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Population regulation in a changing environment: Long-term changes in growth, condition and survival of sprat, *Sprattus sprattus* L. in the Bristol Channel, UK

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ABSTRACT

Sprat, *Sprattus sprattus*, is the dominant pelagic species in British inshore and estuarine waters. Within the Bristol Channel the population is almost totally composed of fish <3 years old with the adults overwintering in Bridgwater Bay. Sprat follow regular seasonal migrations and occasionally form huge aggregations which together generate considerable between sample variability. Using a 36-year monthly time series collected in the Bristol Channel since 1980, together with two periods of intensive daily and weekly sampling, sprat growth is shown to have declined almost linearly over the last 36 years coincident with increasing late summer-autumn seawater temperatures. Longevity has also declined, with age 3+ sprat >140 mm standard length lost to the population by 1999. Further, adult condition, measured as the average weight of a 103 mm standard length adult, declined rapidly from 13.7 g in 2007 to 9 g in 2011. Despite these changes, which would have reduced age-specific fecundity, a sign-rank test showed abundance of adult sprat has shown no long-term trend and Bulmer's test indicates density-dependent regulation is operating. While sprat recruitment is shown to be responding to the sunspot cycle, the North Atlantic Oscillation and sea water temperature, the impact of these variables on adult population density is damped because of density-dependent regulation. The result is that sprat respond to environmental change with large changes in their growth and condition, but the adult abundance is constrained and shows no long-term trend. Recruitment was modelled by combining a Ricker curve with terms for the response of sprat to solar activity, the North Atlantic Oscillation and spring temperature. It is shown that the stock-recruitment relationship does not form a simple curve, but is bounded within a region in which the upper and lower constraints are defined by environmental conditions. Within this bounded region the population trajectory under differing environmental regimes can be predicted.

1. Introduction

Identifying the factors which determine and regulate the abundance of sprat, *Sprattus sprattus* L. 1758, the dominant pelagic species in British inshore and estuarine waters (Henderson, 1989), is of considerable applied and theoretical interest. In inshore European ecosystems, sprat hold a central role feeding upon zooplankton (Baumann et al., 2006a, 2006b) while being preyed upon by fish, mammals, seabirds and man (Jennings et al., 2012; Greenstreet et al., 1998; Thompson et al., 1997). They are one of the most abundant fish along the European Atlantic coast from Portugal to Scotland and their range extends from West Norway to Morocco including the Baltic, northern Mediterranean and Black Seas (Whitehead, 1985). Like other small pelagic fish such as anchovies, *Engraulis encrasicolus*, and sardines, *Sardina pilchardus*, sprat abundance is highly variable (Brochier et al., 2009) and, over short time periods, seemingly random (Peck et al., 2005). However, in the Baltic Sea, studies have shown their population to be responsive to local environmental conditions (Casini et al., 2006). The objective of this study was to build a long-term data set of sprat abundance and age structure of sufficient duration and sampling frequency to understand population regulation within the Bristol Channel sprat population and identify regulatory processes and environmental variables influencing the population. This required an understanding of (1) seasonal movement and recruitment; (2) consistent estimates of annual relative abundance for different age groups over sufficient time to detect density-dependence if operating; (3) contemporaneous time series for physical variables known, or suspected, to influence sprat growth and recruitment; (4) data on the length and weight at age of individual fish to measure level of response of individual fish to the conditions experienced. When the work commenced in October 1980 the duration of the study was not fixed, results are now reported for the first 36 years because statistically robust conclusions can now be reached. The regular monthly sampling is planned to continue for at least the next 10 years.

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The meristic and seasonal distribution studies indicate that the Bristol Channel and Severn estuary holds a local population. Fig. 1 summarises the seasonal distribution of sprat early stages. Sprat spawn in spring and the eggs are most abundant in Carmarthan Bay and off Hartland Point west of Lundy Island in April (Russell, 1980; Williams, 1984). In April, the larvae are concentrated further within the channel, with maximum abundances in Barnstable Bay. Juveniles 20–30 mm SL are observed in Bridgwater Bay in June (Fig. 4) and are first observed in the inner estuary at Oldbury Upon Severn at 35–40 mm SL in August/September (Potter and Claridge, 1985). The decline of adult sprat in samples from Oldbury and Hinkley from February is linked to an offshore movement to the spawning grounds. Potter and Claridge (1985) report that the mean number of fin rays and vertebrae of Bristol Channel sprat differs from that of other British west coast sprat populations. A maximum longevity of 6 years has been reported for British sprat, Bristol Channel sprat do not typically live longer than 4 years (Potter and Claridge, 1985). Adult sprat annually overwinter in Bridgwater Bay between November and mid February.

Studies in the Baltic and Black Seas have shown that sprat are responsive in their growth and condition to environmental conditions (Peck et al., 2012; Casini et al., 2010) with temperature influencing growth (Baumann et al., 2006a, 2006b). Between-year differences in growth in the Bristol Channel were therefore expected, although conditions along the Atlantic coast are more temperate than in the Baltic or Black Seas, so a lower level of variability was anticipated.

While Bristol Channel sprat is no longer commercially exploited, fishery records from the 1800s onwards show the species was abundant throughout the 19th and early 20th centuries (Day, 1890; Day, 1897; Lloyd, 1941). It was the most abundant teleost in plankton samples taken throughout the Bristol Channel between the spring and autumn of 1974 (Potter and Claridge, 1985), and from 1980 it has been the most abundant fish impinged at Hinkley Point, Somerset (Henderson, 2007).

2. Materials and methods

The scale and variability of sprat populations in combination with their shoaling behaviour and mobility makes the collection of adequate samples to study population dynamics particularly demanding. The approach taken here is to use long-term data collected from power station intakes. Sprat are particularly vulnerable to cooling water intakes, and because samples can be collected under all sea conditions a long-term, regular, time series covering all age classes was generated.

Sprat samples were collected from the cooling-water filter screens at Hinkley Point 'B' power station (Fig. 1), situated on the southern bank of the Bristol Channel in Somerset, England (51°14′14.05″N, 3° 8′49.71″W).

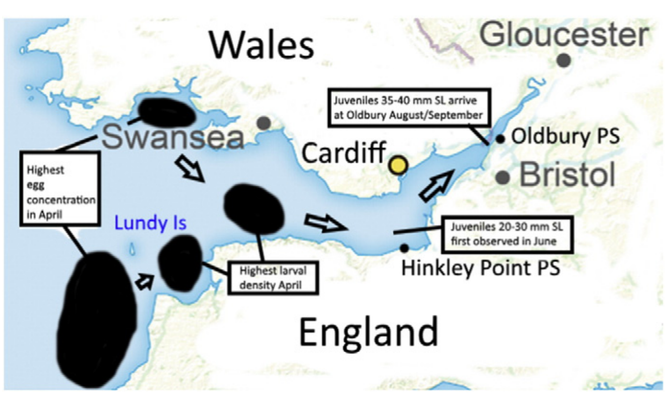

Fig. 1. A map of the study area showing the waters occupied by the Bristol Channel sprat population. In late winter to early spring the adults live predominately to the west of Lundy island, they spawn in March to May in Carmarthan Bay and to the west of Hartland Point. There is a progressive migration up the estuary over the summer. Adults overwinter in Bridgwater Bay near Hinkley Point before moving off-shore in late winter.

The water intakes are in front of a rocky promontory within Bridgwater Bay, while to the East are the 40 km^2 Steart mud flats. Depending upon the tide, the fish were sampled from water varying in depth from about 8 to 18 m. A full description of the intake configuration and sampling methodology is given in (Henderson and Holmes, 1991) and (Henderson and Seaby, 1994). Methodology has not changed over the 36 years of study.

Quantitative sampling commenced in 1980 when 24-hour surveys of the diurnal pattern of capture were undertaken in October and November. From these surveys it was concluded that samples collected during daylight were representative of the 24-h catch, and monthly quantitative sampling commenced in January 1981. The total volume of water sampled per month, which has not varied over the 35-year period, is 4.27×10^5 m^3. To standardise for tidal influence, all sampling dates were chosen for tides halfway between springs and neaps, with sampling commencing at high water (normally about 12:00 h). The number and species of fish and crustaceans collected hourly from two filter screens over a 6-h period were recorded. Monthly samples are taken over 6 h on an intermediate tide in the spring-neap cycle.

The power station intakes at Hinkley Point are an effective sampler because of their location at the edge of a large intertidal mudflat in an estuary with extremely powerful tides that generates suspended solid levels of up to 3 g l^{-1}, so that little light penetrates below 50 cm depth. It is likely that sprats are often unable to see or otherwise detect the intake until they are too close to make an escape. Light is clearly important for avoidance because captures are higher at night at power station intakes situated in clear water. The efficiency of the sampling method is discussed in (Henderson and Holmes, 1991). The filter screens have a solid square mesh of 10 mm and retain few sprats $<$40 mm in length. Using the equation of Turnpenny (1981) a 10 mm mesh will retain all sprat $>$84 mm SL, therefore the condition of larger adult sprat cannot influence their retention on the screens. Between 40 and 84 mm SL retention rate rapidly increases, it is determined by both the orientation of the fish on the screen and also the presence of weed and other debris which block the screen and entangle the fish.

Monthly sampling was not carried out during October 1983 and 1988 or during December 1987 and 1999 because of power station maintenance. A preliminary study was made in October and November 1980 to test for tidal and diurnal changes in the rate of capture. In addition to the standard monthly sampling regime, two shorter periods of intensive sampling were undertaken to study in more detail seasonal presence and growth. The first intensive study comprising twenty-four 24-h samples was undertaken between 8th November 1993 and 10th February 1994 studied changes in the rate of capture over the winter period when the adults enter Bridgwater Bay and followed changes over the spring-neap tidal cycle. The second intensive study was undertaken between February 2009 and March 2010. This comprised forty 24-h samples divided into 10 samples collected in each quarter of the year. Each 24-h sample filtered the fish from 3.416×10^6 m^3 of seawater. The sample dates within each quarter were chosen at random. The purpose of this study was to gain a greater resolution of population structure, check that larger and older sprats observed in the 1980s were not present, obtain large samples for aging and acquire more detail on seasonal change.

Since 1992 the standard length (SL) of all captured fish have been recorded to the nearest mm, prior to this date fish were measured between 1984 and 1990. Commencing in 2000 the catch wet weights of sprat were recorded to the nearest 0.1 g. Sprat condition which was calculated using a double natural logarithm length-weight linear regression. The predicted weight of a 120 mm total length (TL) (103 mm SL) fish was used as a condition measure as was previously used by Casini et al. (2011) for Baltic Sea fish. Individual length-weight data for Hinkley Point suitable for the calculation of condition was collected from 2007 onwards. In 2009/10 sprats were aged using otolith reading.

To allow comparison of the power station impingement catch with a second independent sampling method, pelagic trawls were undertaken