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Larval mortality rates and population dynamics of Lesser Sandeel (*Ammodytes marinus*) in the northwestern North Sea.

Michael R. Heath^{*,a}, Jens Rasmussen^b, Martin C. Bailey^c, John Dunn^b, John Fraser^b, Alejandro Gallego^b, Stephen J Hay^b, Michelle Inglis^d, and Susan Robinson^b

^aUniversity of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH, UK.

^bMarine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, UK.

^cUniversity of Newcastle, School of Marine Science and Technology, Newcastle upon Tyne, NE1 7RU, UK...

^dCentre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, NR33 0HT, UK.

* Corresponding author: Tel: +44 (0)141 548 3591, Fax: +44 (0)141 552 2079.
E-mail address: m.heath@strath.ac.uk (MR Heath)

Journal of Marine Systems – ICES WKMOR special issue

Abstract

Intense fishing of a stock of sandeels (*Ammodytes marinus*) on the sand banks off the Firth of Forth, northeast Scotland, during the 1990's led to a decline in catch per unit effort to uneconomic levels and collateral failures of piscivorous seabird breeding success at nearby colonies. A prohibition on fishing in 1999 was followed by a short-term recovery of stock biomass, but then a sustained decline to very low levels of abundance. Demographic survey data show that despite the decline in stock, recruit abundance was maintained implying an increasing larval survival rate, and that the stock decline was not due to recruitment failure. To verify this hypothesis we analysed a 10-year long data set of weekly catches of sandeel larvae at a nearby plankton monitoring site to determine the patterns of larval mortality and dispersal. We found that the loss rate of larvae up to 20 d age decreased over time, corresponding with the trend in survival rate implied by the stock demography data. The pattern of loss rate in relation to hatchling abundance implied that mortality may have been density dependent. Our study rules out increased larval mortality as the primary cause of decline in the sandeel stock.

Keywords: fish; larvae; otolith; age; length; survival; 55°N 3°W, 58°N 1°W

1. Introduction

Sandeels formed the largest component by weight of annual fishery landings between 1985 and 2000 and are probably the most abundant fish species in the North Sea. However, the fishery for sandeels has been controversial for a number of reasons (Gislason and Kirkegaard, 1998). In particular, the magnitude of sandeel landings (1.1 million t per year in the mid-1990's; ICES, 2009) caused concerns that exploitation might be detrimental to populations of some piscivorous fish, seabird and marine mammal species which rely heavily on sandeels for food (Duant et al., 2008; Frederiksen et al., 2004; Furness, 2002, 2003; Furness and Tasker, 2000, Greenstreet, 2006; Monaghan, 1992; Wright, 1996).

There are in fact several species of sandeels in the North Sea, but by far the most abundant is the Lesser Sandeel (*Ammodytes marinus*). The other main species are the Greater Sandeel (*Hyperoplus lanceolatus*), the Smooth Sandeel *Gymnammodytes semisquamatus*, other species of Lesser Sandeel (*Ammodytes tobianus* and *Ammodytes dubius*), and Raitts Sandeel (*Hyperoplus immaculatus*). The species have characteristically different growth rates, life-span, and spawning times (for example, *A. marinus* spawns in the winter, whilst *A. tobianus* may spawn in the summer). The Lesser Sandeel species are difficult to distinguish morphologically as adults (Mitchell et al., 1998) and especially as larvae. However, a common feature of all the species is their habit of living most of their adult lives buried in seabed sediments, emerging only briefly each year to feed and spawn (Field 1988). This makes assessment of sandeel abundance particularly problematic.

A. marinus is able to bury and survive only in permeable coarse sandy sediments having a small fraction (<10%) by weight of silt grains (Holland et al., 2005; Wright et al., 2000). Eggs are shed during winter and incubate on or in the sediment. Off the east of Scotland larvae hatch in March with a body length of 3-4mm (Macer, 1965; Wright and Bailey, 1996; Winslade, 1971). We do not know if the larvae emerge immediately into the water column or spend a short while in or very close to the sediment, but they begin feeding almost immediately on copepod nauplii, progressing to copepodites and larger prey as they grow (Rasmussen, 2004). By May/June, the survivors have attained a length of 60-70mm and are seeking suitable sediment in which to bury (Wanless et al., 2004). Those individuals which survive the winter in the sediment, emerge again the following spring (April-June) to feed. At the end of this, their second summer, most fish will commit to maturation (Boulcott et al., 2007; Boulcott and Wright, 2008) and spawn for the first time the following winter. Predation from piscivorous fish (cod, haddock, whiting, saithe, mackerel) and some seabirds (e.g. Atlantic puffin) occurs during the first summer (age 0), whilst other avian predators (e.g. guillemot, razorbill, kittiwake and tern) and mammals take mainly age 1 and older fish (Greenstreet, 2006; Greenstreet et al., 2007).

The stock of *A. marinus* in the North Sea is far from a homogeneous unit. Patches of habitat suitable for burial exist throughout the southern North Sea, and in parts of the northern North Sea (ICES, 2007; Christensen et al., 2008). There are large regional variations in growth rate, maturation and weight-at-length between populations occupying the patches in different regions. For example, length-at-age is significantly larger in the central North Sea and Fisher Banks area than in the north-west and at Shetland (Bailey, 1996; Boulcott et al., 2007). Population dynamics have also shown

different patterns, with expansions and contractions in local abundance at Shetland and off the Scottish east coast occurring apparently independently from populations in the central North Sea (ICES, 2007). Tagging data show that settled individuals rarely move more than ~10 km (ICES, 2007, Gauld and Hutcheon, 1990), so connectivity between patches is primarily as a result of advection and diffusion of larvae (Christensen et al., 2008; Proctor et al., 1998). This extent of connectivity is an important issue for both population dynamics and fishery management.

In 1990, fishing fleets located a dense aggregation of sandeels on the shallow (< 50 m) sand banks off the Firth of Forth on the east coast of Scotland (Wee Bankie, Marr Bank; Fig. 1) and the somewhat deeper Berwick's Bank (Duant et al., 2008; Frederiksen et al., 2008). The Danish fleet returned each year thereafter and annual catches from the Banks reached a peak of 100,000 t in 1993. However, by 1999 the catch per unit effort had declined to un-economic levels (Fig. 2). At the same time, kittiwakes, puffin, guillemot and razorbill at the nearby seabird colonies on the Isle of May which foraged almost exclusively for sandeels on the Banks, showed signs of starvation and failure of fledging success (Frederiksen et al., 2008). The fishery was therefore closed in 2000 and has remained so since, except for a supervised small scale monitoring fishery by commercially operated vessels to assess the state of the stock.

Immediately after closure of the fishery at the end of 1999, monitoring fishery catch per unit effort (cpue) increased sharply to a peak in 2001, but then began a sustained decline (Fig. 2; Frederiksen et al., 2008). Almost a decade after the fishery closure, the cpue was extremely low, even compared to the period immediately before the closure of the fishery, with continued detrimental consequences for seabird fledging success. By the mid 2000's, the breeding seabird population on the Isle of May (Fig. 2) which had flourished in the sandeel dominated era, were attempting to meet the dietary demands of their fledglings with a mixture of fish species including sandeel, sprat and snake pipefish, the latter of which appeared in large numbers during 2004-2008 but proved almost indigestible (Harris, 2006; Harris et al., 2007a,b; Wanless et al., 2005).

Additional insight on the post-fishery dynamics of the sandeel population comes from a series of research surveys of the Banks carried out during May or early June annually since 1997 (Greenstreet et al., 2006, 2010). These surveys included hydroacoustic and pelagic trawl surveys for assessing the abundance of sandeels in the water column, together with demersal trawl and dredge surveys of sandeels buried in the sediment, and distinguished between young-of-the-year sandeels (age 0) and older fish (age 1+). The biomass of age 0 fish in the scientific surveys represents the annual recruitment to the Banks population, whilst the 1+ biomass represents the potential spawning stock for the following winter since ~80% of age 1 fish mature in the autumn (Boulcott et al., 2006). The survey results for age 1+ confirmed the cpue data from the monitoring fishery with a rise to a peak in 2000/2001 following the fishery closure and subsequent decline to extremely low abundances by 2006 (Fig. 2). However, the abundances of age 0 fish charted a very different account. Initially there was an increase in age 0 biomass (recruitment) following the closure of the fishery, which approximately tracked the increase in age 1+ fish (Fig. 2). However, after 2001 recruitment was maintained despite declining potential spawning stock (represented by the biomass of age 1+ fish). In principle, this result allows us to narrow down the

cause of the stock decline to a decrease in growth rate or an increase in post-recruitment mortality, so that the population was unable to recover to former levels of abundance even in the absence of fishing mortality.

Possible sources of post-recruit mortality could be predation, though there have been no marked increases in the consumption by, or abundance of, known predators in the region. On the other hand, a long-term decline in the size-at-age of sandeels on the Banks has been documented from analysis of specimens recovered from seabirds returning to their nests, apparently starting before even the onset of the fishery (Wanless et al., 2004). In addition, sea temperatures on the east coast of Scotland have shown a strong warming trend since the mid-1990s, and sandeels may be particularly vulnerable to temperature change. Sandeels lose significant body mass during the over-winter, non-feeding, burial period between late summer and the spawning event in January of the following year (Boulcott et al., 2007; Boulcott and Wright, 2008). Warming temperatures could accelerate the rate of loss leading to enhanced mortality of the overwintering stock.

Particle tracking investigations based on water currents simulated by hydrodynamic models (Christensen et al., 2008; Gallego et al., 2004; Magen, 2000; Proctor et al., 1998) have shown that the areas inshore of the 50 m isobath off the Firth of Forth (which includes the Wee Bankie and Marr Bank) and northwards along the coast as far as Rattray Head (Fig. 1) are highly retentive at the times of year when sandeel larvae are in the water column. In contrast, the models indicate that larvae hatching in deeper areas (Turbot and Berwick's Bank) are expected to be carried away towards the southeast and are unlikely to represent a significant source of immigrants to the inshore Banks. Thus the hydrodynamic evidence suggests that the population on the Banks should be more or less a closed system with no significant immigration or emigration of larvae or settled stages. Under these circumstances, a diagnostic signature of the maintenance of recruitment in the face of declining spawning stock must be decreasing mortality rates of larvae. Independently establishing such a signature would clearly confirm the conclusions reached from the above macro-analysis of stock demography. In this paper we derive the mortality rate of early larval stage *A. marinus* sampled during a 10-year time series of weekly plankton collections at a monitoring site on the northern periphery of the shallow inshore Banks. We ask whether there is any evidence for a temporal trend in mortality rate, and if so, how this may have arisen.

2. Materials and Methods

2.1. Hydrographic and plankton sampling at the monitoring site

The monitoring site ($56^{\circ} 57.83'N$, $002^{\circ} 06.74'W$; Fig. 1) was situated 5km off the town of Stonehaven on the northeast coast of Scotland, at a water depth of 45 m. Peak spring and neap tidal current speeds at the site are 1.4 and 0.7 kn (72 and 36 cm s^{-1} respectively; Admiralty tidal diamond at $56^{\circ} 59.00'N$, $002^{\circ} 00.20'W$), whilst the mean residual flow is of the order of 1-3 cm s^{-1} , equivalent to 0.9-2.5 km d^{-1} , in a south-westerly direction parallel to the coast (Gallego et al., 2004; Magen, 2000). Hydro-chemical and plankton sampling at this site has been conducted each week, weather permitting, since January 1997 (Heath et al., 1999; Bresnan et al., 2009). Initially,

sampling was carried out from the 8m launch *Shuna*, but this was replaced in October 2003 by the 10m catamaran *Temora*.

On each visit to the site, temperature data have been collected with reversing thermometers and CTD probes, water samples collected for salinity, nutrient, chlorophyll concentration and phytoplankton species composition, and zooplankton samples collected using towed nets of various mesh sizes. Plankton sampling with a 100 cm mouth diameter net of 350 μ m mesh was included in the protocol from December 1999 onwards, in order to monitor the abundance of larval fish and macro-zooplankton. The net was towed obliquely at a speed of 1 m.s⁻¹ to within ~3 m of the seabed, with depth below the sea surface being monitored by a Scanmar acoustic telemetry depth sensor. Flow through the net was measured by a TSK mechanical flowmeter mounted in the centre of the mouth opening. Upon recovery of the net, the whole catch was washed into the cod end with pumped seawater filtered through the mesh from the outside. The cod-end was then removed and placed in a 4% borax buffered formalin solution (pH 7.5 - 8.5) to fix the sample for transportation ashore and back to the laboratory, which typically took 1-2 h.

Immediately on return to the laboratory, the cod-end and sample was rinsed with fresh seawater and all fish larvae were picked out and counted. Each sample was picked through twice to ensure all the fish larvae were removed, and the remaining plankton was then preserved in formaldehyde solution. Sandeel larvae were subsequently separated from other fish, and identified to species under a binocular microscope. *A. marinus* was distinguished from the other sandeel species present in the samples (*H. lanceolatus* – the Greater Sandeel, and *A. tobianus*) by the absence of dorsal melanophores. *H. lanceolatus* has melanophores extending onto the caudal fin. All sandeel larvae were then preserved in 80% buffered ethanol (pH 8.0 to 8.5) in labelled 25ml glass vials.

2.2. Sandeel length measurements

Standard lengths (anterior tip of maxillae to end of the notochord) of sandeel larvae collected at Stonehaven during 2000-2003 were measured to 0.1mm resolution using a binocular microscope and calibrated digitising pad connected to a PC. Subsequently, in 2009, larvae collected from 2004 onwards were measured, by scanning images of groups of individuals arranged on a scanner plate, and applying image analysis line-measurement processing software to each individual. Larvae collected during 2002 and 2003 were re-measured using the same system to check that the two methods gave equivalent results.

2.3. Derivation of sandeel larvae abundance

The depth averaged concentration (m⁻³) of sandeel larvae in the water on each sampling occasion at Stonehaven was estimated by dividing the total numbers caught by the volume of water filtered. Total concentration was then disaggregated to 1mm length classes by applying the proportions of measured larvae in each length class. Sea surface area specific abundances (m⁻²) were then the product of depth average concentration and seabed depth. Volume filtered was estimated preferentially from the flowmeter data by applying an instrument-specific calibration factor (*c*, revs m⁻¹) and the net mouth area, to the total flowmeter revs during each tow (area * revs * 1/*c*). In

cases where flowmeter data were missing, volume was estimated from the product of tow duration, speed of the boat through the water, mouth area of the net, and a flow-resistance factor (f). The flow-resistance factor ($f = 0.46$) was estimated from the coefficient of a linear regression between $y = (\text{revs} * 1/c)$ and $x = (\text{duration} * \text{speed})$ based on tows with valid flowmeter data ($r = 0.86$, $n = 191$).

2.4. Otolith preparation

Increment formation in *A. marinus* otolith has previously been shown to occur on a daily basis (Wright, 1993), so that increment counts can be used to estimate the age of individuals from hatching. Sagitta and lapillus otoliths pairs from *A. marinus* larvae collected at the monitoring site each week during 2000 and 2001 were removed using fine dissecting needles and transmitted light under a binocular microscope at x50 magnification. The otoliths from each individual were mounted concave side down on a labelled slide in a thin film of clear nail varnish. Otolith microstructure was then investigated using a Zeiss Axioskop binocular microscope at magnifications of x400 or x1000 (oil immersion). If present, features such as rostral and post-rostral secondary growth centres, check marks, and any other distinguishing features were noted. A count of the total number of increments visible from the hatch check to the otolith edge was made for each otolith. For preference, ring counts were based on mean of three replicate counts for each of the pair of sagittal otoliths.

2.5. Age-length analysis

The age and length measurements on *A. marinus* larvae were analysed to estimate the probability distributions of ages for each 1mm length class. Probabilities were estimated using the continuation-ratio logit method (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). The changes in distribution of age at a given length, as a function of length, were estimated by Generalized Linear Modelling (GLM). Fitting was performed using Maximum Likelihood Estimation code (Stari et al., 2010) developed for the R statistical environment (R Development Core Team, 2008).

Too few otoliths were analysed in 2000 and 2001 to conduct the continuation-ratio logits analysis separately for each year, and none were analysed from 2002-2009. The data were therefore combined to produce an aggregated probability distribution of age given length. We applied this distribution to the abundances in 1mm length classes in each sample, to transform the measured abundance-at-length in each sample, into abundance-at-age.

Larvae of the same age but caught on different sampling dates, must have originated from different hatch dates (hatch date = capture date – age). Hence, for each year we transposed the matrix of abundance by age class and sampling date, into a matrix of abundance by daily age class (rows) and daily intervals of hatch date (columns). Columns in this matrix tracked the development of daily cohorts of larvae, but contained gaps corresponding to ages and hatch dates which were, by chance, not sampled by the weekly sampling scheme. For each year, we therefore aggregated the matrix by averaging each daily age class over 8 x 14 day intervals of hatch date, equivalent to 8 cohorts of larvae per year (days 29-42, 43-56, 57-70, 71-84, 85-98, 99-112, 113-126, and 127-140). The rate of decline in abundance (d^{-1}) down each column of this matrix represented the loss rate of larvae from each hatching cohort.

2.6 Sensitivity of loss rate estimates to variability in growth rates

The application of a fixed probability distribution of age given length derived from the 2000-2001 otolith data in order to transpose the abundance-at-length to abundance-at-age in every sample, carried the implicit assumption that there was no variability in growth rates. In reality, there was highly likely to be variability within and between years due to variations in the temperatures and food abundances experienced by different hatching cohorts. However, we had insufficient data to estimate the magnitude of these variations directly. To assess the sensitivity of the results to inter-annual variations in annual average growth rate, we conducted a bootstrap analysis in which age-length probability distributions representing discrete variations from the 2000-2001 average growth rate were randomly assigned to all the samples collected in each sampling year.

A set of 21 age-length probability distributions was generated to represent discrete annual growth rates in the range $\pm 5\%$ of the 2000-2001 average rate in 0.5% intervals, by rescaling the measured lengths-at-age of individual larvae in the otolith data set and repeating the continuation-ratio logits analysis. Individual lengths were rescaled according to:

$$L_g = L_{\min} + (L - L_{\min}) \cdot g$$

where L was an individual length-at-age measurement in the 2000-2001 data set, L_{\min} was the minimum length in the data set, L_g was the rescaled length-at-age, and g was the growth rate scaling factor ($0.950 \leq g \leq 1.050$, in intervals of 0.005).

The generated distributions were indexed by integer values in the range -10 to +10. We then repeated the process of transposing abundances-at-length to abundances-at-age in each sample through to calculating cohort-specific loss rates, having randomly assigned one of the 21 age-length probability distributions to each year-set of samples. The assignment was carried out by randomly drawing an integer index value for each year from a normal distribution with mean 0 and s.d. 3 (i.e. equivalent to s.d. (g) = 0.015). The value of s.d was qualitatively selected to reflect the scale of inter-annual variation in growth rate that might be expected from variations in temperature and zooplankton abundances, and by reference to published data for larvae of sandeel and other species (Wright and Bailey, 1996; Young et al., 2010). This entire procedure was iterated many times to generate a distribution of loss rate estimates for each year in the study period.

3. Results

A total of 475 sample collections were achieved off Stonehaven during the 10 years between late 1999 and the end of 2009. Sandeel larvae were present on 147 occasions and a total of 15,817 individuals were caught. Of these larvae, the majority (14,651) were identified as *A. marinus*. Of the remaining, 1083 were identified as *H. lanceolatus* and 14 tentatively as *A. tobianus*.

The seasonal distributions of *A. marinus* and *H. lanceolatus* were different. During February and March the catches were composed exclusively of *A. marinus*. *H.*

lanceolatus formed an increasing proportion of the catch from April onwards, attaining 100% by July.

3.1. Length distributions of *A. marinus* larvae

A total of 7145 *A. marinus* larvae were measured from the 10 years of sampling, and the annual distribution of lengths varied between years. The smallest individuals encountered were between 4 and 5mm, and the largest was between 31 and 32mm. However, in some years, individuals larger than approximately 15mm were rare or absent (Fig. 3). The average period over which the smallest larvae (4 mm) were caught (± 1 s.d. around the overall mean date of capture) was day 61-85 (2 – 26 March). Date of capture increased with length whilst the s.d. of catch date decreased (Fig. 4). Within each 1mm length class up to 17 mm, there was inter-annual variability in capture date but no significant linear trends ($p < 0.05$), indicating no trend in annual mean growth rates. Larvae larger than 17 mm were caught in too low numbers to allow an assessment of trends in capture dates.

3.2. Probability of age given length of larvae at the monitoring site

Otolith ages were determined for 307 individual larvae collected at the monitoring site during 2000-2001 (141 in 2000, and 166 in 2001). Ages ranged from 3 to 48 days, and the distribution of individuals with respect to length and age in the two years is shown in Fig. 5. The data indicated that age was approximately proportional to length from the minimum size to around 10mm. Length intervals 11-13 spanned an extreme range of ages (12 to 20), possibly implying a slowing of the growth rate. Beyond 14mm (approximately 23 days age), the age at length was more variable but on average increased approximately lineally with length. The probability of age given length for an example subset of four age classes derived from the continuation-ratio logits analysis is shown in Fig. 5.

3.3. Abundance of larvae at the monitoring site in relation to age and hatch date

The production of larvae over the hatching period of each year was represented by the mean abundance of the youngest larvae (3-5 d old) in each 14 day hatch date interval (Fig. 6). We examined the development of each of these the hatch date cohorts by plotting abundance against daily age, for each cohort (Fig. 7). The results show that cohort abundance declined with age as expected, but in many of the years there was a strong discontinuity at around 20 d. The discontinuities implied that larvae older than ~20 d at capture, could not have originated from the same location as younger larvae in the same hatch date cohort. Their declining abundance with age clearly followed a different trajectory which implied a different abundance at hatch (age 0). Particularly striking examples were 2001 and 2002, where there were two distinct trajectories of abundance for larvae having hatch dates in the day ranges 71-84 and 85-91. Clearly, larvae caught at a very young age (<5 d) must have hatched near to the monitoring site (within ~5 km given typical advection rates), whilst those belonging to the trajectories which was only appeared in the samples as individuals older than 20 d could have hatched at more distant locations (20-50 km) depending on the advection regime. We concluded that the sampling off Stonehaven collected larvae from both local and distant spawning locations. Locally produced larvae declined in abundance due to the combination of mortality and dispersal (advection

and diffusion), so that they were absent or below the abundance detection threshold of the sampling by 20 d. Depending on the advection regime, larvae from distant spawning areas might be carried into the vicinity of the sampling site, but the distance to upstream spawning locations was such that few if any of those that arrived were younger than 20 d old.

3.4. Loss rate of locally produced larvae

The decline in log-abundance between ages 3 and 20, of individuals belonging to the same hatch date cohort, should be a direct measure of the exponential loss or dissipation rate from the local hatching due to the combination of mortality and dispersal. For each year, we estimated this loss rate from the linear regression coefficient of log-transformed abundance against age, for all larvae age 3 to 20d in the same hatch date cohort. Out of 80 possible sets of regression data (8 hatch date intervals x 10 years), 61 comprised 3 or more data pairs, and of these 39 resulted in significant regressions ($p < 0.05$). A Generalised Additive Model (GAM, Hastie and Tibshirani, 1990) was then fitted to these 39 data in order to derive the underlying trends of loss rate with respect to hatch date and year. The optimum GAM, which explained >92% of the deviance in the data, took the form:

$$\text{Loss rate} = s(\text{hatch date interval}) + s(\text{hatch date interval}, \text{year}) + \text{error}$$

where s refers to a smoothing function, in this case a tensor-product spline (GCV score 0.037, $n=39$; intercept: $p=1.03 \times 10^{-15}$, $s(\text{hatch date interval})$: $p=1.86 \times 10^{-2}$ $s(\text{hatch date interval}, \text{year})$: $p=2.54 \times 10^{-2}$). The dominant effect in the data was a declining loss rate with progressively later hatch dates, with superimposed inter-annual variations (Fig. 8).

Annual loss rate was a compound function of the inter-annual variation in loss rate of each hatch date cohort and, since earlier hatch dates suffered a higher loss rate, the distribution of hatching abundance across hatch dates in a given year. Taking the mean abundances of age 3-5 d old larvae in each of the 8 hatch date cohorts as measures of abundance of hatchlings (Fig. 6), we applied the hatch date specific loss rates from the GAM (Fig. 8) to predict the abundance of larvae surviving at age 20d in each cohort. Then, by averaging over the 8 cohorts for each year, we estimated the annual average abundance of hatchlings and survivors to age 20d from the local hatching. Annual loss rate was then given by $\ln(\text{annual hatchlings}) - \ln(\text{annual survivors})$. The results showed that there was no relationship between the measured annual abundance of hatchlings and predicted abundance of survivors (Fig. 9). Hatchling abundance showed a declining trend between 2001 and 2009, whilst there was no trend in predicted survivors. Annual loss rate showed a significant ($p < 0.05$) declining trend between 2000 and 2009, possibly in two phases: 2000-2004 and 2006-2009, and was possibly related to annual hatchling abundance by a dome-shaped or saturating relationship. The pattern of loss rate was correlated with the annual larval phase mortality rate ($M_y = \text{mortality rate in year } y$) derived from the scientific survey data on sandeel demography on the Banks off the Forth of Forth ($M_y = -(\ln(B_{1y-1}) - \ln(B_{0y}))$), where B_1 = biomass of age 1+, and B_0 = biomass of age 0).

3.5 Sensitivity of survivor abundance and loss rate estimates to growth rate variability

The analysis described above assumed a fixed probability distribution of age given length for all samples, based on the otoliths collected in 2000 and 2001. In reality, we can expect year-to-year differences in the probability distribution due to variations in growth rate. The bootstrap analysis of growth rate variability allowed us to assess the uncertainty in the results as a consequence of assuming a fixed probability distribution.

Assuming annual average growth rates to be normally distributed with s.d. equivalent to a coefficient of variation equivalent to 1.5% (i.e. $\sim 7.5\%$ (2.5 s.d.) variation between fastest and slowest annual rates), the bootstrap analysis derived the consequent uncertainty in the predicted annual mean abundance at age 20 d, and the annual loss rate (Fig. 10). The results showed that the uncertainty did not invalidate the earlier conclusions since the decrease in loss rate post-2006, and the maintenance of predicted survivor numbers despite declining abundance of hatchlings were still evident.

4. Discussion

Although the pattern of loss rates of larvae with time at Stonehaven appeared to concur with that expected from the pattern of recruitment on the Banks, there were a number of potentially qualifying factors:

- First, particle tracking models indicate that the inshore waters along the coast (<50 m depth) including the Stonehaven monitoring site and the shallow Banks to the south (Fig. 1) are more or less a closed system with respect to sandeel larvae dispersal. We have to accept that this is the case and that immigration of larvae from the extensive areas of habitat in deeper water to the northeast, such as Turbot Bank (Fig. 1) was negligible.
- Second, we were unable to infer mortality rates of larvae off Stonehaven, only the loss rate which was a combination of mortality and dispersal. For our results to support the original hypothesis, we have to assume that inter-annual variations in dispersal were either small compared to those in mortality or relatively constant from year to year.
- Finally, our results imply that recruitment is effectively determined within 20 d of hatching. This is a surprising result, implying that the density dependent processes which dictate the shape of the stock-recruitment relationship operate during the early larval stage. Most studies of fish recruitment processes have concluded that density dependent variations in mortality rate are most likely to result from processes acting in later larval stages or at settlement (Cushing, 1974, 1983; Holm, 1990; Partridge and DeVries, 1999; Taggart and Leggett, 1987)

4.1. Immigration of larvae and connectivity with the Banks sandeel stock

Samples collected off Stonehaven were taken in coastal waters where the prevailing south-westerly residual current stream is weak compared to tidal flows (<5% of peak tidal flow), and hydro-biological data (salinity, nutrient concentrations, and plankton composition and abundance) are representative of the wider area shallower than 50 m, including the Banks region off the Firth of Forth (Heath et al., 1999). Our analysis indicates that two groups of larvae were found off Stonehaven. The first comprised individuals which must have hatched locally since they appeared in our samples from

a young age (minimum 3 d old). Seabed surveys (Serpetti et al., 2011) have found various patches of sandeel habitat within 2 km of the sampling site where the local group could have originated from. The second group of larvae were non-local and must have hatched into the along-shore flow some distance upstream since they did not appear in our samples until around 20 d age. In some years, no larvae arrived from upstream hatchings, but we do not know whether this was due to variation in transport, mortality prior to arrival off Stonehaven, or lack of spawning. However, there was no evidence of increased retention of locally hatched larvae in years when no non-local larvae appeared.

The distance over which the non-local larvae might have been carried before arriving off Stonehaven should be in the range 20-50km assuming 1-3 cm.s⁻¹ residual flow, or somewhat further if we also take diffusion into account. The likely origin was inshore patches of coarse sandy sediment between Stonehaven and Rattray Head (Fig. 1), rather than the more distant and extensive area of commercially fished sandeel habitat on Turbot Bank, which is further offshore to the north-east. Turbot Bank is located in deeper water and a very different hydrographic and hydrodynamic regime with strong advective flows to the south-east. Immigration of larvae from this region to Stonehaven would have been obvious as the appearance of a distinct, and probably more abundant cohort trajectory accompanied by a substantial increase in salinity, but no such events occurred during the 10 year study period. Hence, we conclude that the non-local larvae detected off Stonehaven were immigrants to the monitoring site, but not to the inshore waters (<50 m depth) which delineate the Banks sandeel stock.

We would expect larvae hatched local to Stonehaven and in the inshore waters extending to Rattray Head, to be mixed and advected south-west towards the Banks. The abundance of recently hatched *A. marinus* larvae (Fig 9. upper left panel, bars), and by inference the spawning biomass, off Stonehaven declined by more than an order of magnitude from a peak in 2001 over the course of our sampling programme. This pattern corresponded closely with the cpue of sandeels in the Danish Monitoring Fishery (Fig 1. upper panel, line plot, correlation with larvae abundance $r^2 = 0.656$, $p < 0.01$), and with the preceding year biomass of age 1+ fish in the May/June scientific surveys on the Banks (Fig 1. lower panel, line plot, correlation with larvae abundance $r^2 = 0.583$, $p < 0.01$). All the evidence points to the conclusion that the spawning patches local to Stonehaven are effectively part of an inshore (<50 m water depth) stock of sandeels which has its main centre of abundance on the Banks, and that there is little immigration from other major spawning groups such as a Turbot Bank.

4.2. Magnitude and consistency of dispersal relative to mortality

A key requirement of any attempt at estimating mortality in a population by sequential head-counts of individuals, is that the entire population shall be surveyed on each occasion. This approach is notoriously challenging in the marine field due to the complications of advection, mixing and diffusion and the cost and difficulty of achieving full synoptic coverage. Our sampling approach clearly made no attempt at sampling the whole population, but what we lacked in spatial coverage, we gained in terms of temporal resolution. This was a key factor because the duration over which larvae were hatching was of a similar order to the age-span over which we were aiming to estimate the loss rate. Hence, the ability to track the dissipation of discrete hatch date cohorts within the annual production of larvae was vital for the study, and

could only be meaningfully achieved by high temporal resolution sampling. Obviously, the down-side of our approach was that we were only able to measure the loss, or dissipation rate of larvae at the sampling site, which should be greater than the mortality rate and included contributions from advection and diffusion.

The highly conservative pattern of loss rate with respect to hatch date suggests that dispersal was not the major determinant. Our results show that loss rate was consistently greater for early hatching cohorts than late hatching. A similar pattern of survival with respect to hatch date was found for sandeel larvae at Shetland in the northern North Sea (Wright and Bailey, 1996). There are many biological reasons why mortality should conform to such a pattern, whilst it is difficult imagine an oceanographic explanation as to why dispersal should be so consistently dependent on hatch date. Early hatching larvae potentially experience consistently different food, predator and temperature environments from those hatching later in the season. In addition, although we know that *A. marinus* produce only a single batch of eggs per year (Boulcott et al., 2007; Boulcott and Wright, 2008), we do not know whether they spawn synchronously, i.e. all individuals in a patch spawn together on the same date, or progressively over a period of time. If synchronously, then the observed duration of the hatching period implies that early hatching eggs must have undergone very much shorter incubation periods than the late hatching eggs, with possible consequences for the fitness of the emerging larvae.

4.3. Inter-annual variation in growth rate

In the absence of otolith data from each hatch date interval and year of monitoring at Stonehaven, we based our transposition of the abundance of larvae at length to abundance-at-age in every sample, on a composite analysis of otolith data collected only in 2000 and 2001. Hence we implicitly assumed no temporal trend or variability in growth rate. Clearly, this was a limitation since spatial and year-to-year variations in size at date, and size at age, of recruited sandeels (age ~3 months) are particularly large (Wright and Bailey, 1996; Wanless et al., 2004). The question is, are such variations present between the hatch date and annual cohorts of larvae that we sampled off Stonehaven, and could they significantly affect our conclusions?

The bootstrap sensitivity analysis showed that uncertainty in the results as a consequence of assuming a fixed growth rate across all years was not sufficient to invalidate the estimated patterns in annual survivor abundance and loss rate, at least provided that the s.d. of inter-annual variations in growth rate were limited to 1.5% around the 2000-2001 average with no underlying trend. Our data showed that there was inter-annual variability in the mean and s.d of capture-date-at-length, some of which could be explained by the variations in hatch date, and some probably by variations in growth rate. However there was no trend in the capture date of any of the length classes of larvae over the monitoring period, at least up to 17 mm length. The implication of this result is that there was no trend in growth rate, at least up to approximately 20 d age. Nevertheless, data on the lengths of 0-group sandeel gathered by Atlantic puffins foraging on the Wee Bankie between late May and mid July, indicate a long-term decline in length-at-date of both 0-group and 1+ group sandeels on the Banks, extending back over a period of 30 years (Wanless et al., 2004). 0-group sandeels on 1 July 2002, were found to be on average 14.5% smaller than on the same date in 1973. However, was no evidence of any trend in growth rate within

the 6-7 weeks each year when the puffins were foraging, so by implication the origins of the decline in size-at-date must be in the period between hatching and late May, either due to changes in growth rate, hatch date, or the pattern of survival with respect to hatch date (Wright and Bailey, 1996). Our data indicate that the trend did not arise from the early stage larvae, at least over the years 2000-2009.

4.4. Mortality process and the survival of sandeel larvae

The consistencies between a) hatchling abundance at Stonehaven and cpue and potential spawning biomass on the Banks, and b) loss rate at Stonehaven and larval phase mortality implied by the demographic data from the Banks surveys, suggest that the major part of the variability in survival which dictated variability in recruitment had already occurred by 20 d age. This being the case, and loss rate at Stonehaven being primarily due to mortality, the dome shaped or saturating relationship between annual mean loss rate and annual mean abundance of hatchlings (Fig. 9) could be more than coincidental, and diagnostic of the underlying processes regulating the recruitment dynamics. Given that there was no trend in the growth rate of larvae, we must conclude that the changes in loss rate arose mainly from variations in predation. We do not know for sure what species might be the predators of 0-20 d old sandeel larvae, but we can suggest that small planktivorous fish (juvenile herring and sprat) may be at least partly responsible since they are particularly abundant in the inshore waters off the east coast of Scotland at the time when sandeel larvae are hatching (ICES FishMap, and ad hoc hydro-acoustic observations during visits to the monitoring site).

The simplest predation-orientated explanation of the observed decline in loss rates would be that the abundance of predators had declined, and any relationship between loss rate and hatchling abundance was purely coincidental. However, an intriguing alternative, based on the apparent dome-shaped or saturating relationship between loss rate and hatchling abundance, is that mortality rates were density dependent. If we can speculate for the moment, that the abundance of predators was effectively constant over time, then the pattern of loss rate with respect to hatchling abundance (Fig. 9) was diagnostic of a Type III functional response (Holling, 1959a,b). This density dependent response occurs when predators vary their search rate or prey preference in response to prey abundance. At low prey densities, mortality first increases with density as predators are attracted to the prey, but eventually begins to decline as prey density increases beyond a threshold where the per-capita uptake rate of the prey (but not necessarily all prey) by the predator becomes saturated (Hixon and Carr, 1997; Holling, 1965; Morris, 1965; Takahashi, 1964). Thus, zooplankton may remain the dominant dietary component of planktivorous fish, but the incidence of attacks on sandeel larvae changes disproportionately to their abundance. A key proviso of this interpretation of the results is that abundance of predators must have remained more or less constant over the observation period for the observed relationship to have emerged. This would have to be the first aspect of the hypothesis to assess in any follow up investigation.

4.5 North Sea context

At the scale of the North Sea, sandeel stocks underwent a steep decline in abundance in 2003, largely due to poor recruitment of the 2002 year class. Since then, survival of recruiting year classes has been largely confined to the southern North Sea, and sandeel abundance in the north has continued to decline (ICES, 2007). The stock trajectory on the Banks off the Firth of Forth is consistent with this assessment, but it is clear from our analysis that the elevated mortality of recruiting year classes which is preventing stock recovery, is not occurring during the first three months of life. In fact, age class 0 abundance in May/June has been maintained despite diminishing spawning stock. Some time between their first summer of life and the following spring, the fish are suffering unusually high mortality and not surviving to participate in spawning. North Sea herring have also suffered a decrease in recruitment rates since 2000 due to diminished overwinter survival of larvae. It has been noted that the onset of poor survival of herring larvae coincided with a change in plankton and temperature conditions, though the precise mechanism has not been identified (Payne et al., 2009). In the case of sandeels in the north-western North Sea, our analysis has helped to narrow down the possible mechanism of diminished survival by eliminating the proposition that early larval stages were involved. The next hypothesis to examine should be that survival of post-recruits during their first overwinter fasting period whilst buried in the sediment, has been compromised by a combination of summer feeding conditions and warming sea temperatures.

5. Conclusions

The key implication of the population demography data collected during the scientific surveys on the Banks (Greenstreet et al., 2006, 2010) was that recruitment had been maintained over the decade following the fishery closure, despite the decline in spawning stock from 2001/2002 onwards. We determined that the expected signature of this pattern was a reduction in the mortality rate (increased survival) of larvae. Our results show that the loss rate of early stage larvae off Stonehaven declined over the study period in a manner which was correlated with the annual mortality rate implied by the population demography data from the Banks. Hence, we have confirmed that an increased larval mortality was not the immediate cause of the decline in sandeel abundance.

Acknowledgements

The long-term commitment to weekly sampling at the Stonehaven site was provided by the Scottish Government. Length measurements and species identification of archived sandeel larvae samples, analysis of the data, and writing of the manuscript were supported by the EU FP6 project RECLAIM (044133 (SSP8) and Scottish Funding Council support to MH through the MASTS marine science pooling initiative. We also gratefully acknowledge the assistance of the crew members of the survey vessels *Shuna* and *Temora*, especially Raymond Cargill and Paul Macdonald, who helped with the sampling in all weathers throughout the 10 year period.

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Figure legends

Fig. 1. Location of the monitoring site of Stonehaven (star symbol) in relation the major expanses of sandeel habitat (black filled areas) identified from geological survey data, fisheries effort statistics, and fishing survey data (digitised from ICES 2007). Additional minor patches of sandeel habitat are widespread in inshore waters along the east coast of Scotland. The heavy dashed line delineates the area closed to sandeel trawling in 1999. The pale grey shaded area enclosed by the thin dashed line represents waters shallower than 50 m. Additional bathymetric contours are shown at 80 m (grey thin dashed) and 110m (grey thin solid). The solid black line delineates the area covered by the scientific surveys of sandeel abundance (Greenstreet *et al.* 2006, 2010).

Fig. 2. Upper panel: Landings (bars, tonnes) and catch per unit effort (line and filled symbols, tonnes per kilo-watt hour) from the Danish sandeel fishery off the Firth of Forth. Between 1990 and 1999 the data are derived from analysis of vessel log-books. From 2000 onwards the data are from the supervised monitoring fishery undertaken to provide stock assessment data. Landings and effort data up to 2005 digitised from Frederiksen *et al.* (2008). Catch per unit effort data for 2006 and 2007 from H. Jensen, Danish Institute for Fisheries Research. Lower panel: Biomass of age 0, and age 1+ sandeels (buried in the sediment plus swimming in the water column combined) measured during May/June each year by the scientific surveys (data digitised from Greenstreet *et al.* 2006 and 2010). The area covered by the scientific surveys is shown in Figure 2.

Fig. 3. Annual mean abundances (m^{-2}) of *A. marinus* larvae length classes, averaged over all samples collected during each year.

Fig. 4. Changes in capture date of *A. marinus* larvae with length averaged over the 10 years of sampling. Bold line indicate the mean capture date of 1 mm length classes. Fine lines without symbols indicate ± 1 s.d. around the mean date.

Fig. 5. Upper panel: Individual length and age estimates of *A. marinus* larvae captured in 2000 (filled symbols) and 2001 (open symbols) at the monitoring site. Lower panel: Fitted probability distributions of age given length from the continuation logit method, for larvae collected in 2000 and 2001 at the monitoring site. Probabilities shown for only every 10th age class.

Fig. 6. Mean abundance (m^{-2}) of 3-5 day old larvae in each of the 8 hatch date cohorts (days 29-42, 43-56, 57-70, 71-84, 85-98, 99-112, 113-126, and 127-140) for each year of sampling.

Fig. 7. Log abundance (m^{-2}) in relation to age at capture, for larvae originating from, as an example, hatch date interval 4 (days 71-84). Lines represent fitted linear relationships for larvae ≤ 20 d old where these were significant ($p < 0.05$).

Fig. 8. Loss rates (d^{-1}) of larvae up to 20 days age, in relation to hatch date for each year of sampling. Symbols represent observed data, bars represent GAM values fitted to the observed loss rates with hatch date interval and year as explanatory variables.

Fig. 9. Upper left: Annual mean abundance (m^{-2}) of local hatchlings at Stonehaven, represented by age 3-5 d old larvae (bars), and predicted annual mean abundance of larvae age 20 d ($100 m^{-2}$; symbols and lines). Upper right: Annual loss rate (d^{-1}) of larvae from local hatching at Stonehaven. Lower left: Annual loss rate of locally hatching larvae in relation to annual mean hatching abundance (m^{-2}). Lower right: Relationship between the mortality rate of larvae implied by the scientific survey data on the Banks (M_y), and loss rate of locally hatching larvae at Stonehaven (d^{-1}) (multiple $r^2 = 0.51$, $F = 6.193$ on 1 and 6 df, $p < 0.05$).

Fig. 10. Bootstrap estimates of the uncertainty in predicted annual mean abundance (m^{-2}) of larvae at age 20 d (upper panel), and annual loss rate (d^{-1}) of larvae from local hatching at Stonehaven (lower panel) after 135 iterations of the data processing. Each box-and-whisker plot shows the extremes (whiskers), quartiles (box) and median (horizontal line) of the estimated values for each year, as a consequence of imposing normally distributed variability in annual average growth rates with s.d. equivalent to a coefficient of variation of 1.5% and mean equal to the 2000-2001 aggregate rate.

Figure 1

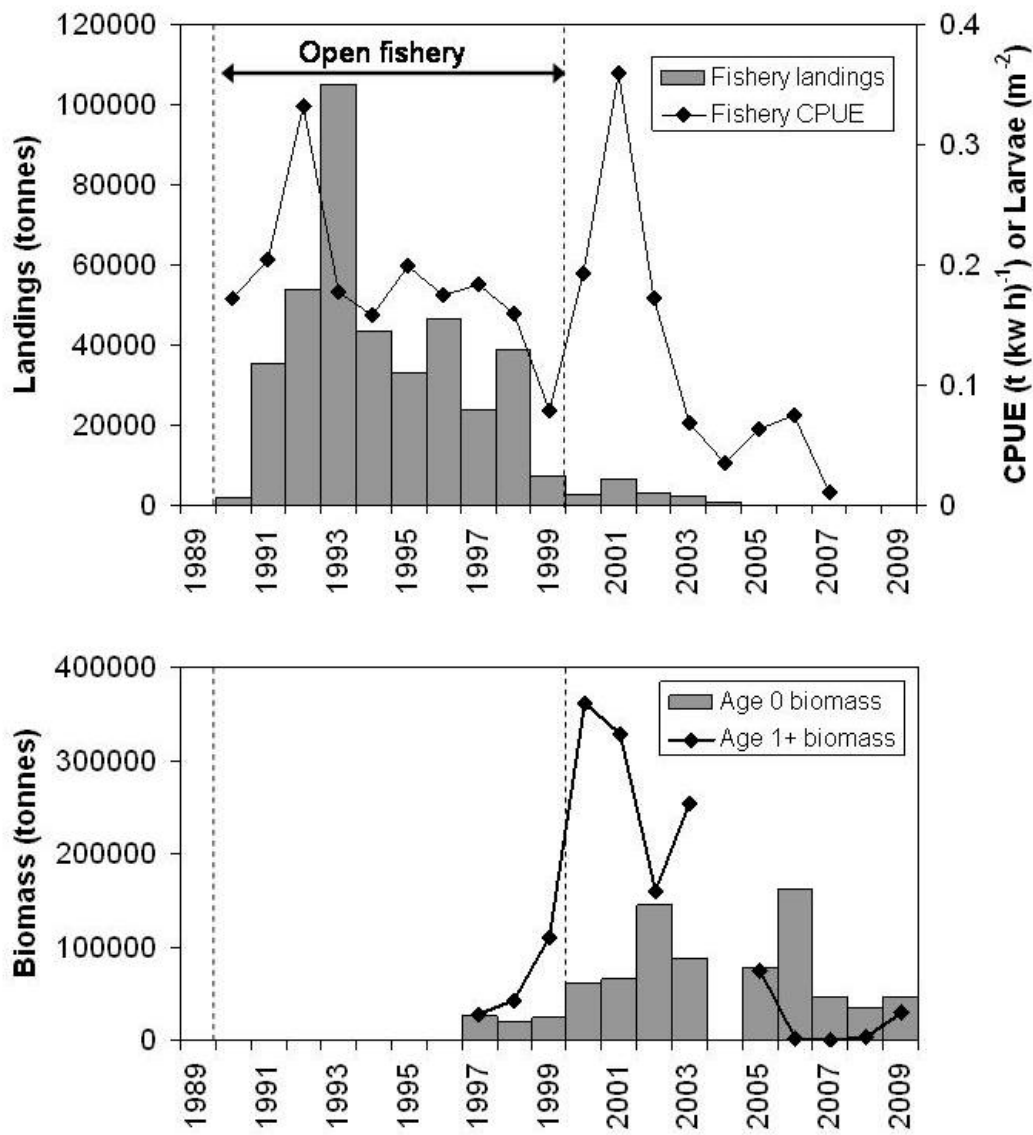


Figure 2

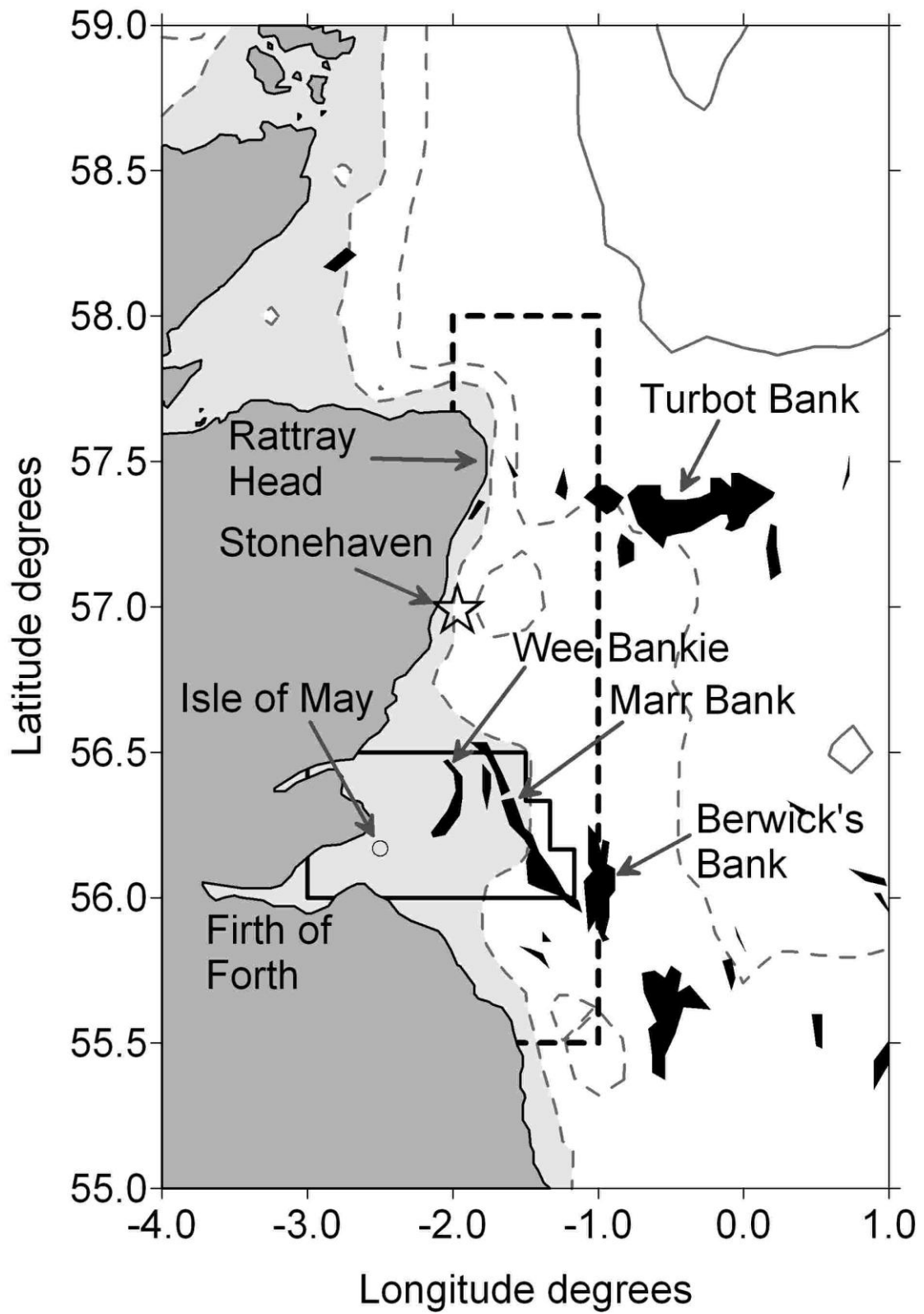


Figure 3

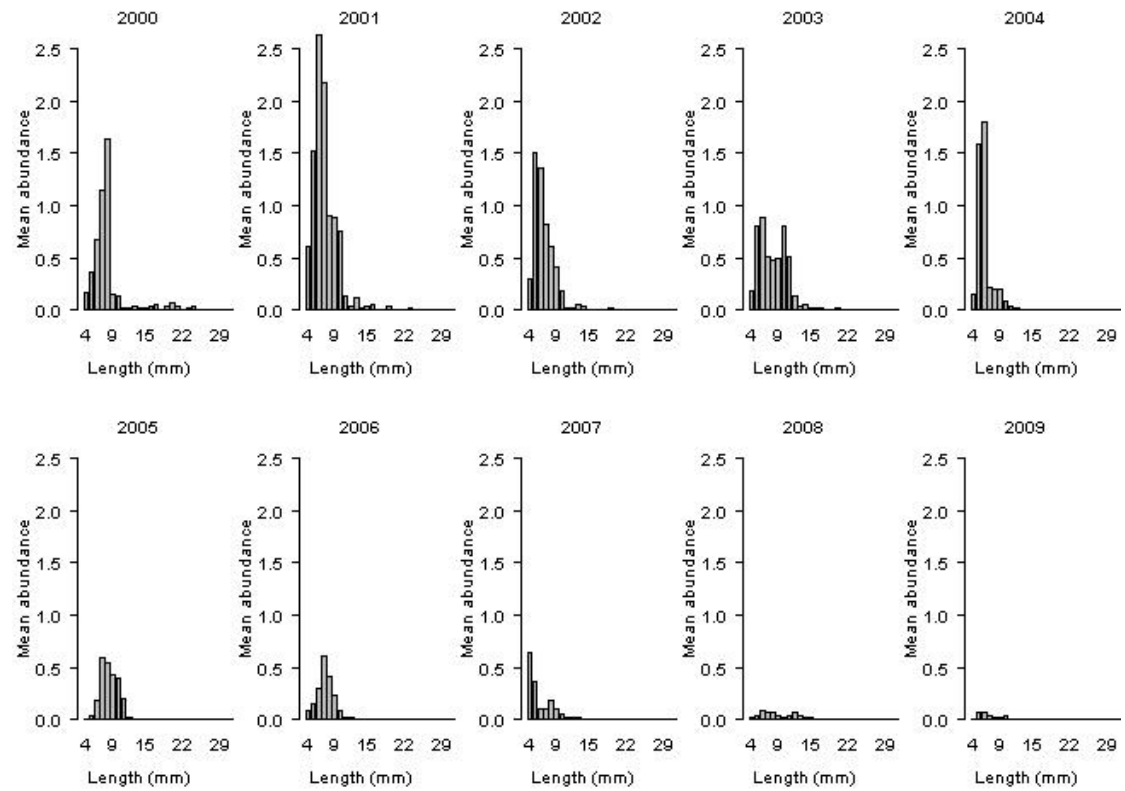


Figure 4

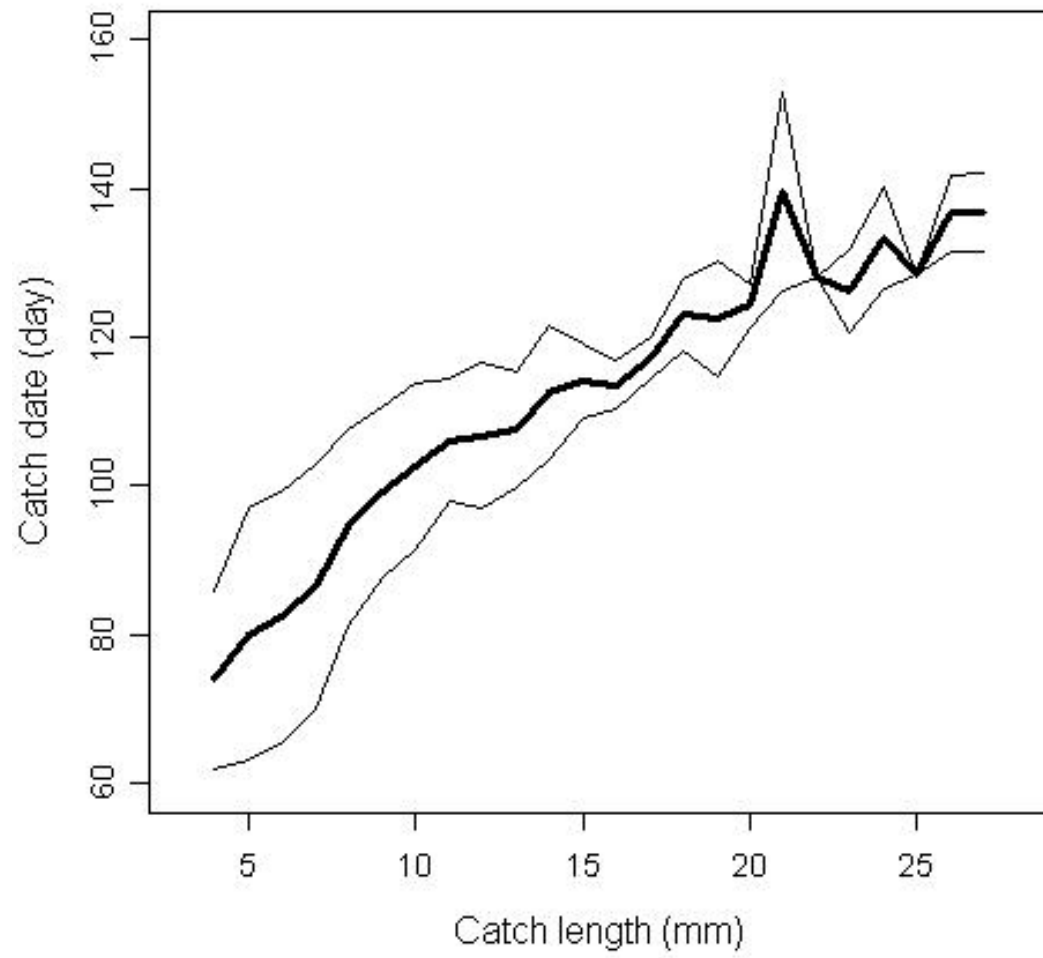


Figure 5

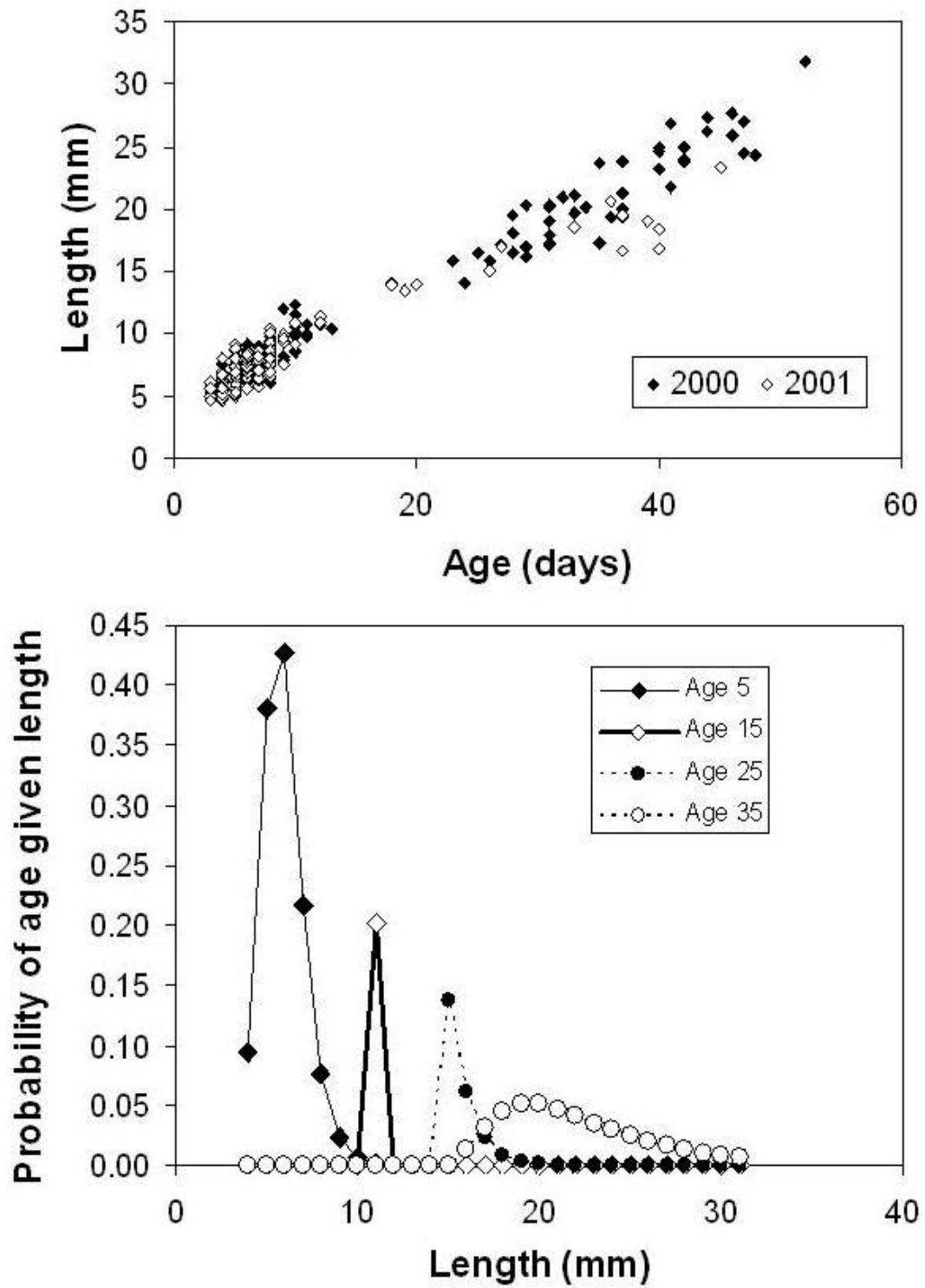


Figure 6

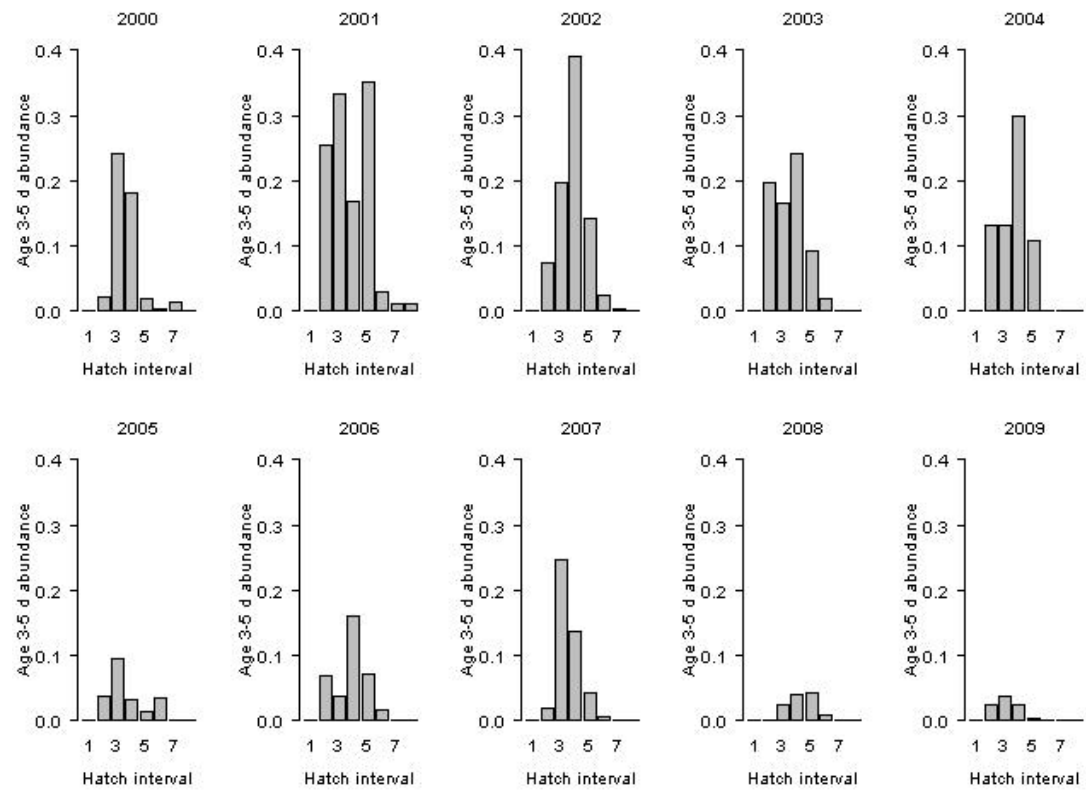


Figure 7

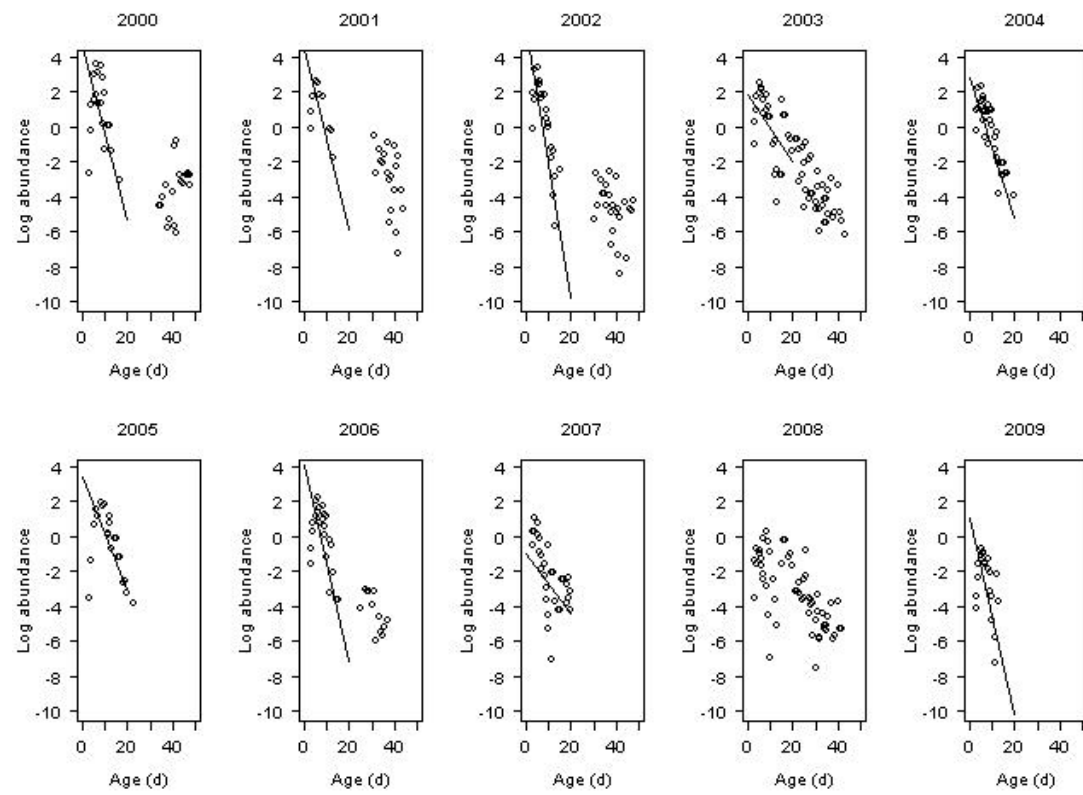


Figure 8

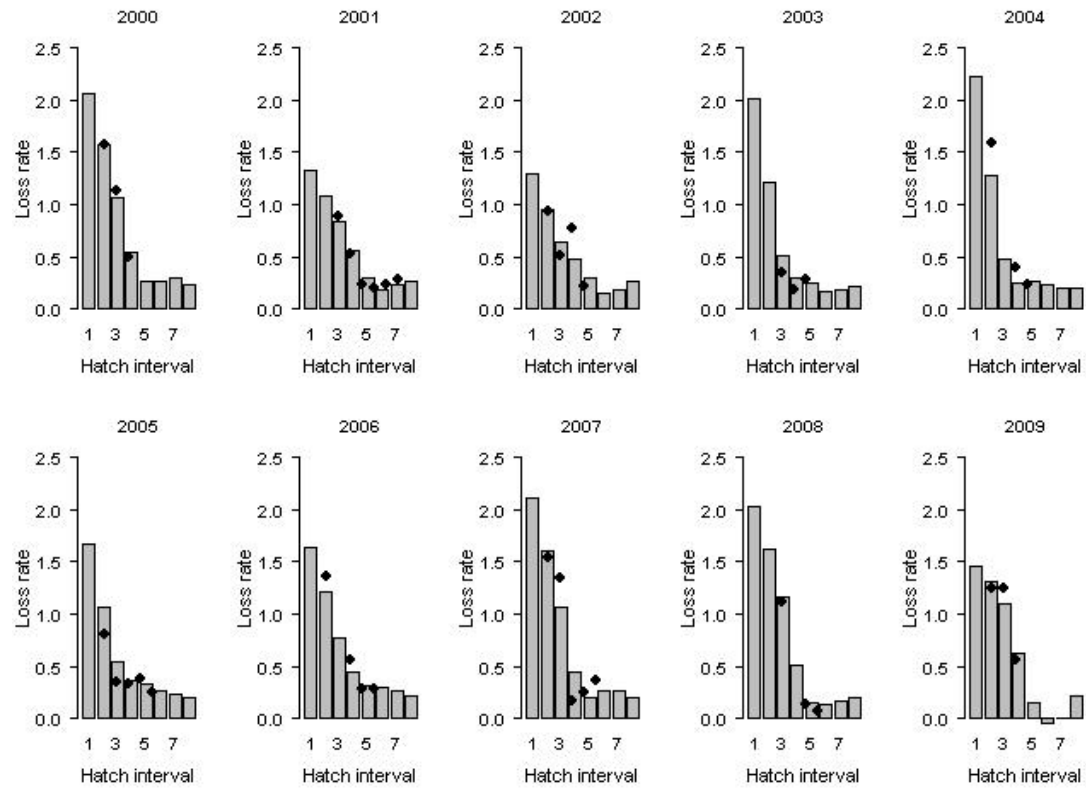


Figure 9

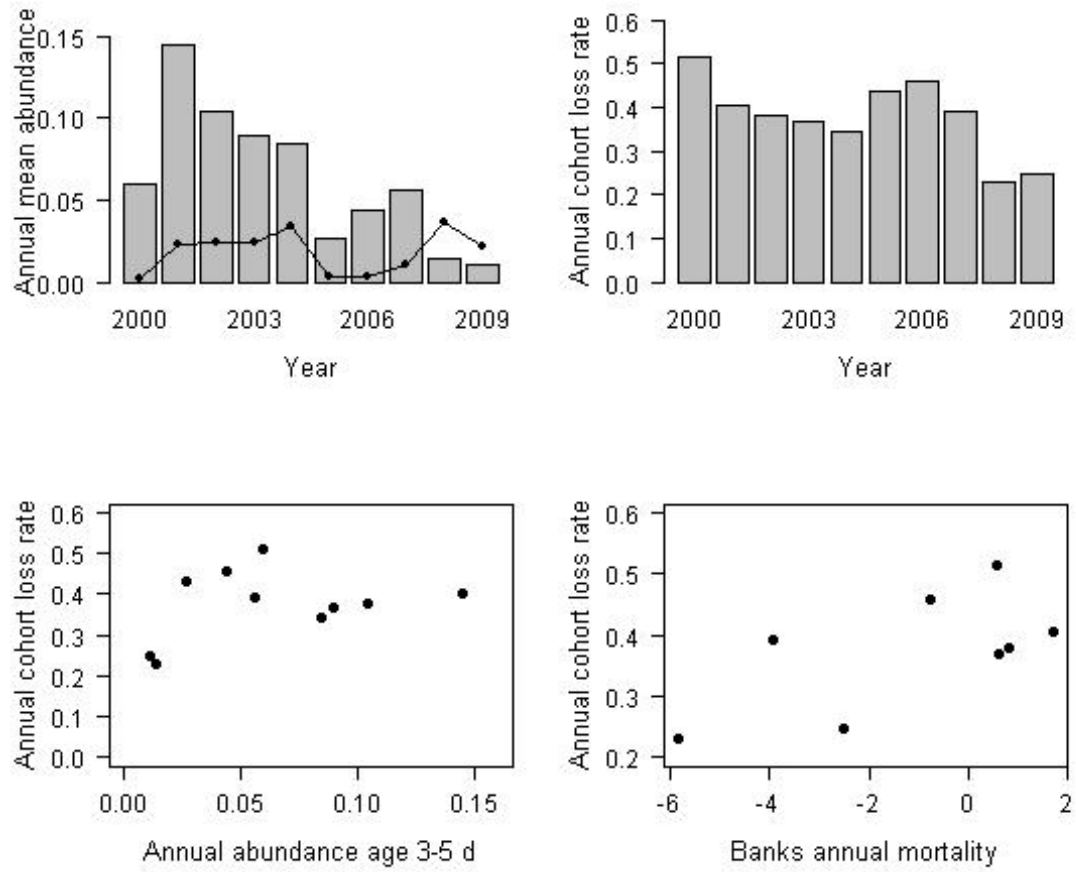


Figure 10

