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The spatial dimension of ecosystem structure and dynamics

Distribution of herring (*Clupea harengus*) and zooplankton in the Norwegian Sea, as determined from generalised additive models

Esben Moland Olsen, W. Melle, S. Kaartvedt, J. C. Holst, and K. A. Mork

We analyse the variability in the distribution and feeding of the Norwegian spring-spawning herring in the period from 1995 to 2004, using survey data collected throughout the Norwegian Sea each year in May - June. The spatial component is handled by fitting generalised additive models (GAMs) to the data. GAMs are an extention of generalised linear models, allowing flexible nonparametric effects of covariates such as latitude and longitude. We also describe the spatial and temporal variability in zooplankton biomass, water temperature and salinity. The data suggest that both herring body size, stomach fullness and zooplankton biomass was higher in the western part of the ocean basin, and that herring generally had a relatively wide and patchy distribution.

Keywords: Generalised additive models, herring, Norwegian Sea, salinity, temperature, zooplankton

Contact author:
Esben Moland Olsen: Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, PB 1066 Blindern, N-0316 Oslo, Norway [tel: +47 22 85 50 65, fax: +47 22 85 40 01, e-mail: e.m.olsen@bio.uio.no].

Introduction

The Norwegian spring-spawning herring is the worlds largest herring stock (Devold 1963, Dragesund et al. 1980, Toresen and Østvedt 2000), and is a major consumer of zooplankton in the Norwegian Sea (Dommasnes et al. 2004). The stock collapsed to the state of commercial extinction in the late 1960s, but is now considered to be fully recovered. During spring and summer, the Norwegian spring-spawning herring forage in the open waters of the Norwegian Sea, building energy reserves for future overwintering and spawning in Norwegian coastal waters (Holst et al. 2004). Historically, there has been much variability in the spatial extent of the herring feeding migration (Holst et al. 2004).

Here, we present a decade of survey data on herring distribution and feeding in the Norwegian Sea during spring and early summer, on an ocean basin scale. We discuss how herring distribution and feeding is linked to the distribution of zooplankton biomass.

Material and Methods

Surveys were conducted in the Norwegian Sea in spring 1995 - 2004. Hydrographical measurements were made using a Sea Bird CTD-probe from 1000 – 0 m depth. Zooplankton was sampled in vertical hauls from 200 – 0 m depth using a WP-2 plankton net with mesh size 180 μm, hauled with a speed of 0.5 ms^{-1}. From each retrieved zooplankton sample, larger jellyfish were removed and the remaining sample divided into two sub-samples. One sub-sample was preserved in formaldehyde. The remaining sub-sample was dried at 70ºC for 24 hours, frozen, and later weighed to the nearest 0.001 g (for details, see: Melle et al. 2004). Herring abundance was estimated continuously from calibrated echo integration systems (38 kHz Simrad EK 500 or EK60). The allocation of area backscattering strengths (s_A) to species was made by comparison of the appearance of the echo recordings to trawl catches. Trawl catches were also used for obtaining individual data on herring body length and stomach fullness. Herring body length was measured to the nearest mm. Herring stomach fullness was quantified on a scale from 1 (empty) to 5 (fully distended) by visual inspection.

Spatial and temporal variation in salinity and sea temperature (averaged for the upper 200 m of the water column) was described by fitting a local polynomial regression (loess) model to the data. We used. We then used the loess model to predict sea temperature and salinity every 0.1 longitude and latitude, on a regular grid throughout the ocean basin. Temperature and salinity isoclines were extracted from these predicted values, removing observations from outside the range of the actual survey.

We fitted generalised additive models (GAMs) to the survey data on zooplankton biomass (g dry weight m^{-2}), herring abundance (s_A values, averaged over 5 nautical miles), herring body length (mean within each trawl haul), and herring stomach fullness (mean within each trawl haul). GAMs are an extension of generalised linear models (GLMs) allowing flexible nonparametric effects of covariates such as latitude and longitude (Fox et al. 2000, Barry and Welsh 2002), and thus handle the spatial component of these data. Model selection was based on the generalised cross validation (GCV) score, which measures the compromise between roughness and smoothness of a fitted curve (Wood 2000). Residual plots were used for checking the fit of the models. For herring abundance, as much as 41 % of the observations in the data set had a s_A value of zero. Due to this, we could not model herring abundance directly, but instead modelled herring abundance conditional on abundance being greater than zero (see, Fox et al. 2000).

Results and discussion

Average sea temperature in the upper 200 m varied from about 8 °C close to the coast of western Norway down to about 2 °C in the north-western part of the Norwegian sea (Fig. 1). Average salinity was generally highest in the southern and central Norwegian Sea (up to about 35.2 ‰), and lower towards the Norwegian coast and the western part of the ocean basin (down to about 34.8 ‰) (Fig. 2). The data indicates that both the shape and the position of the temperature and salinity isoclines varied considerably among years (Fig. 1 and 2).

Zooplankton biomass varied both spatially and temporally (Fig. 3). The preferred GAM model indicates that biomass is often higher in the western part of the Norwegian Sea (Fig. 3). However, this pattern varied substantially among years, and in some years there also appeared to be relatively high zooplankton biomass off the coast of northern Norway (Fig. 3). Zooplankton biomass seems to have been particularly low in 1997 and relatively high in 1999 (Fig. 3).

Herring abundance, mean herring body length, and the mean herring stomach fullness varied temporally and spatially (Fig. 4 – 6). Herring had a relatively wide, but patchy, distribution throughout the Norwegian sea (Fig. 4). Herring abundance seemed relatively high in 2001 and low in 2003 (Fig. 4). Both mean herring body size and mean herring stomach fullness tended to increase towards the western part of the Norwegian Sea (Fig. 5 - 6), where food availability (zooplankton biomass) appeared to be greatest.

In conclusion, we provide fundamental information on the distribution and feeding of one of the main pelagic predators - the herring - and its prey - the zooplankton - throughout the Norwegian Sea basin during the timespan of one decade.

References

Barry, S. C., and Welsh, A. H. 2002. Generalized additive modelling and zero inflated count data. Ecological Modelling 157: 179-188.

Devold, F. 1963. The life history of the Atlanto-Scandian herring. Conseil Permanent International pour l´Exploration de la Mer: Rapports Procès-Verbaux des Réunions 154: 98-108.

Dommasnes, A., Melle, W., Dalpadado, P., and Ellertsen, B. 2004. Herring as a major consumer in the Norwegian Sea. ICES Journal of Marine Science 61: 739-751.

Dragesund, O. Hamre, J., and Ulltang, Ø. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapport et Procès-verbaux des Réunions du Conseil international pour l'Exploration de la mer 177: 43-71.

Fox, C. J., O'Brien, C. M., Dickey-Collas, M., and Nash, R. D. M. 2000. Patterns in the spawning of cod (*Gadus morhua* L.), sole (*Solea solea* L.) and plaice (*Pleuronectes platessa* L.) in the Irish Sea as determined by generalized additive modelling. Fisheries Oceanography 9: 33-49.

Holst, J. C., Røttingen, I., and Melle, W. 2004. The Herring. *In* The Norwegian Sea ecosytem. *Edited by* H. R. Skjoldal. Tapir Academic Press, Trondheim, Norway. pp. 203-226.

Melle, W., Ellertsen, B., and Skjoldal, H. R. 2004. Zooplankton: The link to higher trophic levels. *In* The Norwegian Sea ecosytem. *Edited by* H. R. Skjoldal. Tapir Academic Press, Trondheim, Norway. pp. 137-202.

Toresen, T., and Østvedt, O. J. 2000. Variations in abundance off Norwegian spring-spawning herring (*Clupea harengus*, Clupeidea) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries 1: 231-256.

Wood, S. N. 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. J R Statistical Society B 62: 413-428.

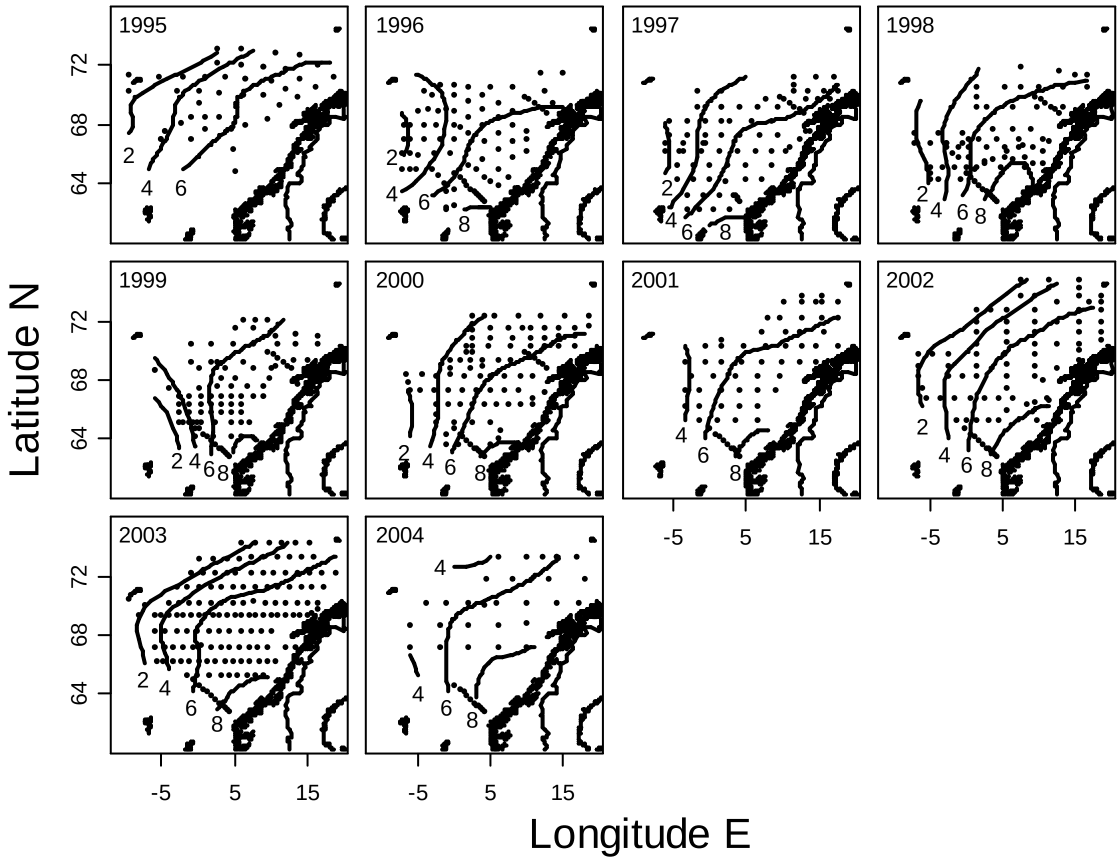

Figure 1. Norwegian Sea water temperatures in the period from 1995 to 2004 (average ºC in the upper 200 m).

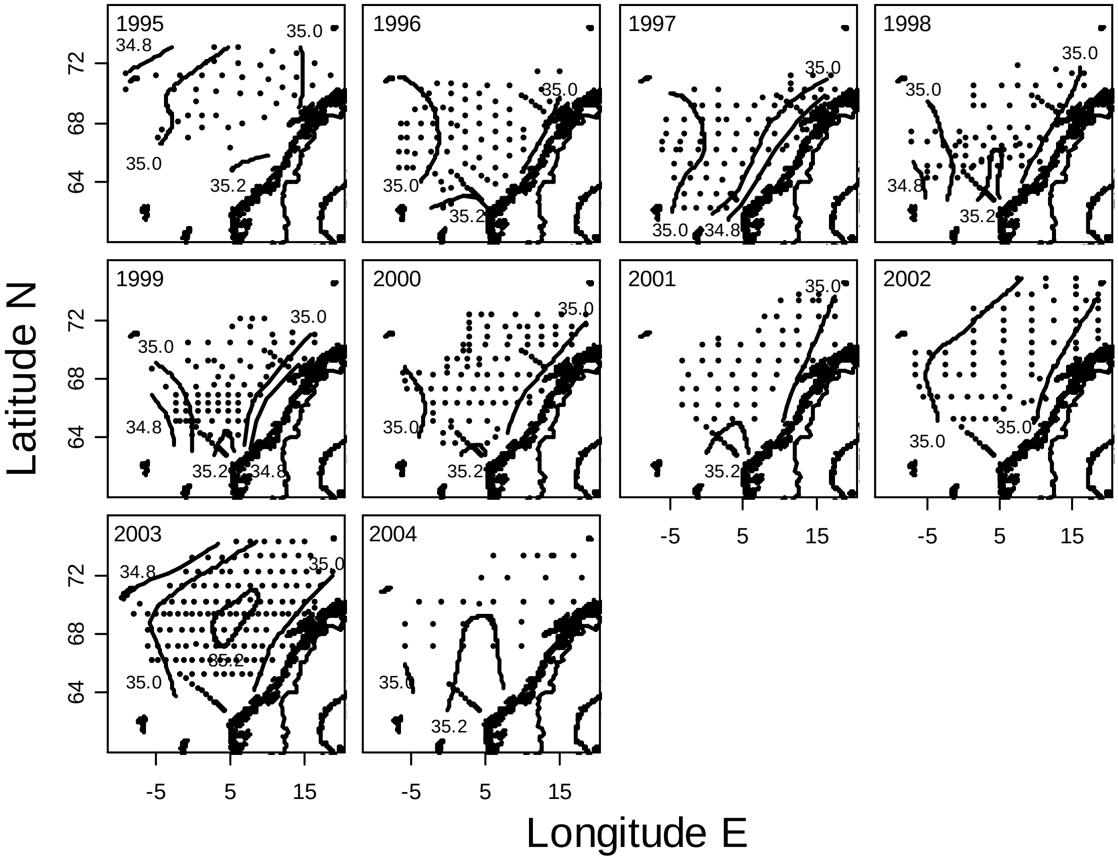

Figure 2. Norwegian Sea salinities in the period from 1995 to 2004 (average ‰ for the upper 200 m).

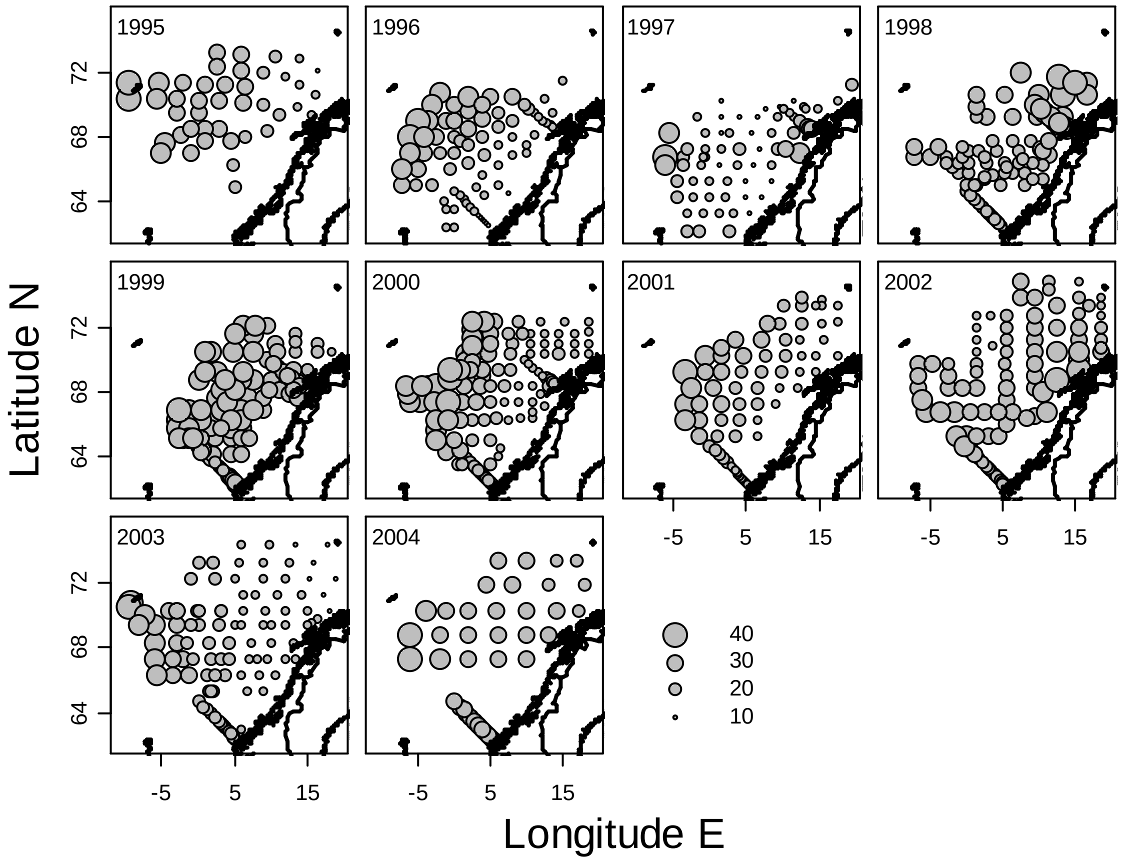

Figure 3. Zooplankton biomass in the Norwegian Sea (g dryweight m^{-2}), as predicted from a generalised additive model (GAM).

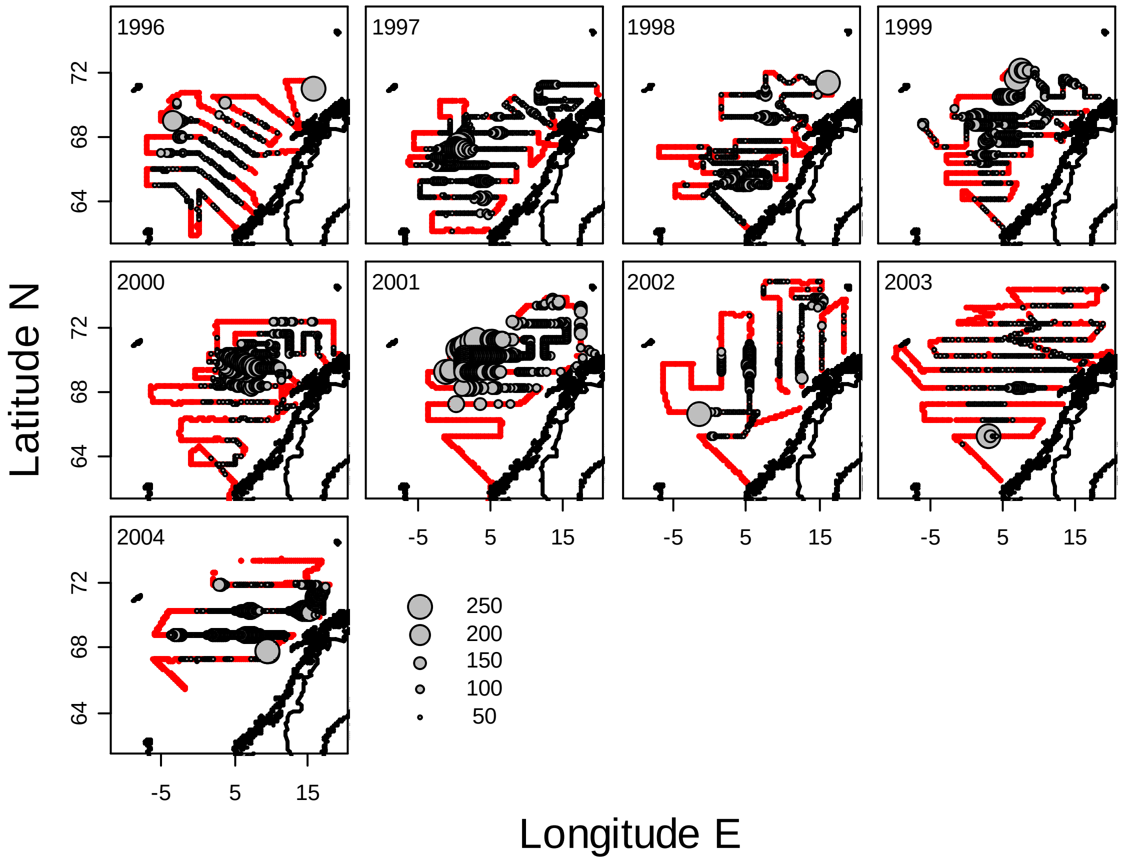

Figure 4. Herring abundance (s_A values, averaged over 5 nautical miles) in the Norwegian Sea, as predicted from a generalised additive model (GAM). Observations of zero herring abundance are shown in red.

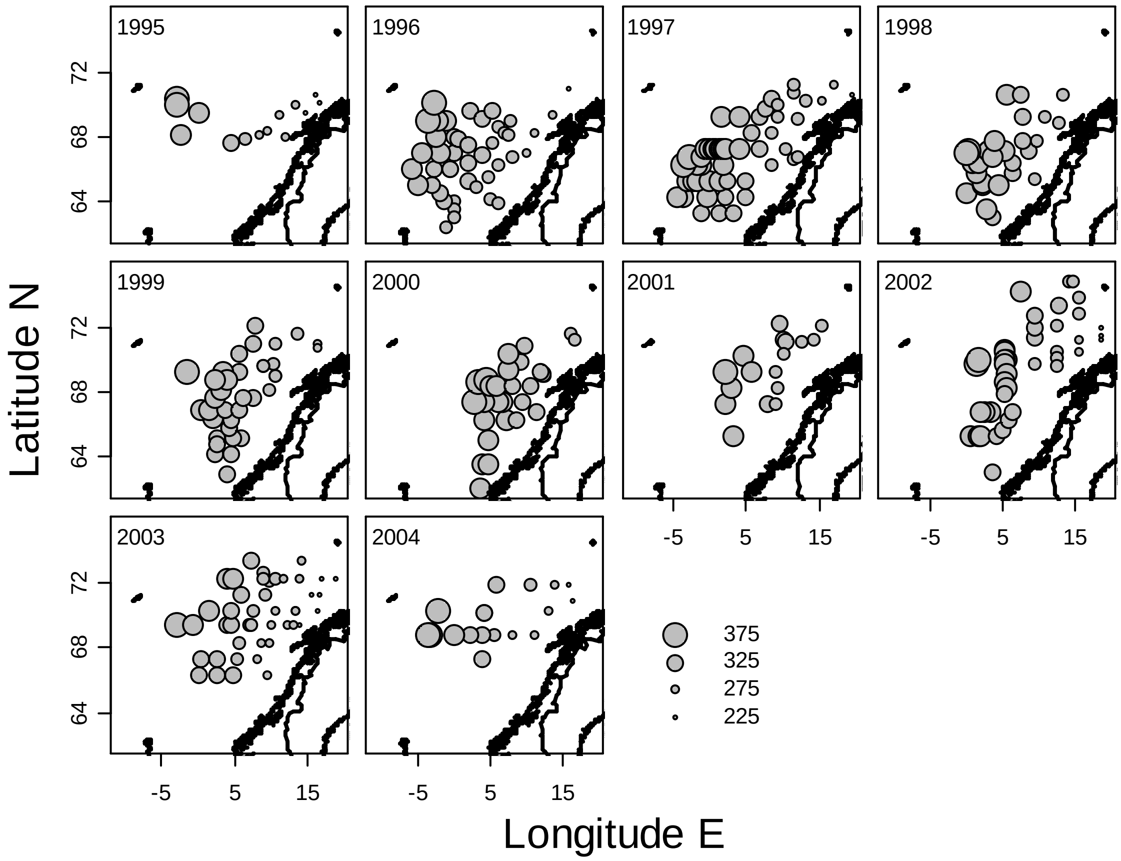

Figure 5. Mean body length of Norwegian spring-spawning herring, as predicted from a generalised additive model (GAM).

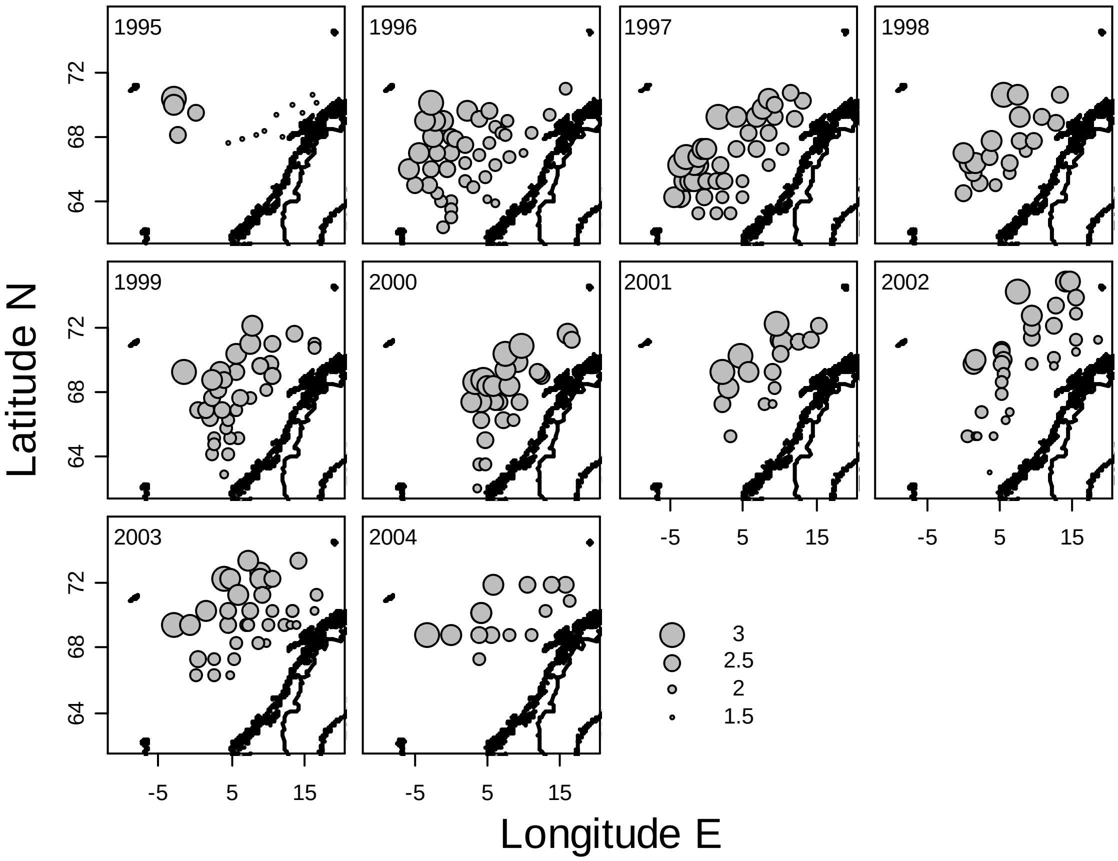

Figure 6. Mean stomach fullness of Norwegian spring-spawning herring, as predicted from a generalised additive model (GAM).