3 years and was contained within the 5th and 95th quantiles in all years).

Particle tracking and survival

The spatial distribution of particle releases was constant from year to year, reflecting the fixed locations of spawning grounds. However, the locations of release sites that produced particles which arrived in the study area off the east coast of Scotland in February varied from year to year, reflecting interannual variations in the transport patterns (Figure 3). It is worth noting that all particles that reached the target area in the month of February originated from the Orkney-Shetland and Buchan spawning areas (41 950 and 10 675 particles released yearly, respectively).

The total number of particles recorded in the study area during February showed marked differences between years (Figure 5a). The year- and area-specific SCAI also varied among years and between the two areas contributing particles to the study area (Figure 5b). Overall, the Orkney-Shetland spawning area contributed the largest amount of simulated larvae to the study area in all years (79.5–99.0%) with a peak in contribution from the Buchan spawning area for the 2002 year class (Figure 5c).

The expected total abundance of herring larvae in the study area based on these model results varied between years with a prominent peak in the 2002 year class (Figure 6a). This variation could not be attributed solely to either of the two sources of variation examined with the particle drift simulation but was the result of both interannual differences in transport pattern and area- and year-specific differences in larval production.

The observed abundance in February in the study area, calculated from local survey data, also varied among years, with higher values in the early part of the study period and again in the last 2 year classes (Figure 6a). The resulting clear variation in survival among years of herring larvae caught within the study area was adequate for investigating the relation between survival and potential causal factors (Figure 6b).

In contrast to the North Sea-wide survival, which was consistently low for all year classes between 2002 and 2006 (Figure 6b), the local survival index was more varied and shows increasing survival of the two latest year classes investigated. While numbers of herring larvae in the MIK surveys remained low for the North Sea as a whole, the proportion captured within the study area increased considerably in the last years included in this analysis, accounting for up to 28% of the total population in the North Sea (Figure 7).

### Herring larvae feeding and diet

We dissected a minimum of 30 herring larvae per year for the period 1995–2007 (1994–2006 year class), adding up to a total of 454 larvae for the study. Parasite and prey incidence was recorded for all 454 larvae dissected. For the majority of the larvae, a full analysis of gut content was also carried out. For 21 of the dissected larvae, only parasite and feeding incidence was noted (Table 1).

A total of 1641 prey items were identified from the dissected intestines (Table 1). Over the entire study period, small calanoid copepods (31%), the cyclopoid *Oithona* spp. (38%), and copepod nauplii (12%) dominated the diet by numbers. This highlights the importance of small copepods in the diet of herring larvae in the study area. The calanoid copepods were almost entirely *Paracalanus* sp. (50%), *Pseudocalanus* sp. (21%), and *Acartia* sp. (8%).
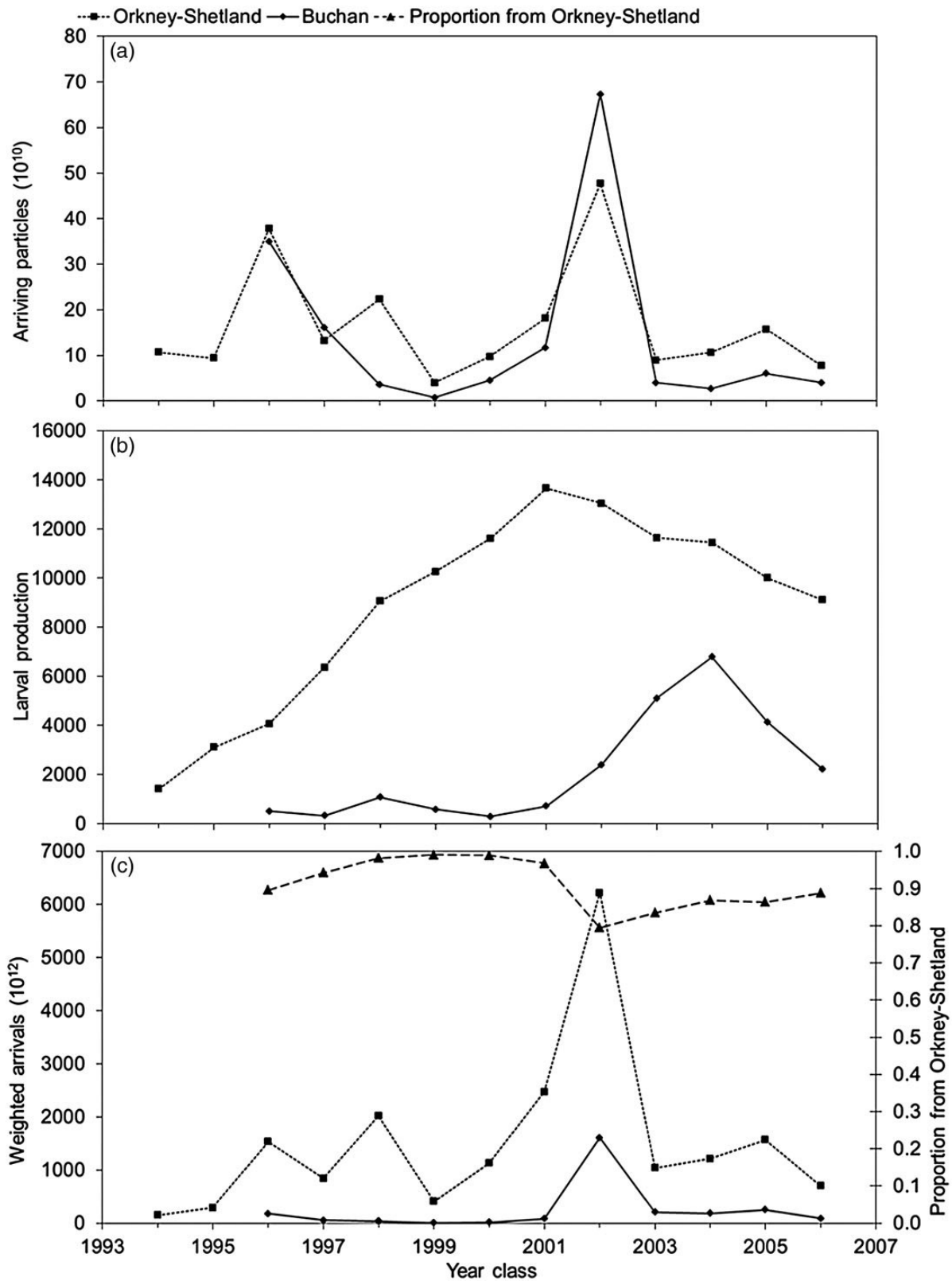
Figure 5. (a) Number of particles representing herring larvae modelled to have arrived in study area during February after release on 15 September in the previous year in Orkney-Shetland and Buchan spawning areas. (b) Size of larval production in Orkney-Shetland and Buchan spawning areas given as SCAI. (c) Relative number of larvae expected to arrive in study area from Orkney-Shetland and Buchan spawning grounds as number of particles arriving weighted by size of larval production at the origin (SCAI). Proportional contribution of the Orkney-Shetland spawning area is also indicated. Year class refers to the year particles were released, i.e. when larvae hatched.
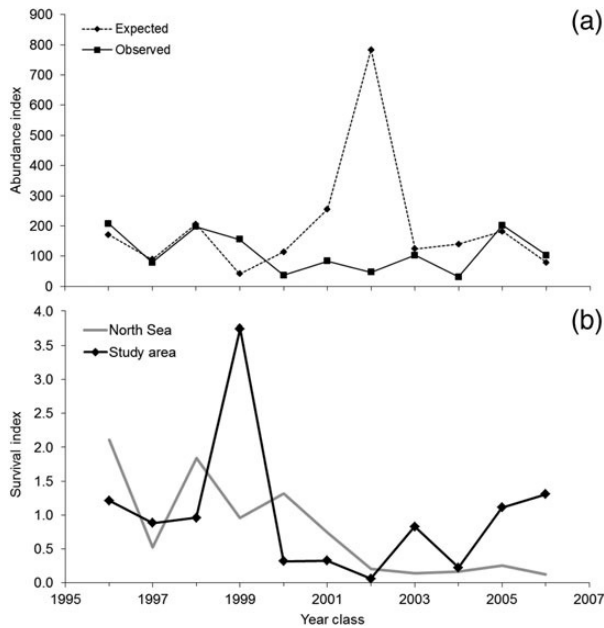
Figure 6. (a) Indices of expected abundance of herring larvae in study area (assuming no mortalities sustained during drift phase) based on particle tracking model (abundance $\times 10^{13}$) and the actual observed abundance in study area calculated from the MIK survey data (abundance $\times 10^{8}$). (b) Indices of survival in the study area, calculated in this study, and the entire North Sea expressed as a ratio between the summed SCAI's and the IBTS0.
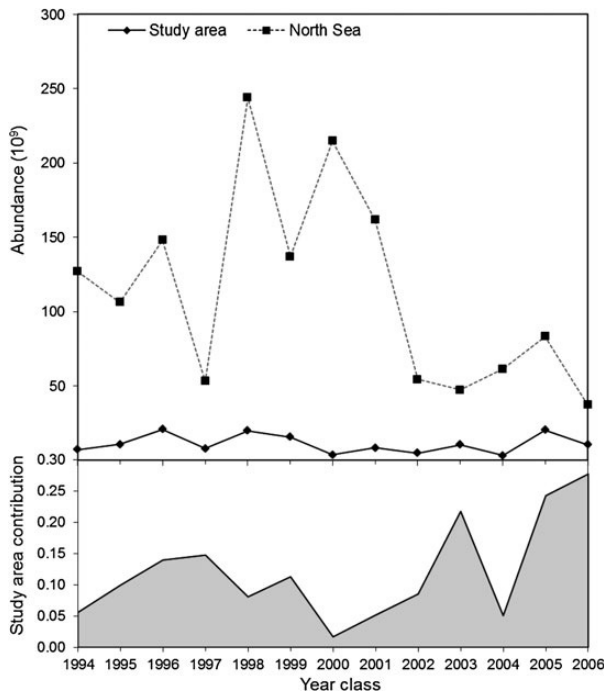
Figure 7. Total abundance of herring larvae in North Sea, the IBTS0 index, and in study area during MIK surveys in the North Sea between 1995 and 2012 (1994–2011 year classes). Lower panel indicates proportion within study area.

Prey items were observed in 117 (26%) of the guts examined. This proportion varied widely among years between 0 and 80%, resulting in very little or no data available for some years with

respect to food composition (Table 1). Since herring larvae are visual predators and generally do not feed at night, the incidence of prey items in the guts was expected to decline with time after sunset. For some years, all samples in the study area were taken very late in the night and for these years, very few larvae had any prey items in them (1994 and 1997 year class in particular, Table 1). The very small proportion of guts containing prey items in these years made it inappropriate to perform further detailed analyses regarding changes in prey composition among years.

Parasites in herring larvae

Two types of parasitic helminths were found in the intestines of the larval herring. One was a digenean trematode (*D. varicus*) and the other was larvae of tetraphyllidean cestodes otherwise known under the species complex *Scolex pleuronectis*. The prevalence (proportion of larvae carrying parasites) of both parasite types showed marked variation among years ranging from 0 to 0.35 for digeneans and 0.03 to 0.33 for tetraphyllideans (Figure 8). The mean prevalence over the entire study period was higher for tetraphyllideans (0.15 ± 0.05) than for digeneans (0.09 ± 0.05). The intensity (number of parasites per larvae) of digeneans only ever exceeded one in the 1999 year class, whereas it was common to find several tetraphyllideans in a single herring larva, with three being the maximum observed (Figure 8). The intensity of infection of tetraphyllideans seemed to be higher in year classes with high prevalence. The two types of parasites were co-occurring in seven herring larvae (Table 2). This was considered too few to justify inclusion as a category in the analysis, but since there was no information available as to the possible effects of the two parasite types being present simultaneously in one larva, these were excluded from the subsequent analyses on the effects of parasites on herring larvae feeding and survival.

Survival and parasites

We tested the hypothesis that survival of herring larvae was influenced by the prevalence of tetraphyllidean and digenean parasites. A model including an effect of the interaction between the two parasite species in Table 3 was the best fitting model based on the AIC_c. This best fitting model indicated that digenean prevalence had a negative effect on survival and that there was a significant positive interaction between tetraphyllidean and digenean prevalence (Table 4). The model provided a good fit to the data and explained 53% of the variation in survival (Table 3). There was little support to keep the main effect of tetraphyllidean prevalence in the model (Table 3). The fitted model met the assumptions for general linear models (Figure 1, Supplementary data).

The significant interaction between the prevalence of the two parasites indicates that the effect of the digenean parasite on survival depends on the level of tetraphyllidean prevalence (Figure 9). When the prevalence of tetraphyllideans was low, there was a strong negative effect of digenean prevalence on survival, but with increasing prevalence of tetraphyllidean cestodes, this negative effect was eliminated and at higher levels of tetraphyllidean prevalence, there was no effect of prevalence of either parasite on survival (Figure 9).

**Feeding incidence**

We also tested the hypothesis that feeding incidence of herring larvae in the study area was similar for larvae with and without parasites using a generalized linear mixed-effects modelling approach.

With a ratio of residual deviance to residual degrees of freedom of 0.75 ($\chi^2 = 332.5$, d.f. $= 442$, $p = 1$), the model was not found to be

Table 1. Analysis and feeding information (four top rows), and number of prey items by year and type found in herring larvae captured between 1995 and 2007 (1994–2006 year classes).

	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Total
Larvae dissected	30	32	83	34	31	31	31	30	30	30	32	30	30	454
Larvae with prey	0	15	17	1	9	8	9	10	5	12	2	5	24	117
Feeding incidence (%)	0	47	20	3	29	26	29	33	17	40	6	17	80	26
Larvae with full prey identification	0	15	17	1	9	8	9	10	2	11	1	5	8	96
Calanoid copepods		77	78	0	5	8	47	54	11	60	5	102	62	509
Cyclopoid copepods		106	105	0	52	21	37	68	7	94	0	109	25	624
Harpacticoid copepods		0	0	0	0	0	0	1	0	0	0	0	0	1
Poecilostomatoid copepods		0	13	0	2	0	1	0	0	0	0	0	3	19
Copepod unspecified		1	3	0	3	1	2	10	0	7	0	15	9	51
Nauplii		58	40	0	41	0	5	9	1	34	0	0	4	192
Isopoda		0	0	0	1	0	0	0	1	0	0	0	0	2
Crustacean remains		1	0	0	2	0	0	2	0	0	0	0	1	6
Eggs		7	8	0	28	2	8	8	1	0	0	3	8	73
Molluscs		3	42	0	59	1	1	1	0	2	0	1	3	113
Unidentified prey		10	0	1	12	7	0	7	0	3	0	3	8	51
Grand total		263	289	1	205	40	101	160	21	200	5	233	123	1 641
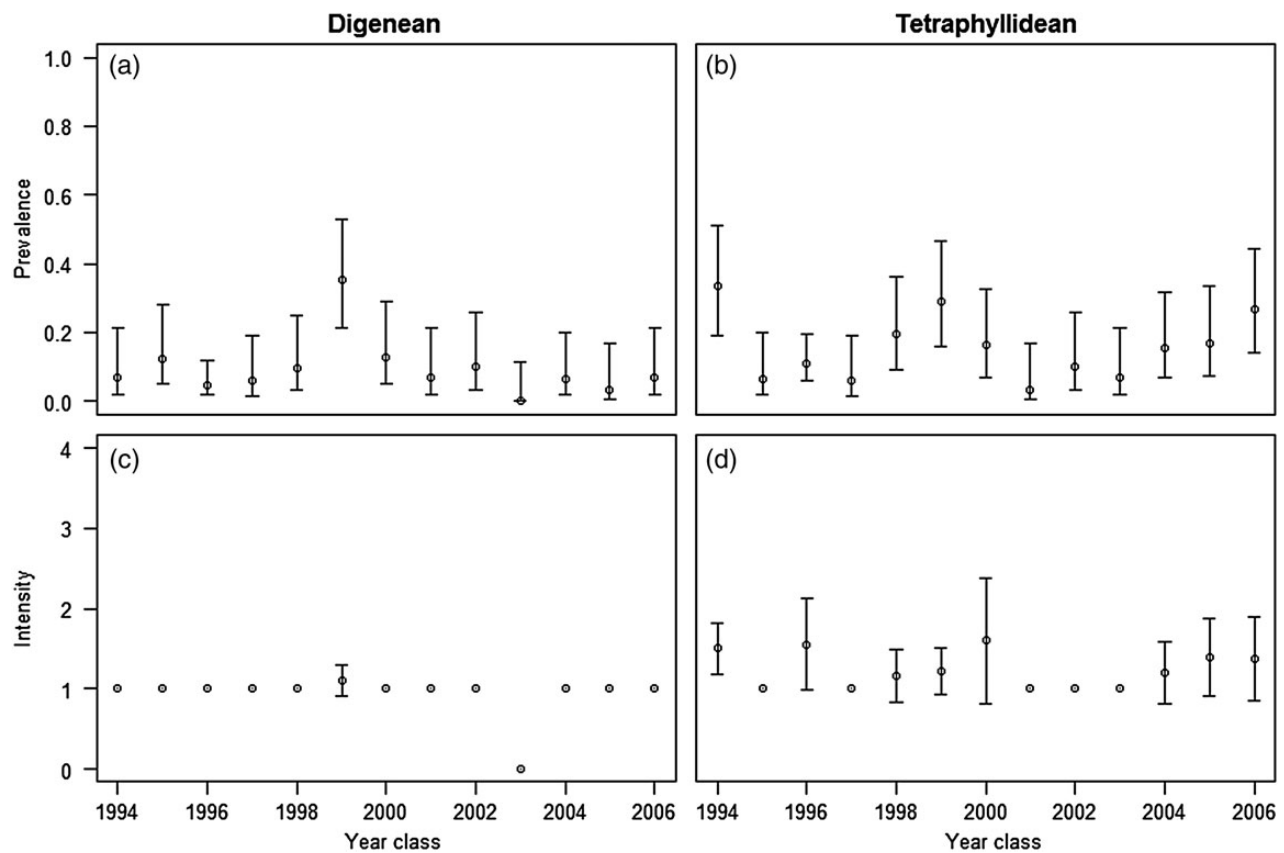
Figure 8. Prevalence and intensity of digeneans (a and c) and tetraphyllidean larvae (b and d) in herring larvae collected in the study area between 1995 and 2007 (year classes 1994–2006). Prevalence in this figure refers to the proportion of individuals investigated that are infected, and intensity meaning the average number of parasites encountered in infected individuals. Error bars represent 95% confidence intervals. The 95% confidence intervals for prevalence were calculated using Wilson's score method without correction for continuity (Newcombe, 1998).

overdispersed. The residuals pattern was investigated using the "binnedplot" function in the "arm" package in R (Gelman and Su, 2013). The binned Pearson residuals showed no distinct pattern against the residual values.

Once the random effect of haul had been accounted for, we found that feeding incidence did indeed significantly decrease with time from sunset (Table 5 and Figure 10). In addition, parasite presence influenced feeding incidence and the direction in which likelihood

Table 2. Annual summaries of parasite prevalence in herring larvae collected in the study area between 1995 and 2007 (1994 – 2006 year classes).

Year class	Larvae sampled	Number infected		Prevalence		Joint occurrence
		Tetraphyllideans	Digeneans	Tetraphyllideans	Digeneans	
1994	30	10	2	0.33	0.07	1
1995	32	2	4	0.06	0.13	0
1996	83	9	4	0.11	0.05	0
1997	34	2	2	0.06	0.06	0
1998	31	6	3	0.19	0.10	1
1999	31	9	11	0.29	0.35	2
2000	31	5	4	0.16	0.13	2
2001	30	1	2	0.03	0.07	0
2002	30	3	3	0.10	0.10	1
2003	30	2	0	0.07	0.00	0
2004	32	5	2	0.16	0.06	0
2005	30	5	1	0.17	0.03	0
2006	30	8	2	0.27	0.07	0

Table 3. Candidate linear models describing the relationship between survival of herring larvae and prevalence of two helminth parasites in the northwestern North Sea, 1995 – 2007.

Model	Model parameters	F-statistic	p-value	AIC$_c$	Adjusted R^2
1	log(survival) $\sim$ ptet	$F_{1,9} = 3.04$	0.12	35.30	0.17
2	log(survival) $\sim$ pdig	$F_{1,9} = 1.20$	0.30	37.13	0.02
3	log(survival) $\sim$ ptet + pdig	$F_{2,8} = 1.36$	0.31	37.28	0.07
4	log(survival) $\sim$ pdig $\times$ ptet	$F_{3,7} = 3.92$	0.06	31.66	0.47
5	log(survival) $\sim$ pdig + pdig : ptet	$F_{2,8} = 6.59$	0.02	29.79	0.53

Survival was log-transformed to satisfy the assumption of normality and diagnostic plots confirmed constant variance with the mean after transformation. (pdig and ptet refer to the prevalence of tetraphyllidean and digenean parasites, respectively).

Table 4. Estimates, standard errors of the mean (s.e.), and significance of parameters of best fitting model in Table 3 (pdig and ptet refers to the prevalence of tetraphyllidean and digenean parasites, respectively).

Parameter	Coefficient	s.e.	t-value	p-value
pdig	-30.52	10.886	-2.80	0.02
pdig: ptet	114.51	35.013	3.27	0.01

of feeding was affected differed with the type of parasite (Table 5). There was some indication that larvae infected with digenean trematodes were less likely to have fed than non-parasitized larvae. In contrast, there was strong support in the model that larvae carrying tetraphyllidean cestode larvae were more likely to have fed than non-parasitized larvae (Table 5 and Figure 11). It is worth noting that we obtained similar results using a generalized linear model approach. However, the significance of these effects was less pronounced given that pseudo-replication was not accounted for. In addition, a GLMM (not presented), which did not account for the fixed effect of parasite (GLMM-NOparasite), was not supported by the data when contrasted with the model above (AIC$_{GLMM-parasite}$ = 392.8, AIC$_{GLMM-NOparasite}$ = 402.4).

Discussion

The availability of archived herring larvae from a succession of years with both high and low recruitment of North Sea herring provided an opportunity to investigate a potential relationship between feeding, infection with intestinal parasites, and overwinter survival of herring larvae. The use of a biophysical model to factor out the direct effect of oceanographic transport variability allowed us to use early larval abundance survey data to account for interannual spawning variability and estimate reliable annual indices of survival for the relevant stocks.

A particle tracking modelling approach was used to identify the origin of the larvae sampled in the study area and to account for interannual transport variability. This methodology is critically dependent on the suitability of the underlying hydrodynamic model. SNAC (Logemann *et al.*, 2004) is a statistical representation of HAMSOM (Backhaus and Hainbucher, 1987) that has been used comprehensively for similar applications in the general domain of interest [e.g. see Gallego (2011) and references therein]. As a comparative exercise, we carried out a similar set of particle tracking simulations using a different hydrodynamic model (POLCOMS; Holt and James, 1999), though for a shorter time-series available to us (1994–2003). The new simulations (not presented here) resulted in the same origin of all larvae sampled in our study (Orkney-Shetland and Buchan) and a similar pattern of years with high and low transport success, although there were some differences in their relative magnitude and POLCOMS-based simulations resulted in a consistently higher (∼3 times) number of particles reaching the target area. However, the latter would in effect act as a scaling factor which should not affect the statistical outcome of our analyses, which was the same for the common time-series. Therefore, we felt justified to use the SNAC-based simulations over the full series when survey and hydrodynamic model data were available to us (1994/1995–2006/2007).

The modelling approach also made a number of simplifying assumptions in the way herring biology was represented (for model
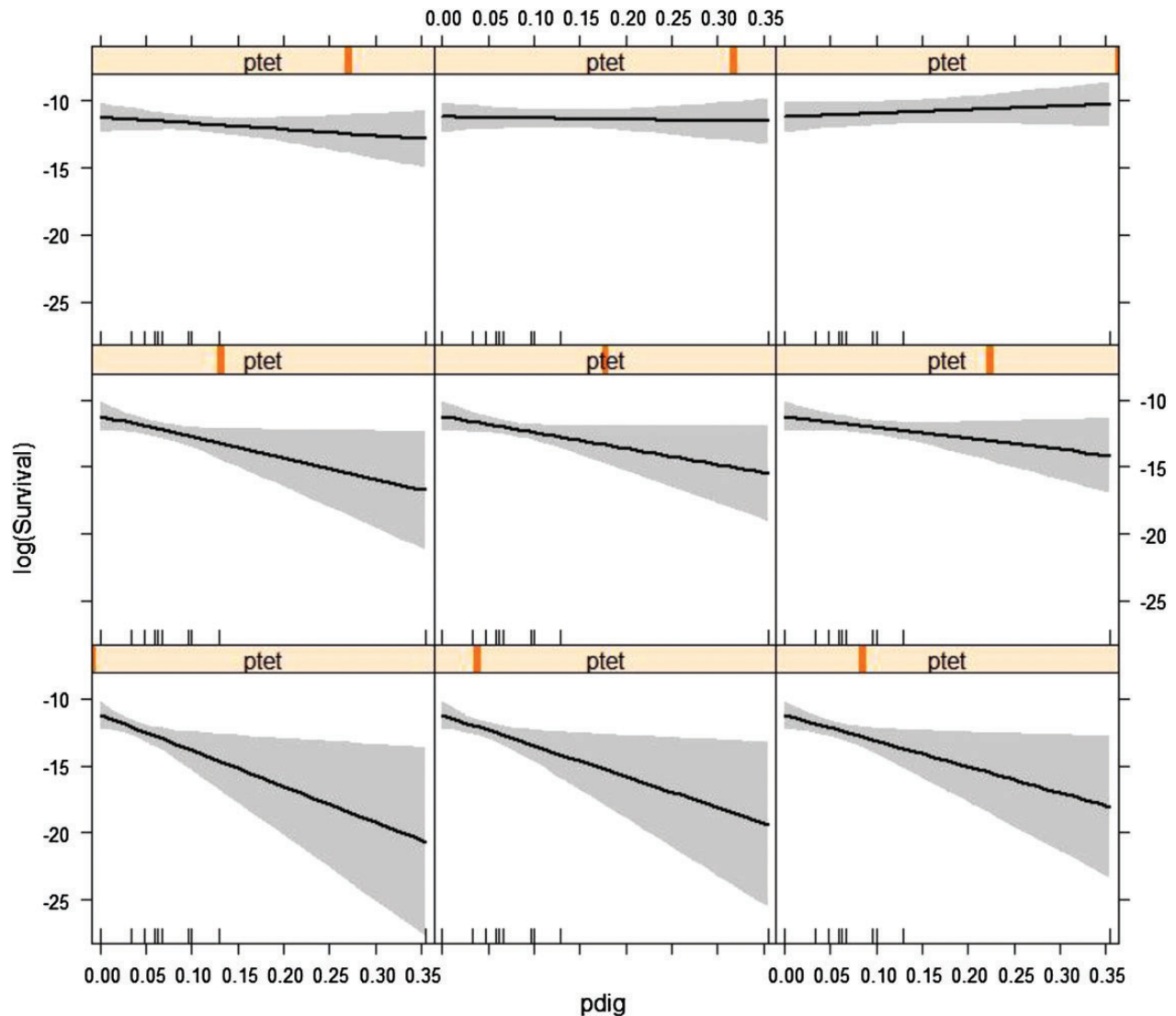
Figure 9. Interaction plot of the effect of prevalence of digenean (pdig) and tetraphyllidean (ptet) parasites on survival of larval herring in the northwestern North Sea. The plot shows the effect of digenean prevalence on log-transformed survival at different levels of tetraphyllidean prevalence.

Table 5. Contrasts summary estimates, standard errors of the mean (s.e.), and significance of parameters from the generalized linear mixed-effects model (prey present ~ state + sunset + (1 | haul), see text) describing the relationship between presence of two types of parasites on the likelihood of feeding in larval herring taking into account time of capture (hours after sunset) and haul effects.

| Parameter	Estimate	s.e.	Z-value	p-value
State (no parasite)	0.41	0.458	0.89	0.37
State (digenean)	−1.30	0.647	−2.02	0.04
State (tetraphyllidean)	1.12	0.403	2.78	0.006
Hours after sunset	−0.45	0.0962	−4.70	<0.0001

The estimated variance for the random effect (haul) was 1.715 (44 hauls, 447 larvae), AIC = 392.8.

sensitivity analyses, see Gallego, 2011). One important assumption was the selected particles release date (representing hatching date). Herring spawning time varies between spawning stocks and, even within a given spawning stock, there is some interannual variability (Heath, 1993). However, in the absence of detailed multi-annual spatially and temporally resolved information on timing of spawning, it was unfeasible to incorporate spawning time variability into our model. Consequently, we selected a single larval hatch date (15 September) as a single particles release date from all spawning locations. For all areas that could contribute larvae to our study area, based on widely accepted oceanographic transport patterns, the west coast of Scotland herring stock spawns predominantly from August to October (Rankine, 1986), while spawning in the Orkney-Shetland area is from the end of August through September and in Buchan in September–October (Heath, 1993). In the years considered in our study, the larval surveys covering the Orkney-Shetland and Buchan areas were carried out in the second half of September. The particles release date of 15 September, therefore, allowed us to use the survey data as a weighting factor for spawning in our analysis. The average growth rates required for those larvae to reach the selected size interval of 24–28 mm in the month of
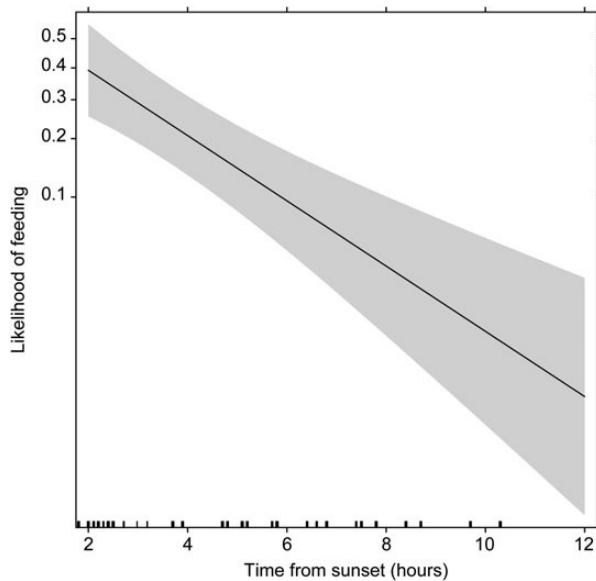
Figure 10. Predicted partial effect from the generalized linear mixed effects model (prey present ∼ state + sunset + (1 | haul), see text) showing the significant negative effect of time-lag from sunset to capture time (time from sunset) on likelihood of feeding.
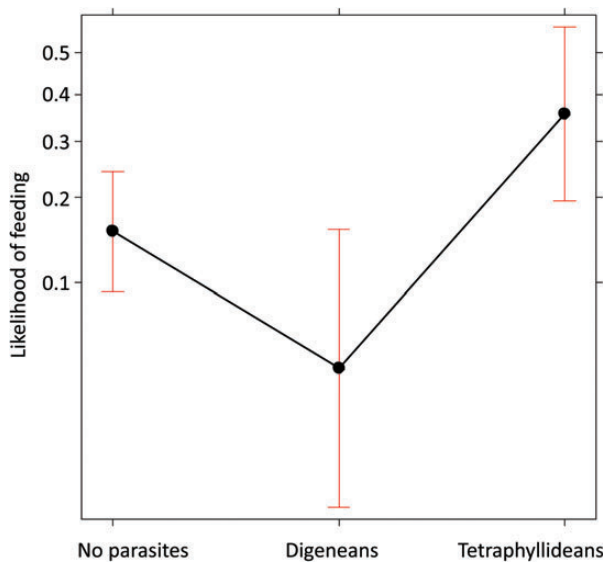
Figure 11. Predicted partial effects plot from the generalized mixed-effects model (prey present ∼ state + sunset + (1 | haul), see text) showing the difference in likelihood of feeding between non-parasitized larvae and larvae carrying digeneans and tetraphyllideans. Vertical error bars represent 95% confidence intervals.

February are 0.13–0.15 mm d^{-1}, which are well within the range reported in the literature (Lough *et al.*, 1982; Gamble *et al.*, 1985; Geffen, 1986). The selection of a fixed length interval for all years may have introduced additional variability into our analysis, as this common range may have resulted in the selection of slower or faster growing components of the population, from year to year. However, the selected range was contained within the 5th and 95th quantiles every year and spanned the median of the length

distribution for most years, thus minimizing this potential short-coming. Additionally, selecting a variable length interval between years would have introduced additional ontogenetic diet variability effects.

At the basis of our investigation was the hypothesis that herring larval overwintering survival could be regulated by parasite infection. The two types of parasites, tetraphyllidean cestode larvae and digenean trematodes, which were identified from herring larvae digestive tracts, have previously been reported from herring larvae in the Northeast Atlantic and the North Sea (Rosenthal, 1967; Heath and Nicoll, 1991; Karlsbakk *et al.*, 2003; Tolonen and Karlsbakk, 2003). The prevalences and intensities we report are well within the range reported in these studies and the effects we describe here are therefore not the result of abnormally high or low levels of parasite prevalence or intensity. Our analyses indicate an interaction at the population level between the effects of the two parasites; the different way that these two types of parasites affect herring larvae may provide the explanation. Herring larvae survival is impacted by digenean parasites through the physical damage to individual larvae, affecting their ability to feed (Ivanchenko and Grozdilova, 1985). However, in years of good cumulative feeding conditions, as indicated by high prevalence of the relatively benign tetraphyllidean cestode larvae, the negative impact of the digeneans is offset by better survival of herring larvae overall. This scenario is further supported by the differences found in feeding incidence between the three categories of larvae. There was some indication that larvae with digeneans had lower feeding incidence than non-parasitized larvae, in agreement with the parasites causing physical damage inhibiting feeding. The larvae with tetraphyllidean cestodes, on the other hand, had significantly higher feeding incidence. Rather than being a direct consequence of the presence of the parasite, it is likely to simply reflect the better feeding conditions they have been subject to which in turn also caused the higher prevalence of tetraphyllideans.

In contrast to this study, Heath and Nicoll (1991) found lower feeding incidence in larvae infected with tetraphyllidean cestode larvae. However, they did not take into account in their analysis that feeding incidence might have been impacted by the time of day of capture of the larvae. We found a significant negative relationship between feeding incidence and the elapsed time between sunset and capture. This relationship is commonly described for herring larvae that are visual predators and rely on some level of light for effective prey capture (e.g. Cohen and Lough, 1983) and should be taken into account whenever feeding incidence is being used to measure feeding success (Llopiz, 2013). Similarly, gut evacuation at capture has the potential to influence feeding success estimates in herring larvae (Hay, 1981). In this study, we used simple presence/absence data to infer feeding incidence rather than number of prey items or stomach fullness, an index that is only sensitive to total evacuation of the gut during capture. In line with Heath and Nicoll (1991), we consider it unlikely that there is a difference in the incidence of full evacuation of stomachs between parasitized and non-parasitized larvae that could have biased our results.

Differences among years in tetraphyllidean and digenean prevalence in the herring larvae could simply reflect differences in the availability of infectious parasites in the zooplankton. If this is the case, there seems to be a link between factors influencing parasite availability, particularly tetraphyllideans, and herring larvae survival. The differences in circulation pattern and consequently transport patterns among years could be one such factor. A detailed investigation of the potential mechanisms causing such a link is

beyond the scope of this paper, but could possibly further illuminate factors affecting the survival of herring larvae in the North Sea.

Although we did investigate diet of late stage herring larvae, the very low sample sizes and the paucity of data on diet for several of the years in our study period mean that the conclusions that could be drawn regarding the interannual differences in the importance of different prey is speculative at best. However, it is worth noting that in general, the food items that were abundant in stomachs in this study such as *Paracalanus* sp.*, Pseudocalanus* sp., *Oithona* sp., and other small calanoid copepods have also previously been recorded as important food items for herring larvae in the North Atlantic (Schnack, 1972; Checkley, 1982; Cohen and Lough, 1983). In any case, the information on stomach contents collected from our samples provides only a snapshot in time of the diet and food consumption of the herring larvae immediately before sampling. However, larvae survival from hatching is a product of the integrated diet and consumption over many months. In this study, we have used data on benign parasites acquired through feeding to make inference regarding feeding of herring larvae over a much longer time-scale. The main diet items reported in this study are also the zooplankton groups that have been linked to the transfer of the parasites found in the herring larvae (Køie, 1979; Marcogliese, 1995), further supporting that these parasites are indicators of cumulative food intake.

Although our results support overwintering as a critical period for the survival of larval herring, it is not possible to test whether this corresponds to the onset of exogenous feeding, as in Hjort's "critical period" hypothesis (Hjort, 1914), or some other time during that stage. The exact time at which larvae are most affected is still unknown, since by analysing larvae collected in February, we are only considering the survivors. Herring larvae are susceptible to infection with both parasite types once they exceed ∼15 mm in length (Rosenthal, 1967; Heath and Nicoll, 1991). This means that the larvae we investigated started accumulating parasites well before even reaching the study area. The next step to further unravel the exact link between feeding and survival should be to consider temporal differences in zooplankton composition over the lifespan of larvae as well as spatial differences along the advection route of the larvae. Furthermore, as diet of herring larvae changes as they grow (Checkley, 1982; Cohen and Lough, 1983; Munk, 1992), consideration should be given to changes in prey preference over the larval lifespan and therefore along the advection route.

The increased survival in our study area towards the end of the study period is in contrast to the continued low North Sea-wide survival (ICES, 2007; Payne et al., 2009). The proportionally higher contribution from the study area to the total abundance of late stage larvae in the North Sea for this later period indicates that the differences in herring larvae survival are real and not just an artefact of the particle tracking approach or the indices used to estimate larval production. This discrepancy between temporal changes in survival locally and North Sea-wide makes it difficult to extrapolate the findings from our study area to a North Sea-wide scenario. While our results indicate that the improvement in the study area could be due to improved food intake, this does not necessarily imply that, conversely, the continued low survival in the wider North Sea is due to poor feeding conditions. However, a recent study by Payne et al. (2013) demonstrated lower growth rates in herring larvae in the central North Sea in years of poor (North Sea wide) survival, further supporting the link between survival and feeding conditions. A more detailed analysis of transport patterns of herring larvae and concurrent spatial

variation in appropriate prey organisms and parasites could further clarify these potential links.

It is not necessarily surprising that the local survival differs from the North Sea-wide survival. The North Sea-wide survival estimate is integrated over a large and environmentally diverse area, and regional differences should be expected. Fässler et al. (2011) provided strong evidence of highly increased mortality in herring larvae, particularly from the Northern spawning components coinciding with the drop in overall North Sea-wide survival. As these are also the spawning components considered in this study, the two observations appear contradictory. However, Fässler et al. (2011) looked at mortalities in the very young larvae (<30 days). Therefore, the two studies are not directly comparable and our conclusions, at the temporal resolution of our study, are not incompatible with finer scale temporal variability in survival patterns.

Estimating survival from successive surveys of larvae is particularly difficult due to factors such as year-to-year differences in the sampling coverage. The SCAI model approach compensates for variations in timing and spatial coverage in the derivation of North Sea-wide abundance indices (Payne, 2010). However, timing and distribution of spawning has not been investigated recently, but it is assumed that the areas and times surveyed still represent the areas and times of peak larval production (ICES, 2008). The coverage of the Buchan and Orkney-Shetland spawning areas has averaged over 80% of the survey stations over the period of this study (coverage data provided by Dr Jörn Schmidt, IFM-Geomar, Germany). The only time that coverage has fallen significantly below this level was in 1996 in Orkney-Shetland, where only 49% of the stations were covered and consequently the survival index for 1996 could be either over- or underestimated.

A correlation between changes in the North Sea plankton community around 2000 and the reduction in North Sea-wide survival of herring larvae has been identified by other authors (Payne et al., 2009). However, this observation by itself does not offer any explanation of how or why survival may have changed in terms of the mechanisms involved.

In this study, we provide evidence that winter survival of herring larvae in a coastal strip off the Northeast of Scotland is detectably influenced by interannual variations in cumulative food intake, as indicated by the incidence of a benign parasite acquired with the natural diet. In addition, there are suggestions of an additive detrimental effect due to digenean trematode parasites when feeding conditions are poor.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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