



Environmental stressors may cause unpredicted, notably lagged life-history responses in adults of the planktivorous Atlantic herring

Thassya C. dos Santos Schmidt^{a,b,*,1}, Jennifer A. Devine^{a,1,2}, Aril Slotte^a, Marion Claireaux^{a,b}, Arne Johannessen^b, Katja Enberg^b, Gudmundur J. Óskarsson^c, James Kennedy^{c,d}, Yutaka Kurita^e, Olav Sigurd Kjesbu^{a,1}

^a Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway

^b Department of Biological Science, University of Bergen, PO Box 7803, N-5020 Bergen, Norway

^c Marine and Freshwater Research Institute, Skulagata 4, PO Box 1390, 121 Reykjavik, Iceland

^d Biopol, 545 Skagaströnd, Iceland

^e Tohoku National Fisheries Research Institute, Japan Fisheries Research and Education Agency, 3-27-5 Shinhama, Shiogama, Miyagi 985-0001, Japan

ARTICLE INFO

Keywords:

Energy allocation
Prey
Climate change
Competition
Growth
Body condition
Fecundity

ABSTRACT

Here we challenge traditional views on the direction of change in teleost body condition and reproductive traits in response to abiotic and biotic factors by studying the data-rich, planktivorous Norwegian spring-spawning herring (NSSH), a member of the abundant Atlantic herring (*Clupea harengus*) stock complex. To test potential influential factors, we focused on the last twenty years, i.e. a period with ocean warming, a transient but significant drop in zooplankton biomass, and accelerating interspecific competition resulting from primarily Atlantic mackerel (*Scomber scombrus*) entering these high-latitude waters in large quantities, “the new mackerel era” in the Nordic Seas. Adult NSSH concurrently allocated relatively less to growth in length than weight resulting in higher body condition. Growth likely decreased in warmer waters under stiff prey competition to support reproductive costs. Condition and reproductive responses were not only immediate but were also lagged by three seasons, corresponding to the period when new oocytes are produced. Furthermore, fecundity increased in warmer waters while egg size dropped. Hence, fine-tuned trade-off mechanisms were apparent and varied. We demonstrate that evaluations of reproductive trade-offs based on pooled data are misleading; poor- and good-condition NSSH followed different reproductive trajectories. These findings emphasize difficult-to-predict trends in life-history traits should be tracked longitudinally by the individuals and their aggregate cohort, as they are linked to complex overarching environmental phenomena, like ecosystem carrying capacity and climate fluctuations.

1. Introduction

Life-history characteristics, the evolution of which is driven by competitive interactions and environmental conditions, determine the amount of resources allocated to different physiological activities (Ricklefs and Wikelski, 2002). These features therefore induce trade-offs between body growth, length of migration, reproduction, and mortality patterns (Stearns, 1989, 1992; Wootton, 1992; McBride et al., 2015). Resources are mainly allocated to body growth before sexual maturation, after which, investment is heavily directed towards

reproduction (Ware, 1982; Chapman et al., 2011; Rijnsdorp et al., 2015; Irgens et al., 2019). Under favorable environmental conditions, resources are in surplus, growth is fast, and energy is divided between body growth and reproductive costs (Stearns, 1992). However, when food becomes scarce, energy will not be allocated the same way (Wootton, 1990; Arendt, 1997) and investment tends to be more towards reproduction than body growth, even though this may affect adult survival rate (Stearns, 1992; Ware, 1982). Reproductive activities, including the onset of the reproductive cycle, degree of reproductive investment, and the decision to abort gametogenesis, are influenced by

* Corresponding author at: Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.

E-mail addresses: thassya@hi.no (T.C. dos Santos Schmidt), Jennifer.Devine@niwa.co.nz (J.A. Devine), aril.slotte@hi.no (A. Slotte), marion.claireaux@gmail.com (M. Claireaux), Arne.Johannessen@uib.no (A. Johannessen), Katja.Enberg@uib.no (K. Enberg), gjos@hafogvatn.is (G.J. Óskarsson), james.kennedy@hafogvatn.is (J. Kennedy), kurita@affrc.go.jp (Y. Kurita), olav.kjesbu@hi.no (O.S. Kjesbu).

¹ Thassya C dos Santos Schmidt, Jennifer A. Devine and Olav Sigurd Kjesbu contributed equally to this work.

² Current address: National Institute of Water & Atmospheric Research Ltd (NIWA), 217 Akersten St, Port Nelson, Nelson 7010, New Zealand.

body reserves (Rideout et al., 2005; Kennedy et al., 2011a; Pellerin et al., 2016). The optimum body condition is characterized by the amount of energy available for reproductive investment and the amount saved for post-spawning somatic activity and growth (Rijnsdorp, 1990). An individual must therefore “choose” between maintaining body size and adjusting relatively costly gamete production (Roff, 1982; van Noordwijk and Jong, 1986).

The planktivorous teleost Norwegian spring-spawning herring (*Clupea harengus*) (NSSH) is considered ideal to investigate the possible scope for plasticity in reproductive and somatic allocations under naturally fluctuating or changing high-latitude conditions (Sundby et al., 2016). NSSH has adapted a life-history strategy where adults make extensive migrations between oceanic feeding, overwintering, and coastal spawning areas (Dragesund et al., 1980, 1997). Winter survival and capital breeding depend on feeding success during the relatively short summer season, after which zooplankton (prey) becomes inaccessible by descending to overwintering depths (Holst et al., 2004). Consequently, several life-history traits of this long-lived (for Clupeids) species (expected maximum age > 20 years) exhibit distinct fluctuations related to body energetics (dos Santos Schmidt et al., 2017).

NSSH is one of the largest commercial fish stocks in the world and has been targeted by man for centuries (ICES, 2017) (Fig. 1a). Stock size has fluctuated markedly over time. Several factors, including over-exploitation, cooler seawater temperatures, and a series of poor year classes, caused the stock to collapse in the late 1960s, but strict management resulted in a gradual rebuilding (Dragesund et al., 1997; Toresen and Østvedt, 2000). Over the period of stock collapse and recovery, plasticity was observed in body growth and age at first maturity

(from 5 to 6 years during the collapse to 3–4 years during the recovery period) (Toresen, 1990; Engelhard and Heino, 2004), and stock reproductive potential represented by total egg production (varying by three orders of magnitude) (Ndjaula et al., 2010).

Strong interspecific competition can influence energy allocation patterns in NSSH. In addition to herring, two large planktivorous stocks, blue whiting (*Micromesistius poutassou*) (BW) and Northeast Atlantic mackerel (*Scomber scombrus*) (NEAM), are also present in the Norwegian Sea and adjacent waters (Huse et al., 2012a; ICES, 2017) (Fig. 1a). During the last two decades (1994–2014), the spawning stock biomass (SSB) of BW varied, while SSB of NEAM has, until recently, steadily increased (ICES, 2017) (Fig. 1a). The summer distribution of NEAM expanded north- and westwards, likely due to a combined response to ocean warming and increasing stock size (Astthorsson et al., 2012; Nøttestad et al., 2016; Olafsdottir et al., 2019), which increased the amount of spatial overlap with NSSH in the summer feeding areas. Competition for food between these three planktivorous species is well documented, including both type of prey (Langøy et al., 2012; Bachiller et al., 2016; Óskarsson et al., 2016), consumption rate (Bachiller et al., 2018), and spatial overlap (Huse et al., 2012b; Utne and Huse, 2012). Interspecific competition is presumed to be highest between NSSH and NEAM because they feed upon the same plankton species, mainly the dominant copepod *Calanus finmarchicus* (Bachiller et al., 2016). Total zooplankton biomass in the area has declined as the biomass of these planktivorous species increased (Huse et al., 2012a; ICES, 2015a) (Fig. 1).

Finally, the overall rise in temperature (Fig. 1b) may have affected both physiological processes (e.g. timing and frequency of spawning, Óskarsson and Taggart 2009; Somarakis et al., 2018), prey composition and distribution (Beaugrand et al., 2009; Alvarez-Fernandez et al., 2012), and altered trophic networks (Stenseth et al., 2002; Johannessen et al., 2012). Regarding temperature, an increase will accelerate metabolic demands, but also growth rate, provided food is in surplus and ambient temperature is below the physiological optimum (Brett, 1979; Freitas et al., 2010). In contrast, higher temperatures combined with reduced access to food due to stronger competition should result in especially poor habitat conditions for ectotherms like NSSH.

Therefore, a changing climate and competitive environment, coupled with the effects of increased predation on limited prey resources, also influenced by changing temperature conditions (Toresen and Østvedt, 2000; Huse et al., 2012a; IPCC, 2014), should affect energy allocation patterns. Consequently, we hypothesized that energy allocation patterns in NSSH were changed by these stressors (Fig. 1), i.e. affected body growth, condition, and reproductive investment. These changes had systematic, but unexpected, trade-offs in oocyte (egg) size and fecundity.

2. Materials and methods

2.1. Herring time series data

NSSH biometric statistics collected between 1994 and 2014 were extracted from the Institute of Marine Research (IMR) research survey and commercial sampling data bases (Table S1). Data were from two periods: early overwintering (October – November), which is the time of peak body condition and includes the start of fasting period (Slotte, 1999b), and the prespawning period (February), when fish use the remaining stored energy before releasing the gametes (dos Santos Schmidt et al., 2017). Body energy declines between these periods, especially during the spawning migration, where losses can be up to 50% of the remaining energy (Slotte, 1999b).

2.2. Body growth and condition metrics

NSSH males and females were previously pooled in studies on body growth and condition (Engelhard and Heino, 2004) but were analysed

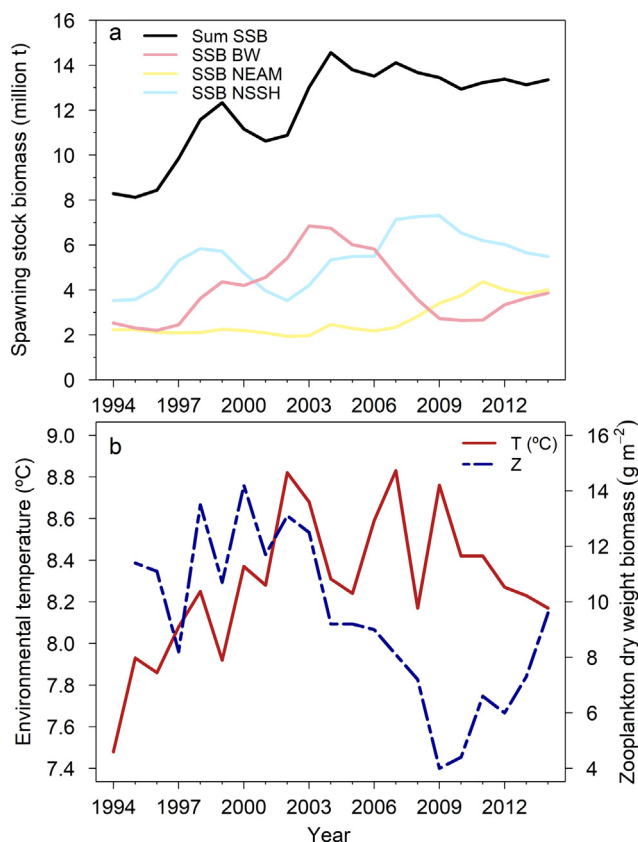


Fig. 1. Trends in pelagic fish stock sizes and environmental conditions in the Norwegian Sea, 1994–2014. (a) Spawning stock biomass of Norwegian spring-spawning herring (NSSH), Northeast Atlantic mackerel (NEAM), blue whiting (BW), and summed spawning stock biomass for all three stocks, and (b) average environmental temperature and total zooplankton biomass.

separately here to examine any differences in gonadal allocation patterns by sex, particularly during the overwintering period (Slotte et al., 2000). Maturity was classified based on eight macroscopic gonadal stages: 1–2, immature; 3–5, maturing and mature; 6, spawning (running); 7, spent; and 8, resting (Mjanger et al., 2006). Fish of all maturity stages, except immature, were considered for the early overwintering period, whereas stages 4 and 5 fish were considered as “prespawning”. For females, stage 4 refers to “the eggs can be seen distinctly and feel like grains; eggs beginning to become transparent” while for stage 5 “most of the eggs are transparent” (Mjanger et al., 2006). Stage 5 was especially in focus in this study because this stage reflects maximum gonad mass prior to any molt or egg release. Total length (“length”; TL; nearest 0.5 cm), whole body weight (“weight”; W; nearest 1 g), age in years (read from scales) (ICES, 2015b), and gonad weight (GW; nearest 1 g) were used to create the following body growth and condition metrics: length- and weight-at-age, cohort growth, weight-at-length, and gonad weight-at-age. Cohort body growth was estimated as the difference between average length- or weight-at-age 7 and 4, for cohorts between 1990 and 2007:

$$\text{Cohort growth in length}_{7y-4y} \text{ (cm)} = \text{Length-at-age } 7_{(t)} - \text{Length-at-age } 4_{(t-3)}$$

$$\text{Cohort growth in weight}_{7y-4y} \text{ (g)} = \text{Weight-at-age } 7_{(t)} - \text{Weight-at-age } 4_{(t-3)}$$

where t is the cohort year; older ages were not included because metrics at these ages overlapped and fewer observations were available (Fig. 2).

2.3. Reproductive investment metrics

Changes in reproductive investment were modelled based on fluctuations in ovary and testes weight (Table S1). Preliminary investigations indicated no trends existed in mean length- and age-at-50% maturity ($p > 0.05$ in all cases) (Fig. S1). Therefore, the size and age of sexually mature fish were restricted to TL ≥ 27 cm and age ≥ 4 years (Engelhard and Heino, 2004; Beverton et al., 2004) (Fig. S1). Any further investigation of plasticity in maturation traits (Engelhard and Heino, 2004; Roff et al., 2006) was considered beyond the scope of this study.

To track temporal changes in gonadal development, determined by the trade-off between fecundity and oocyte size, coverage was expanded by several years and over additional months by including previously published information (Óskarsson et al., 2002; Kurita et al., 2003; Kennedy et al., 2011b; dos Santos Schmidt et al., 2017). Timing of sampling varied in these studies, but in general, covered the onset of new reproductive cycle until the spawning period, i.e. from May to February in the next year (see also Table S2). The 1st May was set as the preliminary start for formation of secondary oocyte growth (cortical alveoli formation followed by true vitellogenesis) (Brown-Peterson et al., 2011; Lowerre-Barbieri et al., 2011), which was later corrected by extrapolation to indicate when cortical alveoli ($> 240 \mu\text{m}$) was present in the samples (see below).

The gonadosomatic index (GSI_S) was used to demonstrate the investment in gonad size during the maturation cycle:

$$GSI_S = 100 \times OW / (W - OW),$$

where OW denotes ovary weight and the denominator is somatic (ovary-free) body weight. Fulton’s condition (K; $K = 100 \times W / TL^3$) was used to demonstrate the interannual variation in relative fecundity according to the fish condition, where $K < 0.7$ indicated fish were in poor condition and $K > 0.7$ were fish in good condition (Óskarsson et al., 2002).

Oocyte size was determined from samples by first preserving a small (“fingernail size”) subsample of ovarian tissue in 3.6% phosphate-buffered formaldehyde for at least two weeks. Diameters of 100 developing

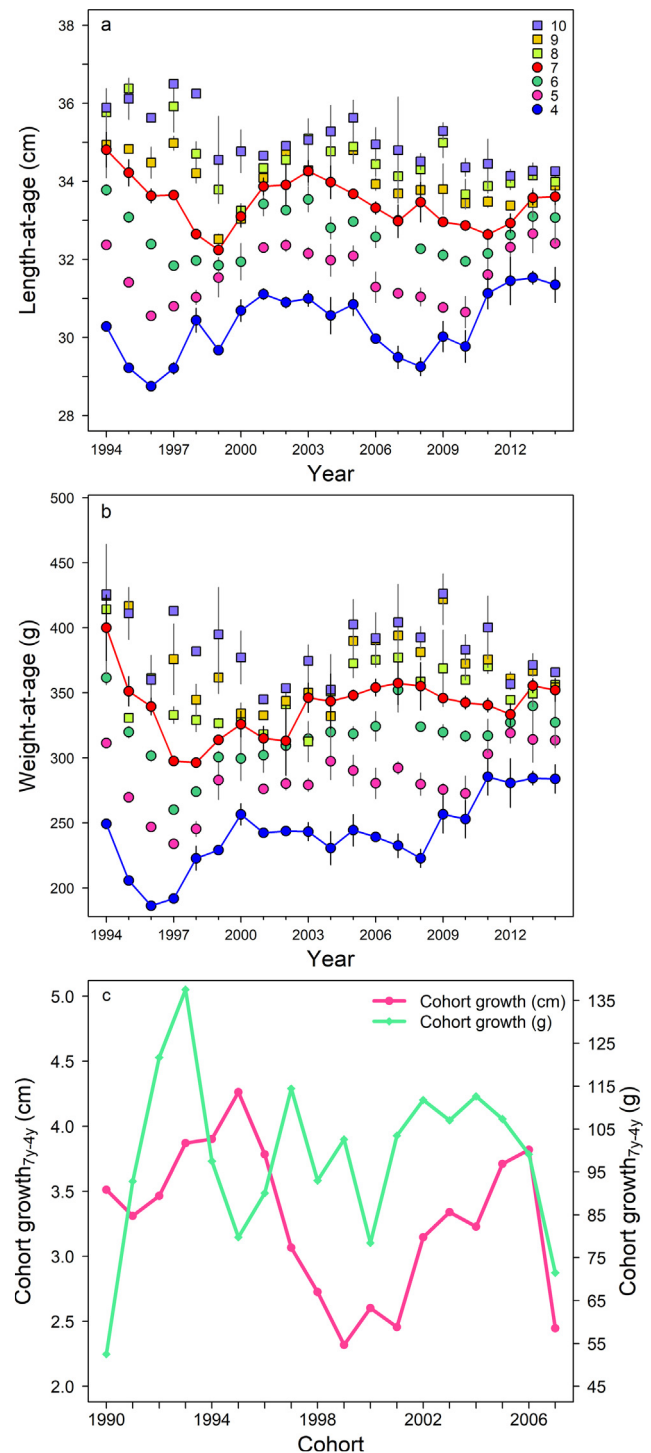


Fig. 2. Trends in body growth of Norwegian spring-spawning herring in the period 1994–2014. (a) Total length-at-age and (b) whole body weight-at-age (mean \pm 95% coefficient interval; CI) during the early overwintering period (October–November) for individuals of both sexes, aged 4–10 years. Ages 4 and 7 were used in cohort growth analyses, connecting here these two data point series by separate lines to emphasize trends. CIs were removed for < 5 individuals. (c) Growth dynamics of single cohorts of Norwegian spring-spawning herring (1990–2007), expressed as the difference in size between age 4 and age 7 years measured for overwintering individuals (males and females combined).

oocytes (starting from cortical alveoli stage until hydration) per female were measured and the mean (OD, in μm) estimated (Thorsen and Kjesbu, 2001). Potential fecundity (F_P) was estimated by $F_P = OW \times 7.474 \times 10^{10} \times OD^{-2.584}$ ($r^2 = 0.96$, $p < 0.001$) (dos

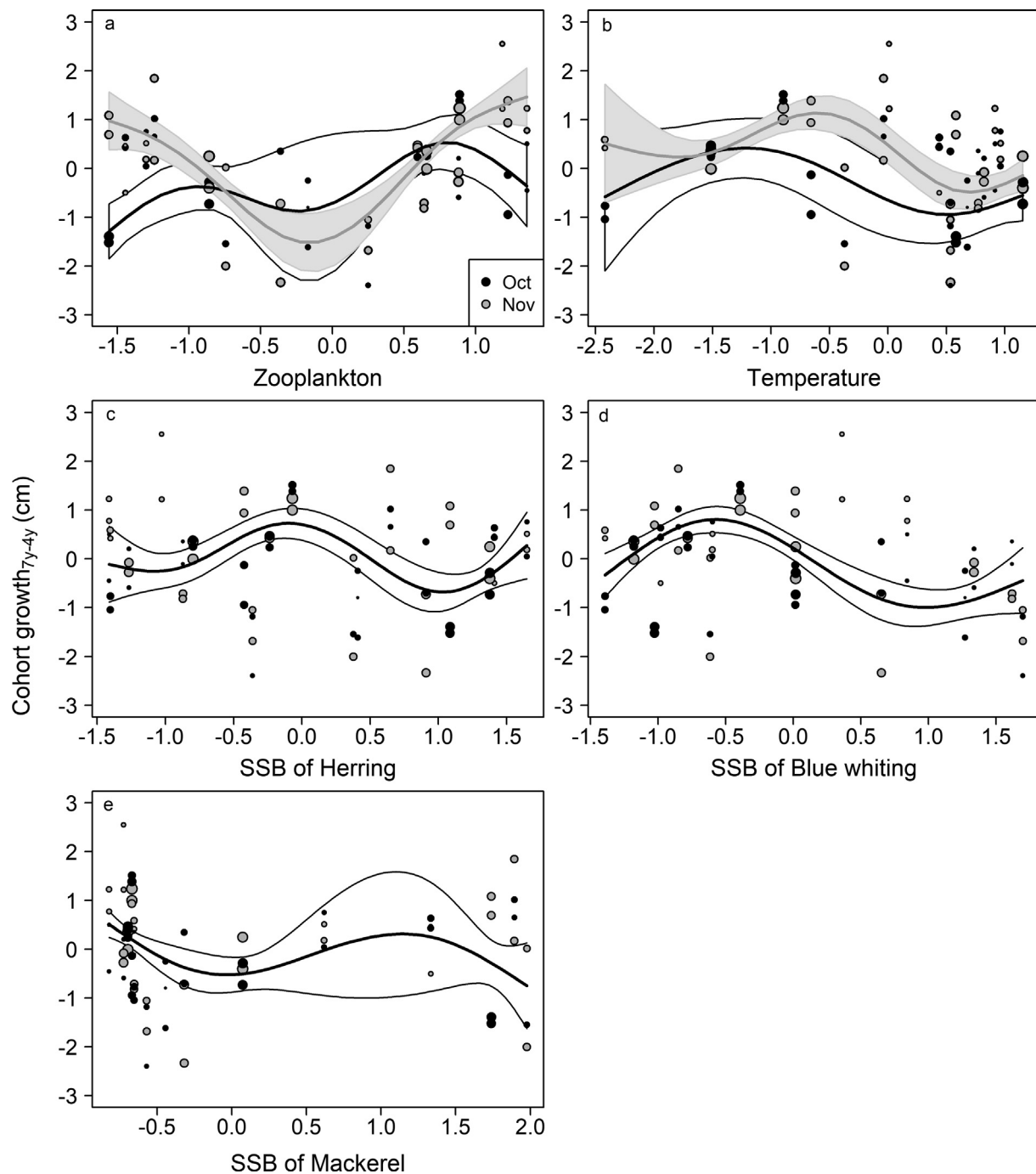


Fig. 3. GAM plots from the Norwegian spring-spawning herring cohort growth in length model. Data are combined for both sexes during overwintering (October–November) in 1994–2011. Variables are organized according to the deviance explained (Table S5). In all panels, thick lines are the smoother and thin lines are 95% CIs. Symbol size is related to the number of observations collected for each cohort.

Santos Schmidt et al., 2017), following oocyte packing density theory (Kurita and Kjesbu, 2009) and using automated methodology (Thorsen and Kjesbu, 2001). Relative length-based fecundity ($RF_{P,TL}$) was given as $RF_{P,TL} = 100 \times F_p / (TL^3)$ (dos Santos Schmidt et al., 2017). Cubic total length was used as the denominator rather than traditional measures of body mass to avoid inflated fecundity values for poor-condition individuals.

Because we were interested in comparing “egg sizes”, represented by oocyte diameter at the fully hydrated stage (OD_{HO}), across seasons, we had to compensate for the changes in oocyte diameter during the final maturation phase through natural swelling (Kurita et al., 2003). A correction factor (1.14) was estimated using data from February 1999,

which contained a mixture of hydrated (u; uncorrected) and late vitellogenic oocytes (Kurita et al., 2003; see their Table 1). This value was then used to convert late vitellogenic oocyte sizes to hydrated sizes (c; corrected) for data from 1997, 1999, and 2006 – 2008. The 2014 samples included only hydrated oocytes (u), therefore no correction was applied. Examinations of macroscopic maturity stages across seasons (February – mid-March) clarified that the examined females were in a spawning capable phase (Brown-Peterson et al., 2011) (Fig. S2). As a supplemental information, oocyte size was also given directly as mean oocyte wet weight (in mg), estimated as $1000 \times OW / F_p$, and thereafter compared with OD.

The physiological effect of environmental temperature (T) on daily

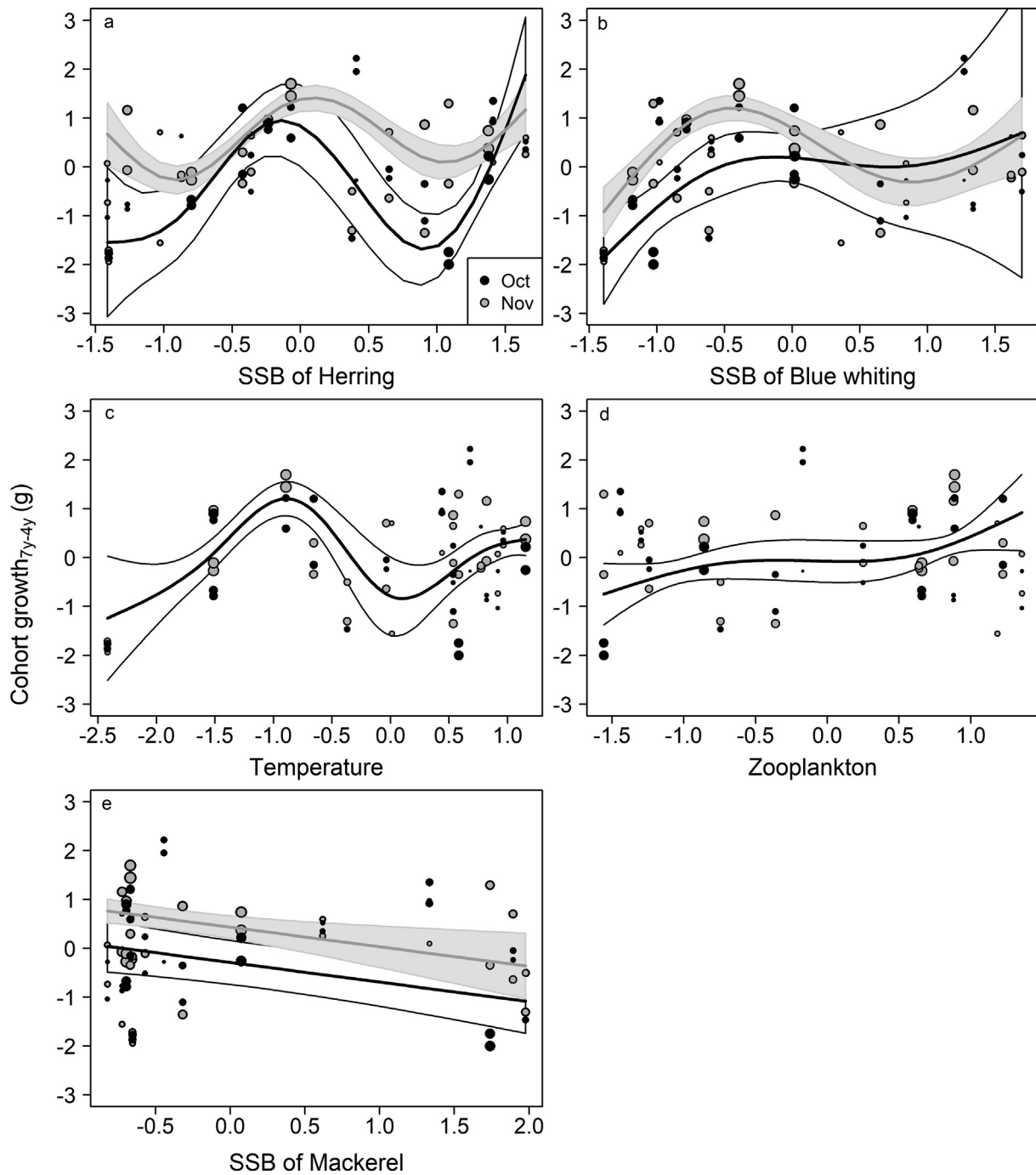


Fig. 4. GAM plots from the Norwegian spring-spawning herring cohort growth in weight model. Data are combined for both sexes during overwintering (October–November) in 1994–2011. Variables are organized according to the deviance explained (Table S5). Thick line is the smoother (a–d) or the regression line (e), and thin lines are 95% CIs. Symbol size is related to the number of observations collected for each cohort.

oocyte growth rate (R_{OD}) was evaluated by the Q_{10} -law (Schmidt-Nielsen, 1983), where data included the studies described above. R_{OD} was calculated by: (1) estimation of the individual increase in OD from the entrance to secondary growth (SG) (referring to the cortical alveoli stage, set at 240 μm for all individuals; Ma et al., 1998) to the observed late vitellogenic stage, i.e. close to the end of SG, but before any change in diameter due to water uptake; (2) estimating of $R_{OD,mean}$ for a given single reproductive cycle (Ganias et al., 2011), i.e. average OD growth divided by the number of days between the starting date, given by extrapolation of the statistical relationship between OD and number of days since 1 April (see Results), and day of sampling; (3) estimation of the Q_{10} -value:

$$Q_{10} = (R_{OD,2,mean}/R_{OD,1,mean})^{10/(T_{2,mean}-T_{1,mean})},$$

where $R_{OD,2,mean}$ and $T_{2,mean}$ are matching daily oocyte growth rate and temperature pairs while $R_{OD,1,mean}$ and $T_{1,mean}$ are the reference values, i.e. $T_{1,mean}$ representing values from the cooler periods (years 1996, 1997, and 1998) (Fig. 1b); and (4) simulation of R_{OD} as a general function of T:

$$\hat{R}_{OD,2} = R_{OD,1,mean} \times (\bar{Q}_{10}(T_2 - T_{1,mean})/10),$$

where \bar{Q}_{10} is the average Q_{10} -value for 1996, 1997, and 1998, and T_2 the highest mean temperature recorded over the studied years.

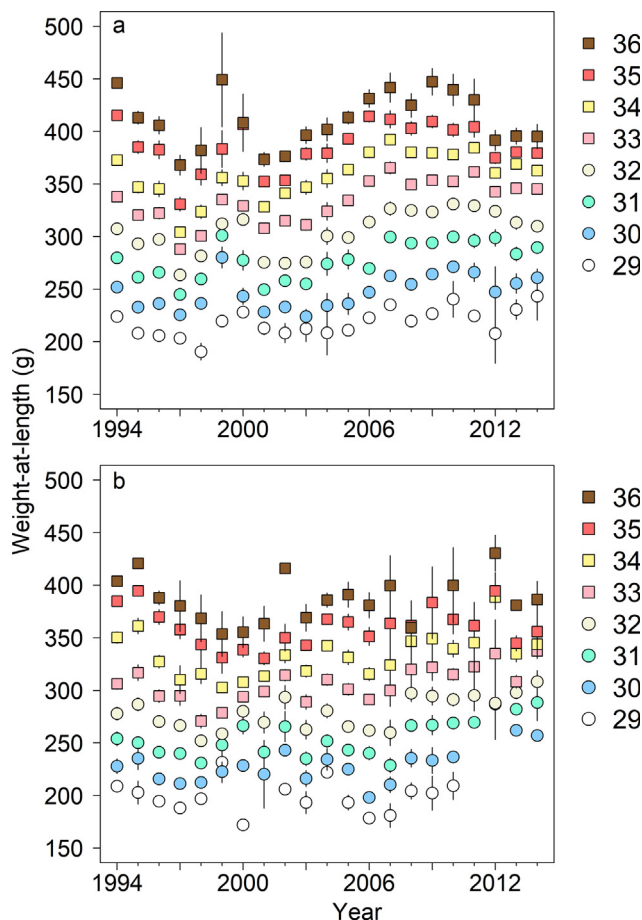


Fig. 5. Trends in body condition of overwintering and prespawning Norwegian spring-spawning herring in the period 1994–2014. (a) Weight-at-length (mean \pm 95% CI) of overwintering individuals ($29 \leq TL \leq 36$ cm) and, correspondingly, (b) prior to spawning. CIs were removed for < 5 individuals. Data for males and females were combined.

2.4. External stressors

The ICES (International Council for the Exploration of the Sea) stock assessments provide data on SSB of NSSH, NEAM, and BW (1994–2014) (ICES, 2017) (Fig. 1a). Estimates of SSB were used as metrics of potential inter- and intraspecific competition, where higher biomasses indicated greater potential for competition for resources. Total biomass was not used as an indicator of competition because only sexually mature fish for all three stocks are generally found in the Norwegian Sea (Skjoldal et al., 2004; Huse et al., 2012a).

Habitat conditions within the Norwegian Sea were inferred from annual temperature data, averaged from the Svinøy hydrographical section ($62^{\circ}22'N$, $4^{\circ}40'E$ – $67^{\circ}43'N$, $10^{\circ}52'W$), 50–200 m depth, 1994–2014 (IMR data) (Fig. 1b). This cross-section of the Norwegian Basin reflects the main feeding areas for the three pelagic stocks (Bachiller et al., 2016) and characterises the Atlantic water inflow (Blindheim, 2004; Mork and Skagseth, 2010). Atlantic water represents the area with highest abundance of zooplankton, mainly *Calanus finmarchicus* and euphausiids (Melle et al., 2004), the main food items of these three fish stocks (Bachiller et al., 2016).

Time series detailing preferred prey were not available, hence total zooplankton biomass was used to provide an index of potential food availability. Zooplankton dry weight (average biomass from May) from the Norwegian Sea (1995–2014) was extracted from ICES (2015a) (Fig. 1b).

2.5. Statistical analyses

Data for cohort growth analyses were standardized to a mean of 0 and standard deviation of 1 because of the wide range of values could influence the model selection. All covariates were estimated as the mean value experienced by a particular cohort as they progressed from age 4 to age 7 years (Fig. S3). Month (October or November) was included to determine whether growth was affected by time of arrival at the overwintering grounds and/or length of fasting (ICES, 2015a; Homrum et al., 2016; ICES, 2016). Because the temporal trends were non-linear, generalized additive models (GAM, R package mgcv; Wood, 2011) were used to determine which factors affected cohort growth ($p < 0.05$). GAMs have the additional advantage of being powerful tools for handling data that are collinear, as these data were, but only up to a certain level of collinearity, if the collinear structure does not change (Dormann et al., 2013), and if concavity is not present (Amodio et al., 2014). Collinearity was high (-0.9 to 0.7) and concavity indices for all terms except month ranged, in the full model, from 0.4 to 1 (Table S3), which meant that selection using multivariate GAMs was problematic. Concavity can complicate statistical interpretation by causing the parameter estimates to become sensitive to e.g. the order of input into the model, the effect of predictors may be enhanced or suppressed depending on the strength and type of correlation (Tomashek et al., 2018). The importance of individual terms was investigated using a double penalty approach, which penalizes the null space in addition to the data range space (Marra and Wood, 2011), a generalized cross-validation (GCV) smoothness selection, and backwards selection of terms after inspecting each model for concavity (Wood, 2006) (Supplementary Information); terms with high concavity (> 0.5) were not used in the same model (Table S3). No significant autocorrelation was apparent (Table S4).

A partial linear regression (PLR) model, with an identity link function and Gaussian distribution, was used to determine the relationship between environmental factors and overwintering body condition, and between overwintering and prior to spawning reproductive investment for the most data rich length classes ($TL = 32, 34, \text{ and } 36$ cm; October – November and February). Data, weight-at-length (classified as body condition) and gonad weight-at-length (i.e., reproductive investment), were standardized to a mean of 0 and standard deviation of 1. The focus was on whether these environmental factors could be shown to influence investment, not to predict future investment given these factors. PLR models were used because of the high multicollinearity between explanatory variables, following the methodology of Legendre and Legendre (1998), where the partitioning effect of each parameter was considered.

The number of individuals was included as weighting factor in each model because sampling was uneven, i.e., data from cohorts that had fewer measurements were given less weight than cohorts that had more data.

For the prespawning period, biotic and abiotic factors were lagged by one year because this relates to the period of gonadal development (May–February, Kurita et al., 2003). When investigating final egg production of NSSH, lags of 0 and 3 years were included for the overwintering period, and of 1 and 4 years for the prespawning period. Fish condition in the period leading up to spawning influences the amount of reproductive material produced (see Discussion).

A power function was used to relate OW with mean OD within years, while the relationship between F_p and OW was described using a linear model. ANCOVA and a *posteriori* Tukey test were used to test for OW-specific differences in F_p and OD among years.

All plots and statistical analyses were performed by using R (version 3.5.2; www.r-project.org).

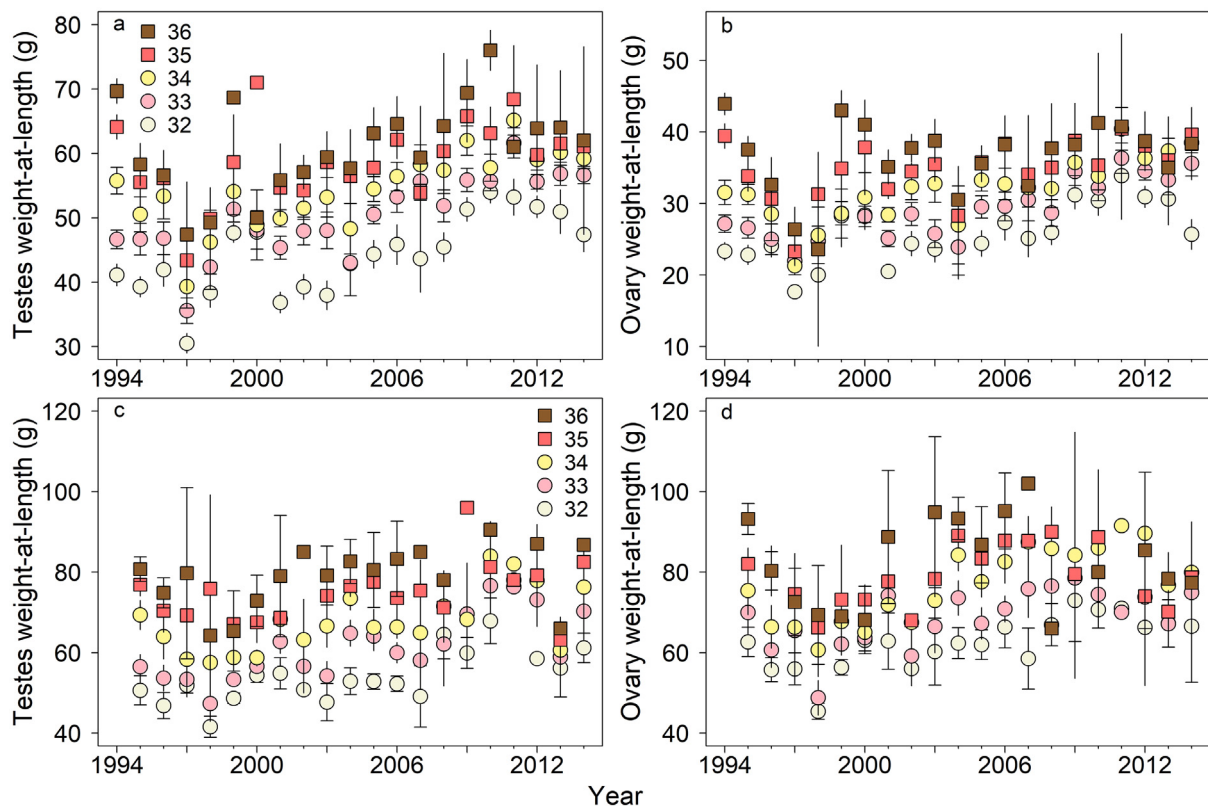


Fig. 6. Interannual changes in overwintering and prespawning testes and ovary weight of Norwegian spring-spawning herring in the period 1994–2014, for fish at 32–36 cm. Gonad weight (mean \pm 95% CI) at overwintering (October–November) for males (a) and females (b), and prior to spawning (February) for males (c) and females (d). CIs were removed for $<$ 5 individuals. Note that the y-axis scales differ between panels.

3. Results

3.1. Cohort growth

Little evidence existed for compensatory growth in length; if the length-at-age of a given cohort was less than average early on, it did not appear to compensate for this later, e.g. individuals aged 4 in 1996 and 2008 were still the shortest in the series at age 7 in 1999 and 2011 (Fig. 2a). This effect was less pronounced in weight-at-age (Fig. 2b), but fish that were smallest in length at age 4 in 1996 and 2008 were among those that increased the most in body weight. After 2010, the difference in body size between younger and older age classes, represented by 4- and 7-year-olds, became less pronounced (Fig. 2a, b). Growth rates in both length and weight typically decreased after age 7, resulting in comparable body sizes for older ages, especially from 2011 onwards (Fig. 2a, b).

Cohort growth in length and weight showed different trends (Fig. 2c). The 18 tracked NSSH cohorts (1990–2007) encountered different living conditions: average temperature varied by almost 1 °C, the relative SSB of NSSH, NEAM, and BW combined increased by ~58%, and zooplankton biomass declined by ~59% (Fig. S3). Significant changes in both length and weight were apparent as fish moved into the overwintering area (Table S5).

Cohort growth in both length and weight was significantly higher in November than October. Because of this significant difference, smooth-factor interactions were investigated for each covariate by month when determining the effect of environmental factors on cohort growth (Figs. 3 and 4, Table S5). Additionally, because of very high concurrency, covariates could not be included in the same model (see Supplementary Information) but had to be tested individually. At low and high zooplankton anomalies, indicated by values either side of zero, fish that were recorded later (November) were generally much larger than those

that recorded earlier (October) (Fig. 3a). At average zooplankton biomass amounts, the opposite was apparent. While fish were, in general, heavier in November, fish did not show much change in weight unless zooplankton biomass was very low or very high (Fig. 4d).

Other clear patterns in cohort growth included the general negative effect of increasing biomass of herring and blue whiting, especially when their biomass was above average (Figs. 3c and d, 4a and b), and the general negative effect of increasing mackerel biomass, but its effect differed on growth in length and in weight, being the negative effect more evident on growth in weight (Fig. 3e and 4e). Although most of the data were collected during positive temperature anomalies, at least cohort growth weight tended to increase as temperature warmed from very low anomalies (Fig. 4c). Because each factor was tested individually with the GAMs and were affected by other parameters, as indicated by the high concurrency estimates, some of the effects, such as the increase in cohort weight with positive anomalies in herring and blue whiting SSB, might be confounded by interactions between the external factors (see also Fig. S4), or alternatively, might also be due fluctuations in the carrying capacity of this Large Marine Ecosystem (Fig. 1).

3.2. Individual body condition

Analyses on NSSH body condition revealed highly dynamic patterns, with notable differences between the length classes, during both overwintering and prior to spawning periods (Fig. 5). Weight-at-length during the overwintering showed an increase from 2000 to 2011, then it became more stable, especially for larger length classes (Fig. 5a). For prior to spawning fish, weight for a given length was significant lower after 1996 but increased after 2008 (Fig. 5b).

A large proportion of the changes in weight-at-length during the overwintering for smaller individuals was explained by the investigated

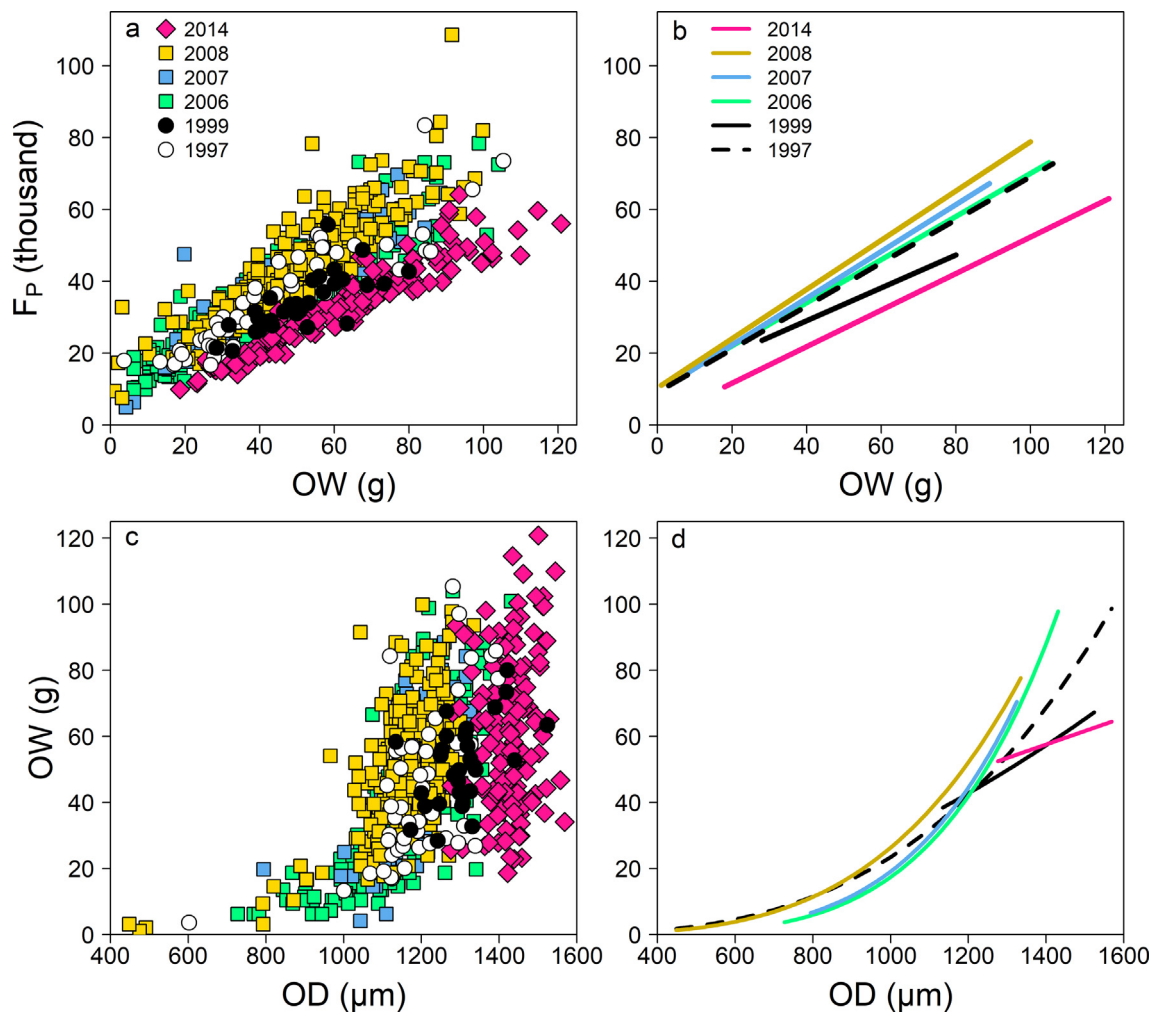


Fig. 7. Links between Norwegian spring-spawning herring fecundity, oocyte size and ovary size. Plots of (a) potential fecundity (F_p) versus ovary weight (OW), (b) the respective linear curve fits, (c) OW versus mean oocyte diameter (OD), and (d) the respective allometric curve fits for years 1997, 1999, 2006–2008, and 2014. Each dot represents an individual between 27 and 40 cm in total length. For annotations in panels (c) and (d), consult panels (a) and (b), respectively.

factors (TL: 32 cm, deviance explained (DE): 42–46%; TL: 34–36 cm, DE: 31–37%) (Table S6), but there was still a large amount left unexplained, which indicated that causal mechanisms may have been missed. Factors lagged of 3 years explained more of the observed changes for the larger length classes. NEAM SSB, month, and zooplankton biomass explained most of the changes, but shared effects were common for all covariates (Table S6). Individuals sampled in October had consistently greater weight for a given length than in November. Preliminary investigation showed that the PLR models explained less than 10% of changes in weight-at-length prior to spawning over the last 21 years (TL: 32 cm, DE: 5.29%; TL: 34 cm, DE: 7.86%; TL: 36 cm, DE: 9.95%; model output not shown), hence no further investigation was performed.

3.3. Gonad size

We found systematic fluctuations in gonad weight of this stock. For both the overwintering and prespawning periods, testes and ovary size declined to their lowest values towards the end of the 1990s, but then increased back to or exceeding previously observed levels (Fig. 6). PLR regression indicated that explanatory factors, including lags, explained more of the patterns in gonad weight during overwintering (DE = 31–55%) than prior to spawning (DE = 13–23%, Table S7). Size-specific gonad weight was significantly different between sexes: testes were heavier during overwintering, but ovaries were heavier

prior to spawning. Most of the change in gonad weight was explained by changes in SSB of each one of the three planktivorous stocks; overall gonads increased in size as stock size increased. Other factors were also significant but explained less of the variability.

3.4. Reproductive trade-offs

Generally, a bigger maturing NSSH ovary as reported in February – mid-March contained more oocytes, i.e. F_p being a linear function of OW (Fig. 7a, b), while the mean size of these oocytes (OD) also affected OW positively but then in an allometric fashion (Fig. 7c, d). Both relationships were significantly different for each year ($p < 0.001$), except for OW vs. OD in 2014 ($p = 0.225$) characterized by high variability in OW, but low variability in OD (Fig. 7c). Two years, 2014 and 2008, stood out; showed similar OWs ($p = 0.612$, $27 \leq TL \leq 40$ cm, see also Fig. 6b, d), but notably different trends in OW vs. F_p and OD (Fig. 7, see also Table S8). This indicated that an ovary approaching spawning could be comprised of either many oocytes of small sizes (2008), or of few but consistently large oocytes (2014). However, in the case of 2006, 2007, and 2008 a minor fraction of the examined material consisted of females that apparently were not prespawning but rather in a preceding developmental phase ($OD < \approx 1000 \mu\text{m}$). An extremely tight relationship existed between OD and mean oocyte wet weight (Fig. S5). For the latter parameter, the presence of ovarian stroma was, however, not accounted for.

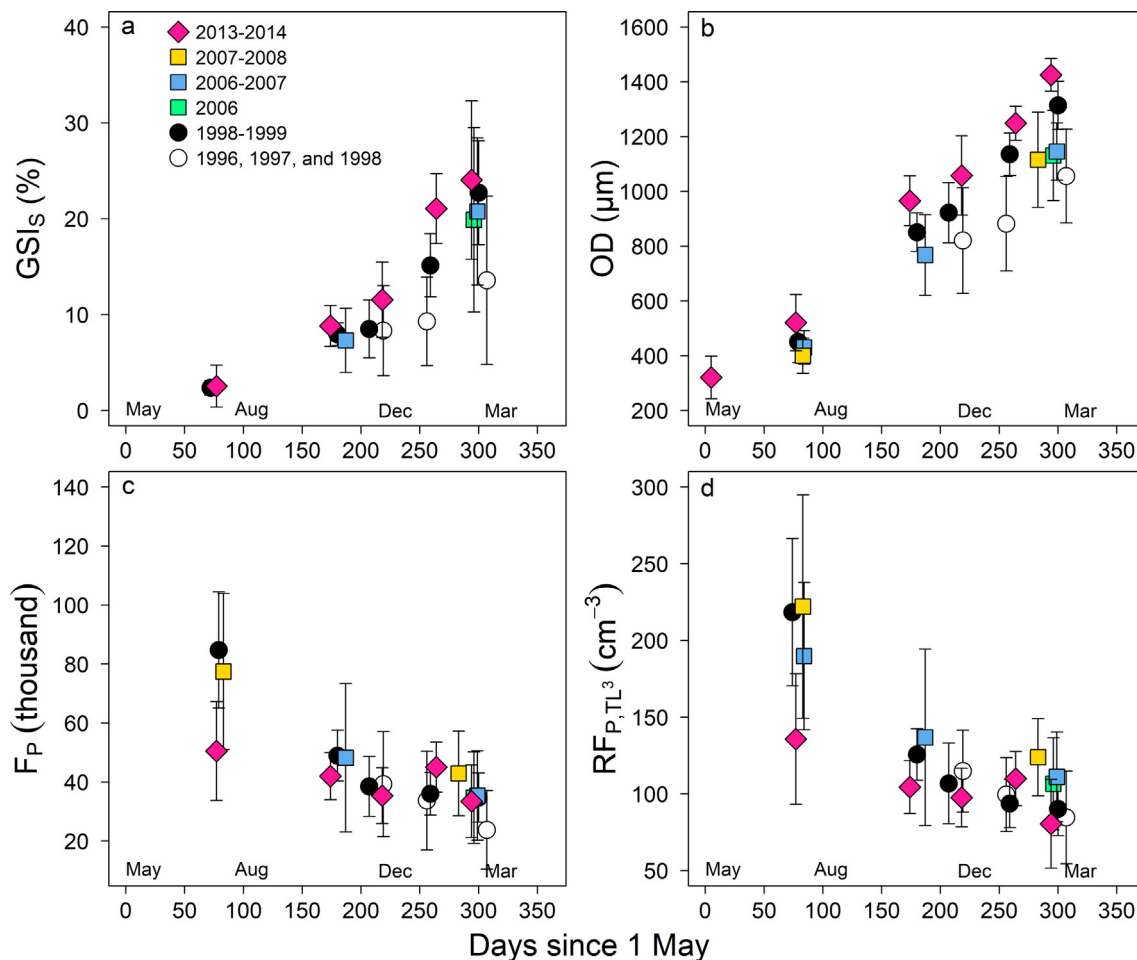


Fig. 8. Development in female Norwegian spring-spawning herring reproductive traits within and between seasons (1996–2014). Mean (\pm SD) of (a) somatic (ovary-free) gonadosomatic index (GSI_s), (b) oocyte diameter (OD), (c) potential fecundity (F_P), and (d) relative length-based potential fecundity (RF_{P,TL³}) throughout the reproductive cycle of female ≥ 32 cm, consulting previously published or own data (Table S2). Day represents the typical sampling day during each field survey. May 1st (Day 0) was assumed to reflect onset of secondary oocyte growth (see further refinements in Fig. 9).

Tracking studies within reproductive cycles evidenced that reproductive traits could change over time in unlike fashions across cycles (Fig. 8). GSI_s grew from about 2–3% to 23–29% (Fig. 8a). Oocytes in the 2013–2014 reproductive cycle were consistently the largest throughout development (Fig. 8b). In contrast, F_P for this cycle was generally the lowest in the time series investigated (Fig. 8c), even after standardizing for body size using relative length-based F_P (RF_{P,TL³}) (Fig. 8d). The patterns seen in 1998–1999 resembled those of 2013–2014 in terms of fecundity and oocyte size development (see also Fig. 7). Although those two cycles differed from the others studied, the estimated degree of down-regulation, i.e. reduction of fecundity through atresia, from July to February was higher in the 1998–1999 than in the 2013–2014 reproductive cycle (59 and 34%, respectively), this difference is most likely due the small sample size in July 1998 (Table S2; $n = 16$). The respective down-regulation estimates for the 2006–2007 and 2007–2008 reproductive cycles were 52 and 44%.

Including additional oocyte development studies expanded the spatio-temporal coverage, which showed that the appearance of cortical alveoli oocytes varied by roughly one month (Fig. 9, Table S9). The subsequent daily growth rate of developing oocytes (R_{OD}) also varied between years ($p < 0.001$; Table S10). The temperature regime had a positive influence on R_{OD} during the reproductive cycle (T_{y-1}) (Fig. S6a) and estimated spawning time was typically earlier in relatively warmer waters (Fig. S6b). Egg size, reported as hydrated oocyte diameter (OD_{HO}), were significantly larger in 1999 and 2014 ($p < 0.001$) than in other years (Fig. S6c). The Q₁₀ value in the 1998–1999

reproductive cycle was significantly higher ($p < 0.001$) than in the other years (Table S10). A positive, but nonsignificant, correlation existed between OD_{HO} and Q₁₀ ($p = 0.187$).

Females prior to spawning were generally in good condition and only $\sim 10\%$ (range 4.8% in 1997 – 25.6% in 1999) had a K below the poor-condition threshold value of 0.7 (Fig. 10a) (Óskarsson et al. 2002). Above this threshold (i.e. fish in good condition), size-specific fecundity, represented by prespawning RF_{P,TL³}, increased with increasing K ($p < 0.001$) (Fig. 10a, Table S11). Condition level significantly influenced RF_{P,TL³} ($p < 0.001$) (Fig. 10a), R_{OD} ($p = 0.010$), but not OD_{HO} ($p = 0.065$). Both R_{OD} and OD_{HO} were significantly negatively related to prespawning RF_{P,TL³}, indicating a clear trade-off between these parameters (Fig. 10b, c and Fig. S11). Lagged temperature had a significant effect on these reproductive parameters; warmer waters resulted in higher prespawning RF_{P,TL³} ($p < 0.001$) and smaller OD_{HO} ($p < 0.001$) in the following year but did not affect R_{OD} ($p = 0.253$) (Fig. 10, Figs. S6 and S7, Tables S10 and S11). Because spawning timing was a function of day of initiation of vitellogenesis and final egg size (OD_{HO}), increased R_{OD} resulted in earlier spawning (Fig. 10d, Fig. S6a). Spawning occurred within distinct segments of the spring (calendar day ~ 35 –85) and was earlier in warmer than in cooler waters ($p < 0.001$) (Fig. 10d).

In summation, NSSH females could apparently modify the egg diameter by nearly 35%, from approximately 1150 to 1550 μm , in parallel with an almost tenfold reduction in prespawning RF_{P,TL³}, from about 235 to 25 cm^{-3} , depending on body condition (K) and the

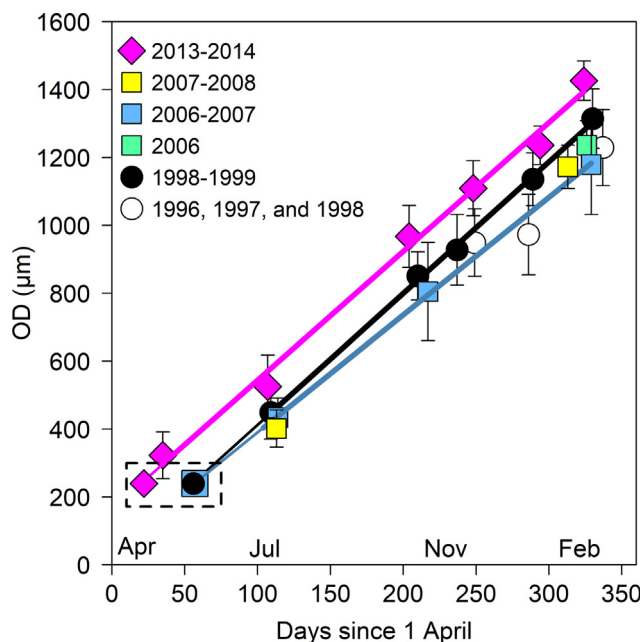


Fig. 9. Growth in oocyte diameter (OD) (mean \pm SD) through the year for distinct temporal periods, where estimated time of appearance of cortical alveoli oocytes (OD = 240 μm ; Ma et al., 1998) is noted (box region). The onset of secondary oocyte growth was defined per model outputs (Table S9); April 1st was set as Day 0. Only fish \geq 32 cm were considered, due the lower number of observations for fish smaller than 32 cm.

environmental conditions met during oogenesis (using T_{y-1} as proxy).

4. Discussion

Norwegian spring-spawning herring (NSSH) showed phenotypic plasticity in body growth, condition, and reproductive investment during a period of changing abiotic and biotic conditions between 1994 and 2014. Theory states that for migrating animals showing indeterminate body growth, increased body condition can be achieved through either greater food (energy) intake or by reducing growth in body length and diverting more of the available energy to body mass (e.g. Stearns, 1992; Ware, 1982). The latter alternative is rarely considered in the teleost literature, at least not directly, but we found that NSSH switch between both alternatives. This has been reported in manipulated, experimental studies for herring (Ma et al., 1998) but has not been reported in wild populations. Cold- (e.g. cod (*Gadus morhua*) and herring) and warm-temperate (e.g. mackerel) teleosts have different strategies to cope with environmental stressors that modify adult body metrics in different ways, and these strategies are often acclimated to the local conditions (Huse et al., 2012b; Olafsdottir et al., 2016; Sundby et al., 2016). Overall, we found that external stressors, represented by SSBs of NSSH, NEAM, and BW, zooplankton biomass, and annual temperature (including lag effects) played significant, but complex roles in cohort growth, body condition (expressed as weight-at-length), and gonad size (measured as gonad weight-at-length).

Plasticity in NSSH appears particularly well developed (e.g. Pörtner and Farrell, 2008; Geffen, 2009). Investigations of physiological principles underlying oocyte development and subsequent reproductive trade-offs strengthened the impression of a high level of reproductive plasticity in NSSH. Condition (K) values under 0.7 are decisively associated with markedly increased levels of atresia in NSSH (Óskarsson et al., 2002). The proportion of fish in poor condition varied both between years (Ndjaula et al., 2010; dos Santos Schmidt et al., 2017; present analysis) and with latitude, where prespawning fish at higher latitudes were more likely to be in poorer condition than fish at lower latitudes (Óskarsson et al., 2016).

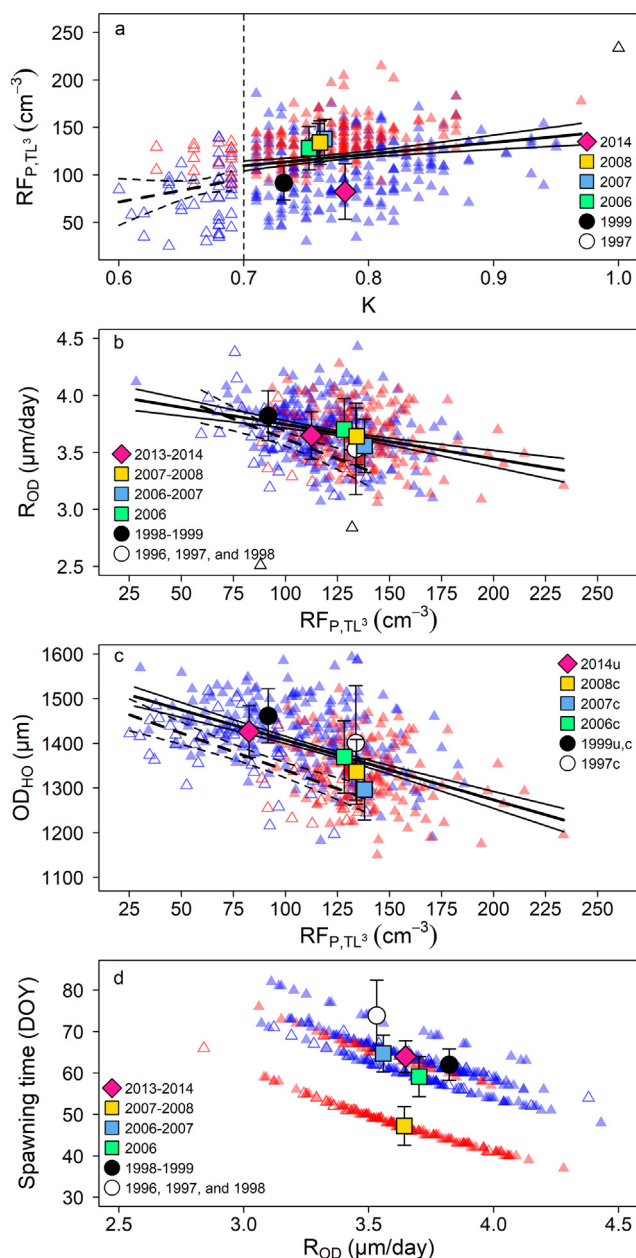


Fig. 10. Reproductive trade-offs and factors influencing spawning time of female Norwegian spring-spawning herring. Mean (\pm standard deviation; SD) of (a) length-specific fecundity (RF_{P,TL^3}) vs. Fulton's condition factor (K), (b) daily oocyte diameter growth rate (R_{OD}) vs. RF_{P,TL^3} , (c) final (hydrated) oocyte diameter (OD_{Ho} , assumed to correspond to "egg size") vs. RF_{P,TL^3} and (d) spawning time vs. R_{OD} over all seasons of the present reproductive study. The data were thereafter split into those representing either individuals in poor condition ($K < 0.7$) (open triangles) or good condition ($K \geq 0.7$) (filled triangles) followed by establishment of linear regression lines (with 95% CI) (a-c). Whether the individual had stayed in relatively warmer (red triangle) or relatively colder water masses (blue triangle) was indicated as an additional factor. In (c) the letters u and c refer to measurements of hydrated oocytes ("uncorrected" diameters) and late vitellogenic oocytes ("corrected" diameters), respectively; the latter diameters were transformed to hydrated diameters by a correction factor (see Material and methods). Note that body size dependency was incorporated via RF_{P,TL^3} . Solid line represents the regression line for females in good condition and dashed line for poor condition. To standardize further, only pre-spawning females \geq 32 cm were considered, because of lower number of females smaller than 32 cm.

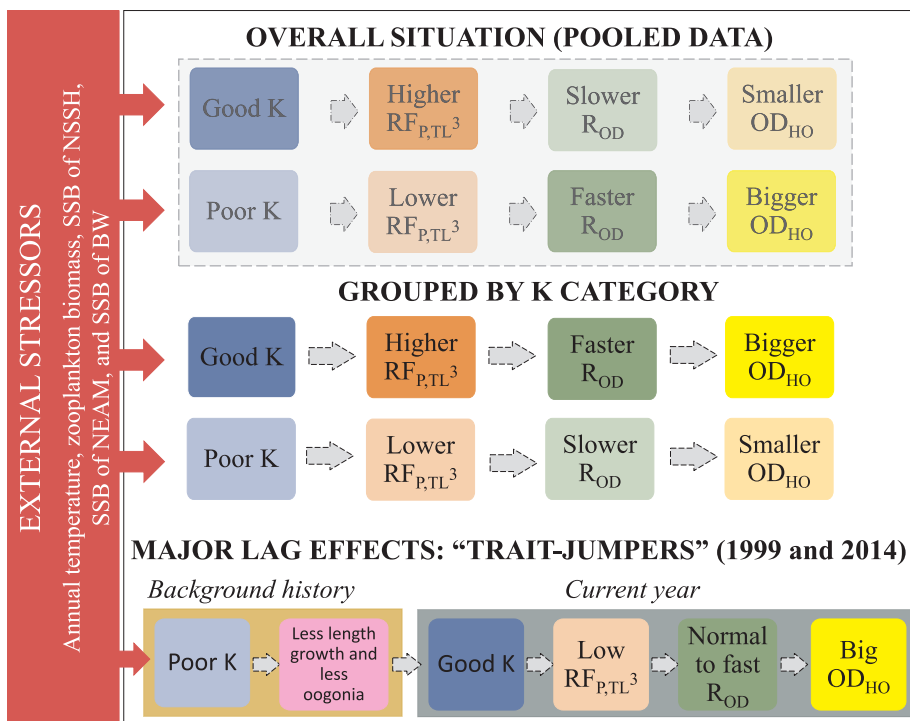


Fig. 11. Flow diagram outlining three perceived scenarios for reproductive trait responses in pre-spawning, female Norwegian spring-spawning herring as a function of body condition (K) under environmental fluctuations, depending on the degree of data resolution. The data were successively sub-divided: pooled (considered an inadequate approach and therefore framed), grouped by K category ($K < 0.7$ or ≥ 0.7) and, ultimately, selecting only those individuals showing signs of a poor background history but in good status currently (1999 and 2014) ("trait-jumpers"), using once more K as reference point (dos Santos Schmidt et al., 2017). Listed external stressors were in the above analyses proven to act importantly as explanatory factors (cf. Table S7). $RF_{P,TL}^3$: length-specific fecundity; R_{OD} : daily oocyte diameter growth rate; OD_{HO} : final (hydrated) oocyte diameter (assumed to reflect egg size).

NSSH reproductive traits supported the notion of well-developed plasticity, but also demonstrated that variation among years may manifest early in the reproductive cycle (Figs. 8 and 9). NSSH exhibited a clear trade-off between fecundity and egg size over the years. The overall plasticity detected in NSSH indicated that females in good condition should produce relatively high numbers of smaller eggs at a slower oocyte growth rate (Fig. 11). The lower growth rate may indicate delayed spawning time, also after taking into account any "holding" of ovulated oocytes in the lumen prior to egg release (Carolsfeld et al., 1996). In contrast, poor-condition females should produce fewer, bigger eggs and spawn earlier (Fig. 11). This is in line with general life-history theory stating that trade-offs between fecundity and egg size are physiological mechanisms working at least across species (e.g. Stearns, 1992). The production of bigger eggs by poor-condition females may be a mechanism to increase offspring survival, often referred as "anticipatory maternal effects" (Marshall et al., 2018). Nonetheless, these interpretations appear only partly relevant for one sub-category of NSSH females, i.e. "trait-jumpers" (Fig. 11), discussed below. The reason for this conflict is that different trajectories are taken by adults, depending on their condition (Fig. 10a–c). Females in good condition produce many, bigger eggs at a faster oocyte growth rate and thus are classified as the "parametric winner" (Fig. 11). Energetically speaking, this makes sense, because of the higher body (fat) reserves in good condition females, which is an example of capital breeder species (Slotte, 1999a; McBride et al., 2015). Hence, any signs of trade-offs between fecundity and egg size become undetectable, along with any anticipatory maternal effect, when the trait response data are grouped by high and poor K rather than uncritically pooled (Fig. 11). Furthermore, this grouped-by-K approach agrees with that the reproductive investment should normally become greater with body size (age) (Barneche et al., 2018), but also agrees with reports on asymptotic body growth in this class of animal (see above), likely related to accelerated reproductive costs.

The models describing gonad weight, although informative regarding factors influencing reproductive investment, failed to pick up major dynamics taking place within the ovary. This was because $RF_{P,TL}^3$ increased but OD_{HO} decreased in warmer waters during the reproductive cycle (T_{y-1}), while the reverse occurs at lower temperatures

(Fig. 10a–c). These opposite influences on ovary size effectively masked any underlying trends in $RF_{P,TL}^3$ and OD_{HO} . The presently noticed influence of temperature raises concerns regarding further anthropogenic climate change (IPCC, 2014; Keenlyside et al., 2008), but T_{y-1} may also be a proxy for a series of related abiotic and biotic processes not specifically investigated in the current study, particularly because temperature is easily measurable whereas the true mechanistic factor may not be so (Rijnsdorp et al., 2009; Sundby et al., 2016). Physiologically speaking, the increase in $RF_{P,TL}^3$ in warmer water because of intensified early oocyte recruitment is logical, especially in NSSH where the oocyte recruitment activity is limited to late spring/early summer due to the clear determinate fecundity style (dos Santos Schmidt et al., 2017). Thus, when the ocean warms, the initial production (proliferation) of oocytes outcompetes the reabsorption of oocytes through atresia, despite the latter process also being accelerated (Kjesbu, 2016). On the other hand, the presence of larger eggs during cooler temperatures is consistent with studies that show more energy is available to oocyte growth due to lower energy costs of e.g. body maintenance (Marshall et al., 2018). Thus, any proper evaluation of trade-offs between fecundity and egg size cannot be detached from environmental signals. The analyses in this study were undertaken within an historical warm period (Kjesbu et al., 2014) and data from contrasting cool periods (e.g. late 1960s to early 1980s, Drinkwater, 2009) were missing or highly limited (dos Santos Schmidt et al., 2017). Because of the lack of contrast, the effect of the included factors may have been underestimated.

We believe that the overall picture regarding reproductive trade-offs in NSSH was distorted by the underlying trends in K (Fig. 11); however, a sub-group exists that does not fit, otherwise known as "trait-jumpers". Trait-jumpers are represented by individuals from the spawning seasons of 1999 and 2014, all in current good condition, but which exhibit the lowest $RF_{P,TL}^3$ (dos Santos Schmidt et al., 2017) along with most likely the largest OD_{HO} (Fig. 11). Mechanistically speaking, the large OD_{HO} for 2014 seems to relate to an early start of the reproductive cycle (Fig. 9) but a normal spawning time (Fig. S6b) resulting in more time to oocyte growth (van Damme et al., 2009), whereas for 1999 this may be explained by the observation that the oocyte growth rate was significantly higher than in the other examined reproductive cycles (Table S10). The fundamental processes underlying these findings are yet

entirely unknown. However, dos Santos Schmidt et al. (2017) documented that poor feeding situations and low K as far back as 3–4 years can cause the production of fewer oogonia (and thereby very small number of oocytes recruited), which negatively affect the future reservoir of these primary oocytes cells. The trait-jumpers clearly fall into the expected patterns outlined in the life-history literature of trade-offs between fecundity and egg size, but also display anticipatory maternal effects (Green, 2008; Marshall et al., 2018). We therefore conclude that NSSH has developed a broad repertoire regarding reproductive trait responses. Under good environmental conditions, NSSH produce many, large eggs, emphasizing parental fitness, while under poor conditions, the strategy is to emphasize offspring fitness by returning stronger later producing fewer, but large eggs (Stearns, 1992).

Similar to previous studies (Bernardo, 1996; Green, 2008; Marshall et al., 2018), we have shown, by using different approaches, that NSSH present a suite of maternal (parental) effects. The results found here should be of interest not only for academia but also for managers because strong links were detected between NSSH life-history trait expressions and population size; the latter is heavily influenced by the implemented harvest rate (ICES, 2017). While the effect of a subset of possible factors describing prey abundance, interspecific competition, density-dependent effects, and climate change were investigated, other factors may be better descriptors of the observed changes. Fishing pressure, at any trophic level, may cause disturbances in top-down processes (Casini et al., 2009) as well as evolutionary changes in life-history (e.g. Enberg et al., 2012; Rijnsdorp et al., 2015; Jørgensen et al., 2007). Moreover, juvenile NSSH inhabit the Barents Sea and thereby experience different living conditions (e.g. Dolgov et al., 2011). Distinct competition pressures that occur in the nursery area may subsequently affect adult life history (Enberg et al., 2012). Therefore, future investigations should also address life-history dynamics of NSSH juveniles. Nevertheless, we have shown that highly sophisticated reproductive trait responses exist in adult NSSH, ranging from immediate to markedly lagged responses.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors are thankful to Kjell Arne Mork for providing quality-assured temperature data, and the technical staff at the Pelagic Research Group for herring field sampling and processing. Svein Sundby, Hein Rune Skjoldal, and Geir Huse, also at the Institute of Marine Research (IMR), are thanked for sharing their profound insights in high-latitude marine ecosystem dynamics. The reviewers are acknowledged for valuable comments and suggestions that improved the manuscript – one identified as Richard S. McBride, NOAA, USA. Thassya C. dos Santos Schmidt was supported by the National Council of Scientific and Technological Development (CNPq), Brazil (grant number 240467/2012–4), Marion Claireaux and Katja Enberg by the Research Council of Norway (grant number 243735), and Olav Sigurd Kjesbu by the Ministry of Trade, Industry and Fisheries/IMR, Norway (grant number 14861).

Contributors

TCSS, AS, and OSK developed the conceptualization of research. TCSS, JAD, AS, GJO, JK, YK, and OSK performed the formal analysis. TCSS, JAD, and OSK wrote the manuscript, with feedback of all the other co-authors AS, MC, AJ, KE, GJO, JK, and YK.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2019.102257>.

References

- Alvarez-Fernandez, S., Lindeboom, H., Meesters, E., 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Mar. Ecol. Prog. Ser.* 462, 21–38. <https://doi.org/10.3354/meps09817>.
- Amodio, S., Aria, M., D'Ambrosia, A., 2014. On concurrency in nonlinear and nonparametric regression models. *Statistica* 74, 85–98. <https://doi.org/10.6092/issn.1973-2201/4599>.
- Arendt, J.D., 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* 72 (2), 149–177.
- Asthorsson, O.S., Valdimarsson, H., Gudmundsdottir, A., Óskarsson, G.J., 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. *ICES J. Mar. Sci.* 69 (7), 1289–1297. <https://doi.org/10.1093/icesjms/fss084>.
- Bachiller, E., Skaret, G., Nøttestad, L., Slotte, A., 2016. Feeding ecology of Northeast Atlantic mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. *PLoS One* 11 (2), e0149238. <https://doi.org/10.1371/journal.pone.0149238>.
- Bachiller, E., Utne, K.R., Jansen, T., Huse, G., 2018. Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLoS One* 13 (1), e0190345. <https://doi.org/10.1371/journal.pone.0190345>.
- Barneche, D.R., Robertson, D.R., White, C.R., Marshall, D.J., 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360, 642–644. <https://doi.org/10.1126/science.1260868>.
- Beaugrand, G., Luczak, C., Edwards, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Change Biol.* 15 (7), 1790–1803. <https://doi.org/10.1111/j.1365-2486.2009.01848.x>.
- Bernardo, J., 1996. Maternal effects in animal ecology. *Am. Zool.* 36, 83–105.
- Beverton, R.J.H., Hylan, A., Østved, O.J., Alvsvaag, J., Iles, T.D., 2004. Growth, maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring. *ICES J. Mar. Sci.* 61 (2), 165–175. <https://doi.org/10.1016/j.icesjms.2004.01.001>.
- Blindheim, J., 2004. Oceanography and climate. In: Skjoldal, H.R. (Ed.), *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp. 65–96.
- Brett, J.R., 1979. Environmental factors and growth. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), *Fish Physiology. Bioenergetics and Growth*, vol. 8. Academic Press, New York, pp. 599–675.
- Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., Lowerre-Barbieri, S.K., 2011. A standardized terminology for describing reproductive development in fishes. *Mar. Coast. Fish.* 3, 52–70. <https://doi.org/10.1080/19425120.2011.555724>.
- Carolsfeld, J., Scott, A.P., Collins, P.M., Sherwood, N.M., 1996. Reproductive steroids during maturation in a primitive teleost, the Pacific herring (*Clupea harengus pallasi*). *Gen. Comp. Endocrinol.* 103, 331–348. <https://doi.org/10.1006/gcen.1996.0129>.
- Casini, M., Hjem, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., Kornilovs, G., 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl. Acad. Sci. USA* 106 (1), 197–202. <https://doi.org/10.1073/pnas.0806649105>.
- Chapman, E.W., Jørgensen, C., Lutcavage, M.E., 2011. Atlantic bluefin tuna (*Thunnus thynnus*): a state-dependent energy allocation model for growth, maturation, and reproductive investment. *Can. J. Fish. Aquat. Sci.* 68 (11), 1934–1951. <https://doi.org/10.1139/f2011-109>.
- Dolgov, A.V., Bogstad, B., Johannesen, E., Skern-Mauritzen, M., 2011. Trophic relationships. In: Jakobsen, T., Ozhigin, V.K. (Eds.), *The Barents Sea: Ecosystem, Resources, Management Half a century of Russian – Norwegian Cooperation*. Tapir Academic Press, Trondheim, pp. 431–494.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36 (1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- dos Santos Schmidt, T.C., Slotte, A., Kennedy, J., Sundby, S., Johannesen, A., Óskarsson, G.J., Kurita, Y., Stenseth, N.C., Kjesbu, O.S., 2017. Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well. *Proc. Natl. Acad. Sci. USA* 114 (10), 2634–2639. <https://doi.org/10.1073/pnas.1700349114>.
- Dragesund, O., Hamre, J., Ulltang, Ø., 1980. Biology and population dynamics of the Norwegian spring-spawning herring. *Rapp. p-v réün – Cons Int. explor. Mer.* 177, 43–71.
- Dragesund, O., Johannesen, A., Ulltang, Ø., 1997. Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia* 82, 97–105.
- Drinkwater, K., 2009. Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s. *Deep Sea Res. Part 2 Top. Stud. Oceanogr.* 56, 2087–2096. <https://doi.org/10.1016/j.dsr2.2008.12.001>.
- Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Bouykal, D.S., Baulier, L., Eliassen, S., Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Mar. Ecol. Prog. Ser.* 33 (1), 1–25. <https://doi.org/10.1111/j.1439-0485.2011.00460.x>.
- Engelhard, G.H., Heino, M., 2004. Maturity changes in Norwegian spring-spawning

- herring before, during, and after a major population collapse. *Fish. Res.* 66 (2–3), 299–310. [https://doi.org/10.1016/S0165-7836\(03\)00195-4](https://doi.org/10.1016/S0165-7836(03)00195-4).
- Freitas, V., Cardoso, J.F.M.F., Lika, K., Peck, M.A., Campos, J., Kooijman, A.L.M., van der Veer, H.W., 2010. Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species. *Phil. Trans. R. Soc.* 365, 3553–3565. <https://doi.org/10.1098/rstb.2010.0049>.
- Ganias, K., Nunes, C., Vavalidis, T., Rakka, M., Stratoudakis, Y., 2011. Estimating oocyte growth rate and its potential relationship to spawning frequency in teleosts with indeterminate fecundity. *Mar. Coast. Fish.* 3, 119–126. <https://doi.org/10.1080/19425120.2011.555729>.
- Geffen, A., 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. *ICES J. Mar. Sci.* 66 (8), 1688–1695. <https://doi.org/10.1093/icesjms/fsp028>.
- Green, B.S., 2008. Maternal effects in fish populations. *Adv. Mar. Biol.* 54, 1–105. [https://doi.org/10.1016/S0065-2881\(08\)00001-1](https://doi.org/10.1016/S0065-2881(08)00001-1).
- Holst, J.C., Rottingen, I., Melle, W., 2004. The herring. In: Skjoldal, H.R. (Ed.), *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp. 203–226.
- Homrum, E.Í., Óskarsson, G.J., Slotte, A., 2016. Spatial, Seasonal and Interannual Variations in Growth and Condition of Norwegian Spring-spawning Herring During 1994–2015. *International Council for the Exploration of the Sea, Copenhagen*.
- Huse, G., Holst, J.C., Utne, K., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., Fenchel, T., Uiblein, F., 2012a. Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea – results of the INFerno project. *Mar. Biol. Res.* 8 (5–6), 415–419. <https://doi.org/10.1080/17451000.2011.653372>.
- Huse, G., Utne, K.R., Fernø, A., 2012b. Vertical distribution of herring and blue whiting in the Norwegian Sea. *Mar. Biol. Res.* 8 (5–6), 488–501. <https://doi.org/10.1080/17451000.2011.639779>.
- ICES, 2015a. Final Report of the Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR). *International Council for the Exploration of the Sea, Copenhagen*.
- ICES, 2015b. Report of the Workshop on age estimation of Norwegian spring spawning herring between, Norway, Denmark, Iceland and the Faroe Islands (WKNSSAGE). *International Council for the Exploration of the Sea, Copenhagen*.
- ICES, 2016. First Interim Report of the Working Group of International Pelagic Surveys (WGIPS). *International Council for the Exploration of the Sea, Copenhagen*.
- ICES, 2017. Report of the Working Group on Widely Distributed Stocks (WGWIDE). *International Council for the Exploration of the Sea, Copenhagen*.
- IPCC, 2014. *The Ocean*. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, United Kingdom, pp. 1655–1731.
- Irgens, C., Folkvord, A., Otterå, H., Kjesbu, O.S., 2019. Otolith growth and zone formation during first maturity and spawning of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* <https://doi.org/10.1139/cjfas-2019-0033>.
- Johannessen, E., Ingvaldsen, R.B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., Knutsen, T., Skern-Mauritzen, M., Stiansen, J.E., 2012. Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES J. Mar. Sci.* 69 (5), 880–889. <https://doi.org/10.1093/icesjms/fss046>.
- Jørgensen, C., Enberg, K., Sunlop, E.S., Arlinghaus, R., Boukal, D.S., 2007. Managing evolving fish stocks. *Science* 318, 1247–1248. <https://doi.org/10.1126/science.1148089>.
- Keenlyside, N.S., Latif, M., Jungclauss, J., Kornbluh, L., Roeckner, E., 2008. Advancing decadal-scale climate prediction in the North Atlantic sector. *Nature* 453, 84–88. <https://doi.org/10.1038/nature06921>.
- Kennedy, J., Skjæraasen, J.E., Nash, R.D.M., Slotte, A., Geffen, A., Kjesbu, O.S., 2011a. Evaluation of the frequency of skipped spawning in Norwegian spring-spawning herring. *J. Sea Res.* 65 (3), 327–332. <https://doi.org/10.1016/j.seares.2011.01.003>.
- Kennedy, J., Nash, R.D.M., Slotte, A., Kjesbu, O.S., 2011b. The role of fecundity regulation and abortive maturation in the reproductive strategy of Norwegian spring-spawning herring (*Clupea harengus*). *Mar. Biol.* 158 (6), 1287–1299. <https://doi.org/10.1007/s00227-011-1648-0>.
- Kjesbu, O.S., 2016. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A., Mokness, E. (Eds.), *Fish Reproductive Biology: Implications for Assessment and Management*. Wiley-Blackwell, Chichester, pp. 321–366.
- Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D.M., Skjæraasen, J.E., 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proc. Natl. Acad. Sci. USA* 111 (9), 3478–3483. <https://doi.org/10.1073/pnas.1316342111>.
- Kurita, Y., Kjesbu, O.S., 2009. Fecundity estimation by oocyte packing density formulae in determinate and indeterminate spawners: Theoretical considerations and applications. *J. Sea Res.* 61 (3), 188–196. <https://doi.org/10.1016/j.seares.2008.10.010>.
- Kurita, Y., Meier, S., Kjesbu, O.S., 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *J. Sea Res.* 49 (3), 203–219. [https://doi.org/10.1016/S1385-1101\(03\)00004-2](https://doi.org/10.1016/S1385-1101(03)00004-2).
- Langøy, H., Nøttestad, L., Skaret, G., Broms, C., Fernø, A., 2012. Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Mar. Biol. Res.* 8 (5–6), 442–460. <https://doi.org/10.1080/17451000.2011.642803>.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science BV, Amsterdam.
- Lowerre-Barbieri, S., Brown-Peterson, N., Murua, H., Tomkiewicz, J., Wyanski, D., Saborido-Rey, F., 2011. Emerging issues and methodological advances in fisheries reproductive biology. *Mar. Coast. Fish.* 3, 32–51. <https://doi.org/10.1080/19425120.2011.555725>.
- Ma, Y., Kjesbu, O.S., Jørgensen, T., 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.* 55 (4), 900–908. <https://doi.org/10.1139/f97-305>.
- Marra, G., Wood, S.N., 2011. Practical variable selection for generalized additive models. *Comput. Stat. Data Anal.* 55 (7), 2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>.
- Marshall, D.J., Pettersen, A.K., Cameron, H., 2018. A global synthesis of offspring size variation, its eco-evolutionary causes and consequences. *Funct. Ecol.* 32, 1436–1446. <https://doi.org/10.1111/1365-2435.13099>.
- McBride, R.S., Somarakis, S., Fitzhugh, G.R., Albert, A., Yarangina, N., Wuenschel, M.J., Alonso-Fernandez, A., Basilone, G., 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish. Fish.* 16 (1), 23–57. <https://doi.org/10.1111/faf.12043>.
- Melle, W., Ellertsen, B., Skjoldal, R., 2004. *Zooplankton: The link to higher trophic levels*. In: Skjoldal, H.R. (Ed.), *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp. 137–202.
- Mjanger, H., Hestenes, K., Olsen, A., Svendsen, B.V., Wenneke, T.d.L., 2006. *Manual for sampling of Fish and Crustaceans*. Institute of Marine Research, Bergen.
- Mork, K.A., Skagseth, Ø., 2010. A quantitative description of the Norwegian Atlantic current by combining altimetry and hydrography. *Ocean. Sci.* 6 (4), 901–911. <https://doi.org/10.5194/os-6-901-2010>.
- Ndjaula, H.O.N., Nash, R.D.M., Slotte, A., Johannessen, A., Kjesbu, O.S., 2010. Long-term changes in the total egg production of Norwegian spring-spawning herring *Clupea harengus* (L.) – Implications of variations in population structure and condition factor. *Fish. Res.* 104 (1–3), 19–26. <https://doi.org/10.1016/j.fishres.2010.04.002>.
- Nøttestad, L., Utne, K.R., Óskarsson, G.J., Jónsson, S.P., Jacobsen, J.A., Tangen, Ø., Anthonypillai, V., Aanes, S., Vølstad, J.H., Bernasconi, M., Debes, H., Smith, L., Sveinbjörnsson, S., Holst, J.C., Janse, T., Slotte, A., 2016. Quantifying changes in abundance, biomass and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2014. *ICES J. Mar. Sci.* 73 (2), 359–373. <https://doi.org/10.1093/icesjms/fsv218>.
- Olafsdóttir, A.H., Slotte, A., Jacobsen, J.A., Óskarsson, G.J., Utne, K.R., Nøttestad, L., 2016. Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: effects of mackerel stock size and herring (*Clupea harengus*) stock size. *ICES J. Mar. Sci.* 73 (4), 1255–1265. <https://doi.org/10.1093/icesjms/fsv142>.
- Olafsdóttir, A.H., Utne, K.R., Jacobsen, J.A., Jansen, T., Óskarsson, G.J., Nøttestad, L., Elvarsson, B.P., Broms, C., Slotte, A., 2019. Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. *Deep Sea Res. Part II* 159, 152–168. <https://doi.org/10.1016/j.dsr2.2018.05.023>.
- Óskarsson, G.J., Taggart, C.T., 2009. Spawning time variation in Icelandic summer-spawning herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.* 66 (10), 1666–1681. <https://doi.org/10.1139/F09-095>.
- Óskarsson, G.J., Kjesbu, O.S., Slotte, A., 2002. Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *J. Sea Res.* 48 (1), 59–79. [https://doi.org/10.1016/S1385-1101\(02\)00135-1](https://doi.org/10.1016/S1385-1101(02)00135-1).
- Óskarsson, G.J., Gudmundsdóttir, A., Sveinbjörnsson, S., Sigurðsson, Þ., 2016. Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. *Mar. Biol.* 12 (1), 16–29. <https://doi.org/10.1080/17451000.2015.1073327>.
- Pellerin, S., Paquette, R., Pelletier, F., Garant, D., Bélisle, M., 2016. The trade-off between clutch size and egg mass in tree swallows *Tachycineta bicolor* is modulated by female body mass. *J. Avian Biol.* 47, 500–507. <https://doi.org/10.1111/jav.00725>.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692. <https://doi.org/10.1126/science.1163156>.
- Ricklefs, R.E., Wikelski, M., 2002. The physiology/life-history nexus. *Trends Ecol. Evol.* 14 (10), 462–468.
- Rideout, R.M., Rose, G.A., Burton, M.P.M., 2005. Skipped spawning in female iteroparous fishes. *Fish. Fish.* 6 (1), 50–72. <https://doi.org/10.1111/j.1467-2679.2005.00174.x>.
- Rijnsdorp, A.D., 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. *Neth. J. Sea Res.* 25 (1–2), 279–289. [https://doi.org/10.1016/0077-7579\(90\)90027-E](https://doi.org/10.1016/0077-7579(90)90027-E).
- Rijnsdorp, A.D., van Damme, C.J.G., Witthames, P.R., 2015. Ecology of reproduction. In: Gibson, R.N., Nash, R.D.M., Geffen, A., van der Veer, H.W. (Eds.), *Flatfishes: Biology and Exploitation*. John Wiley & Sons, United Kingdom, pp. 101–131.
- Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., Pinnegar, J.K., 2009. Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* 66 (7), 1570–1583. <https://doi.org/10.1093/icesjms/fsp056>.
- Roff, D.A., 1982. Reproductive strategies in flatfish: A first synthesis. *Can. J. Fish. Aquat. Sci.* 39, 1686–1698. <https://doi.org/10.1139/f82-225>.
- Roff, D.A., Heibo, E., Vøllestad, L.A., 2006. The importance of growth and mortality costs in the evolution of the optimal life history. *J. Evol. Biol.* 19, 1920–1930. <https://doi.org/10.1111/j.1420-9101.2006.01155.x>.
- Schmidt-Nielsen, K., 1983. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, Cambridge.
- Skjoldal, H.R., Sæther, B.E., Fernø, A., Misund, O.A., Rottingen, I., 2004. *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim.
- Slotte, A., 1999a. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *J. Fish. Biol.* 54, 338–355. <https://doi.org/10.1111/j.1095-8649.1999.tb00834.x>.
- Slotte, A., 1999b. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia* 84 (2), 111–127. <https://doi.org/10.1080/00364827.1999.10420439>.
- Slotte, A., Johannessen, A., Kjesbu, O.S., 2000. Effects of fish size on spawning time in

- Norwegian spring-spawning herring. *J. Fish. Biol.* 56 (2), 295–310. <https://doi.org/10.1111/j.1095-8649.2000.tb02107.x>.
- Somarakis, S., Tsovroula, S., Giannoulaki, M., Schismenou, E., Nikolioudakis, N., 2018. Spawning stock, egg production and larval survival in relation to small pelagic fish recruitment. *Mar. Ecol. Prog. Ser.* 617–618, 113–136. <https://doi.org/10.3354/meps12642>.
- Stearns, S.C., 1989. Trade-offs in life history evolution. *Funct. Ecol.* 3, 259–268. <https://doi.org/10.2307/2389364>.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stenseth, N.C., Myrsetrud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M., 2002. Ecological effects of climate fluctuations. *Science* 297, 1292–1296. <https://doi.org/10.1126/science.1071281>.
- Sundby, S., Drinkwater, K.F., Kjesbu, O.S., 2016. The North Atlantic spring-bloom system – where the changing climate meets the winter dark. *Front. Mar. Sci.* 3 <https://doi.org/10.3389/fmars.2016.00028>. Article 28.
- Thorsen, A., Kjesbu, O.S., 2001. A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. *J. Sea Res.* 46 (3–4), 295–308. [https://doi.org/10.1016/S1385-1101\(01\)00090-9](https://doi.org/10.1016/S1385-1101(01)00090-9).
- Tomaschek, F., Hendrix, P., Baayen, R.H., 2018. Strategies for addressing collinearity in multivariate linguistic data. *J. Phon.* 71, 249–267. <https://doi.org/10.1016/j.wocn.2018.09.004>.
- Toresen, R., 1990. Long-term changes in growth of Norwegian spring spawning herring. *J. Cons. Int. Explor. Mer.* 47, 48–56. <https://doi.org/10.1093/icesjms/47.1.48>.
- Toresen, R., Østvedt, O.J., 2000. Variation in abundance of Norwegian spring spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and influence of climatic fluctuations. *Fish. Fish.* 1, 231–256. <https://doi.org/10.1111/j.1467-2979.2000.00022.x>.
- Utne, K.R., Huse, G., 2012. Estimating the horizontal and temporal overlap of pelagic fish distribution in the Norwegian Sea using individual-based modelling. *Mar. Biol. Res.* 8 (5–6), 548–567. <https://doi.org/10.1080/17451000.2011.639781>.
- van Damme, C.J.G., Dickey-Collas, M., Rijnsdorp, A.D., Kjesbu, O.S., 2009. Fecundity, atresia, and spawning strategies of Atlantic herring (*Clupea harengus*). *Can. J. Fish. Aquat. Sci.* 66, 2130–2141. <https://doi.org/10.1139/F09-153>.
- van Noordwijk, A.J., Jong, G., 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *Amer. Nat.* 128, 137–142.
- Ware, D.M., 1982. Power and evolutionary fitness of teleosts. *Can. J. Fish. Aquat. Sci.* 39, 3–13. <https://doi.org/10.1139/f82-002>.
- Wood, S.N., 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC, Boca Raton.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Series B Stat. Methodol.* 73 (1), 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.
- Wootton, R.J., 1990. *Ecology of Teleost Fishes*. Chapman and Hall, London.
- Wootton, R.J., 1992. Constraints in the evolutionary of fish life histories. *Neth. J. Zool.* 42 (2–3), 291–303. <https://doi.org/10.1163/156854291X00342>.