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Spatio-temporal variation in the reproduction timing of Atlantic Wolffish (*Anarhichas lupus* L) in Icelandic waters and its relationship with size

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ABSTRACT

Biological data were retrieved from 3694 female Atlantic wolffish *Anarhichas lupus* collected in Icelandic waters at four locations during the breeding season using a long–term study spanning from 2002 to 2013. The main objective was to investigate reproduction investment and timing. In the main spawning ground, little temporal differences were observed. In contrast, the peak of the spawning season was different among spawning grounds, suggesting spatial differences in the timing of reproduction. The size of females *A. lupus* was related to the spawning time with the larger fish spawning earlier than smaller ones. In addition, no significant pattern was found between temperature and spawning time. Except at its main spawning area where spawning begins in late September, spawning usually began in late August or beginning of September and was completed in early November.

1. Introduction

In temperate environments, seasonal differences in sea temperature and zooplankton abundance will typically affect the timing of reproduction of many fish. Spawning time, which is cyclical for most temperate fish species, is one of the main features affecting survival and growth of fish progeny, as favourable environments are likely to positively affect both attributes. Mortality is the highest for early life stages and has been related to temperature, food availability and predation (Houde, 1997). Temperature, which is one of the most important abiotic factors for the survival of the larvae (Houde, 1989), is also known to influence growth, mortality and juvenile fish size. It is also generally acknowledged that survival rate of larvae is higher when hatching synchronises to the zooplankton spring bloom and is asynchronous when predators are in highest abundance (Hjort, 1914; Cushing, 1969). Studies have also shown positive relationships between survival ratios of larvae or juvenile fish during their first year and year class strength for several fish species (Campana et al., 1989; Carscadden et al., 2013; Ojaveer et al., 2011; Sundby et al., 1989). The timing of the reproduction is therefore crucial for a successful recruitment and consequently for the stock productivity and sustainability. Reproductive timing has been related to temperature, photoperiod, food availability, demography and genetic diversity, inter-annual variation and differences between locations, and differences in spawning time (Bromage et al., 2001; Kjesbu, 1994; Lapolla and Buckley, 2005; Marteinsdottir et al., 2000; Morgan, 2001; Morgan et al., 2013; Ottera et al., 2012).

The Atlantic wolffish *Anarhichas lupus* L. 1758 is widely distributed in the North Atlantic Ocean and is an important commercial species. Within its distribution, the spawning time of *A. lupus* varies considerably from September to October in Icelandic waters to late July-late September in the White Sea, September in Norwegian waters and autumn in Canadian waters (Jónsson, 1982; Templeman, 1986; Falk-Petersen et al., 1990; Pavlov and Novikov, 1993; Gunnarsson et al., 2006). In Iceland, spawning of *A. lupus* has been observed all around the country (Fig. 1), but a relatively small (2000 km^2) area west of the country is considered to be the main spawning area. *A. lupus* exhibits a rather unusual reproductive strategy; the female coils around the eggs after spawning, and creates a demersal egg cluster that is later guarded by the male during the incubation period which is *c.* 800–1000 °C-days (cumulative days temperature) (Keats et al., 1985; Ringø and Lorentsen, 1987; Pavlov and Moksness, 1995).

In Icelandic waters, the fishery effort using bottom trawl has increased considerably at the main spawning ground during

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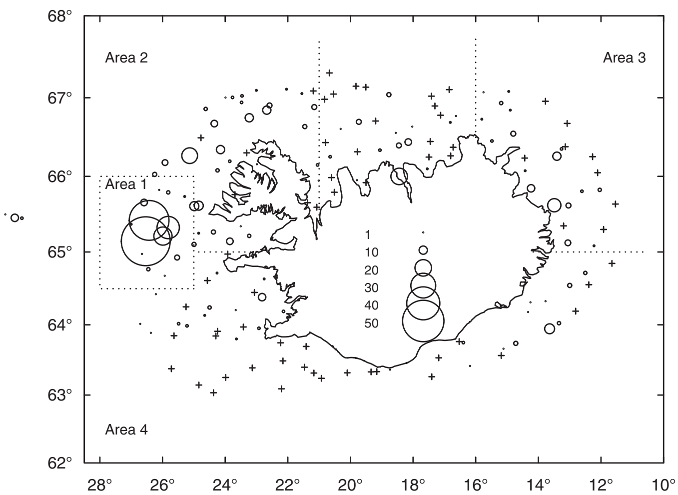

Fig. 1. Spawning (◯) of Atlantic wolffish at Iceland, according to AGFS. The (◯) represents stations where female *A. lupus* were found near spawning or recently spawned, the size of the circles denote number of such fish, (+) represents station where no such females were found.

spawning time from 1999 onwards, as the commercial value of *A. lupus* is highest during this period (S. Pétursson, pers. comm.). Before that, the *A. lupus* fishery was mainly comprised of longliners after the incubation period, outside the spawning areas.

In the year 2002, in an attempt to improve the recruitment of *A. lupus*, part of the main spawning ground was closed during spawning and incubation time (area 1, Fig. 1). As the data and knowledge on spawning of *A. lupus* was scarce, sampling of data on spatial-temporal distribution of spawning in the area was increased. Based on this sampling and logbooks from fishing vessels, the size of the closed area was further extended in 2010 from 500 km^2 to 1000 km^2 and the closure period was extended from 1st of October – 1st of May to 15th of September – 1st of May.

A. lupus abundance has declined drastically during recent years, especially in the north-west Atlantic Ocean where it was listed by the Canadian Species at Risk Act (SARA) as a species of 'special concern' (McCusker et al., 2008). In Icelandic waters, the recruitment was good from 1993 to 1999 but has decreased since then, and been at low level (40% of the highest observed values) from 2010 to 2014. The Marine Research Institute (MRI) of Iceland has given advice based on Maximum Sustainable Yield (MSY) since 2001 but fishing activities exceeded the advised catch for a number of years. However, since 2013, catches have been in accordance with the Total Allowable Catches (TAC) recommended by the MRI (MRI 2015). Concurrently, the fishable stock and the spawning stock have been stable and even increased slightly despite the relatively low recruitment.

Nowadays, the trend in *A. lupus* spawning time is regularly monitored at the main spawning ground to estimate the benefit of the closure period. To observe possible influence of fisheries and environment on spawning time of *A. lupus*, we investigated potential relationships between the reproduction timing, size of the females, and temperature, at the main spawning ground as well as three other areas where this species is known to spawn. We also assessed spatio-temporal differences in spawning trends within these different spawning areas.

2. Materials and methods

2.1. Sampling areas

Sampling areas were chosen to represent both the main spawning area of *A. lupus* (area 1 in Fig. 1) and other spawning areas with different temperature regimes. The area between areas 2 and 3 was excluded from the analysis due to a lack of data (Fig. 1).

2.2. Sampling

Biological samples of female *A. lupus* were collected during 12 consecutive years (2002–2013) from four different areas in Icelandic waters (Fig. 1). All females caught were sampled during the autumn ground fish survey (AGFS) conducted by the MRI from late September to October, using a bottom trawl with 40 mm square mesh codend. In addition, samples were taken for stock assessment purposes from commercial landings from July to December to fully cover the spawning time of the species (Table 1 and Fig. 1). For the analysis of spatial distribution of spawning, only data from the AGFS were used except in 2011 and 2012. In the former year, the survey could not be completed correctly for technical reasons and in the latter, the data collected from areas 3 and 4 were biased. These data were consequently excluded from all analysis. During sampling, the total length (cm) of each female was measured and maturity stages determined visually in the field.

The seabed temperature was measured with Scanmar thermometer which were located on the headline of the trawl and calibrated with Starmon mini temperature recorders before cruise.

2.3. Maturity

Maturity stages were determined according to the maturity scale of Barsukov (1959), revised by Mazhirina (1988). Only two maturity stages were considered during this study, i.e. stage 3 which refers to fish that intend to spawn during the present spawning season and stage 4 which refers to fish that have recently completed spawning or were recovering after spawning (See Gunnarsson et al., 2006 for a full description).

2.4. Statistical analysis

To investigate the effects of female size and spatio-temporal on the time of spawning a multivariate logistic regression model (Cox, 1958) of the form:

$$p_{aldy} = \frac{1}{1 + exp\left(-\beta_{ald} + \gamma_{ay}\right)}$$

was estimated. Here p_{aldy} is the estimated proportion of fish that has spawned in area at length l, day of the year d, year y and

$$\beta_{ald} = \alpha_a + \beta_1 d + \beta_2 l + \beta_{a3} d + \beta_{a4} l + \beta_5 ld + \beta_{a6} ld$$

which represents the effect covariates and γ_{ay} the year—area interaction used as a proxy for the spatio-temporal variability. Here the emphasis is on inferring the time of spawning, and its inter-annual variability, and therefore the year—area interaction were treated as a random effect. The parameters of the model were estimated using restricted maximum likelihood (as described in Bates et al., 2015). Variables were selected to the model by eliminating, using an exhaustive search, those variable combinations that contributed the greatest increase to the Bayesian Information Criterion score or BIC (Schwarz, 1978), resulting in a reduced model where the BIC score could not be improved. Models were considered comparable if the difference in the BIC score was less than 2, as suggested by Kass and Raftery (1995). χ^2 tests were used to compute variable significance in the reduced model.