

Trade-offs between growth and reproduction in wild Atlantic cod

Arild Folkvord, Christian Jørgensen, Knut Korsbrekke, Richard D.M. Nash, Trygve Nilssen, and Jon Egil Skjæraasen

Abstract: Animals partition and trade off their resources between competing needs such as growth, maintenance, and reproduction. Over a lifetime, allocation strategies should result in distinct trajectories for growth, survival, and reproduction, but such longitudinal individual data are difficult to reconstruct for wild animals and especially marine fish. We were able to reconstruct two of these trajectories in wild-caught Northeast Arctic cod (*Gadus morhua*) females: size-at-age was back-calculated from otolith growth increments, and recent spawning history was reconstructed from postovulatory follicles and present oocyte development. Our findings indicate distinct trade-offs between length growth and reproduction. Fish that sexually matured early had attained a larger size at age 3 than immatures, but onset of reproduction caused slower growth compared with immatures. We found that 6- and 7-year-old females skipping spawning grew significantly more in the year of missed spawning than females spawning for the second consecutive year. The latter tentatively supports the hypothesis that skipped spawning may occur as an adaptive life-history strategy, given the potential future fecundity gain with increased size.

Résumé : Les animaux répartissent leurs ressources entre différents besoins concurrents comme la croissance, le maintien et la reproduction. Sur une vie, différentes stratégies d'affectation devraient se traduire par différentes trajectoires de croissance, de survie et de reproduction. Il est toutefois difficile de reconstituer ce genre de données longitudinales individuelles pour des animaux sauvages, particulièrement pour des poissons de mer. Nous avons pu reconstituer deux de ces trajectoires pour des morues (*Gadus morhua*) femelles du nord-est de l'Arctique; la taille selon l'âge a été recalculée à partir d'incrémentes de croissance d'otolithes et l'historique de frai récent a été reconstitué à partir de follicules postovulatoires et du développement des oocytes présents. Nos constatations indiquent différentes répartitions de ressources entre la croissance de la longueur et la reproduction. Les poissons qui atteignent la maturité sexuelle plus tôt sont de taille plus grande à 3 ans que les poissons immatures, mais le début de la reproduction ralentit leur croissance par rapport à celle des individus immatures. Nous avons constaté que les femelles de 6 et 7 ans qui ne frayent pas une année croissent significativement plus durant cette année-là que les femelles qui frayent pour une deuxième année consécutive. Ces observations appuieraient l'hypothèse voulant que le fait de sauter une année de frai puisse constituer une stratégie d'adaptation étant donné la plus grande fécondité future que pourrait permettre une plus grande taille. [Traduit par la Rédaction]

Introduction

Throughout life all organisms face allocation decisions whereby limited resources need to be diverted between several competing needs, such as growth, maintenance, and reproduction (Fisher 1930; Roff 1983, 1992). Increased investment into one of these components necessarily comes at the expense of the others (Arendt 1997; Enberg et al. 2012), e.g., increased investment into body growth will negatively affect the resources invested in offspring and vice versa. Fish generally follow indeterminate growth strategies where resources are prioritized for growth until maturity, after which a considerable and increasing proportion of resources are channelled towards reproduction, thus slowing down growth from maturity onwards (Heino and Kaitala 1999; Kozłowski 1996). This pattern commonly fits well with size-at-age plots from data aggregated at the population level, but such patterns could arise from individual growth trajectories in many different ways. At the population level, trade-offs may also be masked because some individuals manage to reproduce intensely and grow rapidly

(Reznick et al. 2000), likely because they have a higher capability or better strategy for the acquisition of resources (Enberg et al. 2012). Conclusively establishing a negative relationship between reproduction and growth, i.e., demonstrating the trade-off, thus requires knowledge of individual growth trajectories prior to and after maturation, as well as a history of reproductive investments. The optimal allocation pattern may further depend on external factors such as mortality, and in guppies (Poeciliidae) it has been shown that populations living at locations with many predators mature earlier and smaller and give birth to smaller young than guppies living at low-predation sites (Reznick 1982). Patterns of allocation and life histories may also differ markedly between populations because of variation in other ecological factors (Ricklefs and Wikelski 2002; Zera and Harshman 2001).

At the individual level, animals become sexually mature at different ages and sizes, but generally the larger fish in a cohort mature first (Heino et al. 2002a). Differences in size-at-age may arise early in life, whether the causes are environmental or reflect

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different genetically coded growth strategies. Laboratory experiments have shown that early size differences may persist over several years (Koedijk et al. 2010), but compensatory growth may also eliminate these differences (Auer 2010). Such catch-up growth has been documented on a regular basis following reproduction in fish (Pedersen and Jobling 1989) and may have negative consequences for traits other than size (Auer et al. 2010; Metcalfe and Monaghan 2001). It is thus not clear from what age size differences manifest themselves and delayed consequences may be diverse and variable. Using our reconstructed trajectories for growth and reproduction, we are able to compare contrasting groups and retrospectively assess at which ages those differences first emerged.

Although it is generally assumed that iteroparous fish with an annual reproductive cycle spawn every year from sexual maturation onwards, it has become clear that resting, or skipped spawning, may be common both within populations and across species (Jørgensen et al. 2006; Rideout et al. 2005; Rideout and Tomkiewicz 2011). Mechanistically, fish may skip spawning by refraining from investing energy in gonad maturation altogether, invest and develop gonads but reabsorb all nutrients prior to the time spawning should have occurred (mass atresia), or spawn partially and reabsorb remaining nutrients from the gonads (partial atresia) (Rideout et al. 2005). Skipped spawning has been hypothesized to occur as (i) a function of limited energy reserves and (or) (ii) an adaptive strategy whereby younger females increase their lifetime production by investing in growth, which allows for greater fecundity in subsequent years (Jørgensen et al. 2006; Rideout et al. 2005). It should be noted that these explanations are by no means mutually exclusive, as both factors may jointly influence skipped spawning both at the individual and the population level. Recently, skipped spawning was demonstrated to be a frequent phenomenon in Northeast Arctic (NEA) cod (*Gadus morhua*; Skjæraasen et al. 2009, 2012; Yaragina 2010). Skipping individuals generally had smaller livers than spawning females (Skjæraasen et al. 2012), suggesting an energy-linked mechanism.

Establishing spawning history in iteroparous teleosts is in itself challenging given that fish mature at different sizes, which in combination with the seasonality of gonad size and appearance (Schwalme and Chouinard 1999) makes it difficult to, e.g., separate sexually immature fish from those mature fish that are skipping spawning. For cod, postovulatory follicles (POFs) are unequivocal markers of maturation and spawning and persist in the female gonads more than a year after the reproductive act (Witthames et al. 2010). Utilizing this marker in combination with information on present developmental status allowed us to reconstruct individual annual spawning history for female cod and to subdivide females into four categories in the present study: immatures, first-time spawners, repeat spawners, and skippers.

Calcified structures have long been used to estimate age and previous growth history of fish (e.g., Lea 1910; Rollefson 1933). The process of back-calculating size depends on validated annually formed opaque and translucent zones in the selected structure (typically scales or otoliths; hereafter we refer to otoliths) and an estimable relationship between otolith size and fish size. This form of ageing and back-calculation is a common practice in most fisheries laboratories (Francis and Campana 2004). Alternating pairs of translucent and opaque zones constituting annual otolith increments reflect annual variations in environmental and intrinsic conditions experienced by the fish. For Atlantic cod, validation experiments with multimarked, individually tagged cod have documented the utility of back-calculation of previous size and growth (Li et al. 2008). In NEA cod, clearly distinguishable translucent zones are formed during the winter months (Hoie et al. 2009), and we used the occurrence and position of these annual zones as the basis for our size-at-age and growth estimations, since their time of formation also coincided with the timing of the annual research surveys.

Table 1. Number of individuals at age from four reproductive categories used in the present study.

| Age at catch | Immatures | Skippers | First-time spawners | Repeat spawners | Total |
|--------------|-----------|-----------|---------------------|-----------------|-----------|
| 5 | 7 | 4 | 1 | 0 | 12 |
| 6 | 32 | 27 | 9 | 3 | 71 |
| 7 | 3 | 6 | 8 | 10 | 27 |
| 8 | 2 | 8 | 9 | 15 | 34 |
| 9 | 0 | 0 | 1 | 4 | 5 |
| 10 | 0 | 0 | 0 | 1 | 1 |
| All groups | 44 | 45 | 28 | 33 | 150 |

Note: Final analyses are based on fish caught at ages 6 and 7 (in bold). Note that this table refers to nonweighted individual samples taken from a restricted size range obtained primarily in the Barents Sea and does not directly correspond to population-level ratios of immature, skippers, first-time, and repeat spawners for the Northeast Atlantic cod.

Allocation strategies result in distinct lifetime trajectories for growth, survival, and reproduction (e.g., Jørgensen and Fiksen 2010). In the present paper, we have been able to reconstruct two of these trajectories in wild-caught female Atlantic cod. Knowing the individual history of growth and reproduction allows us to address trade-offs in wild-living fish and show how current phenotype and performance may have been shaped by events earlier in life.

Materials and methods

Cod samples

Female NEA cod ranging 60–82 cm and 1.6–5.5 kg were collected using a combination of commercial vessels and dedicated research surveys in February and March 2007 and 2008 in the Barents Sea (Table 1). Aboard the vessels, fish were first weighed to the nearest gram and measured for total length (rounded down to nearest centimetre). The gonad and liver were then weighed (g), and a sample of the gonad was stored on neutral buffered formaldehyde (4%) for subsequent laboratory analyses. Finally, otoliths were removed from all fish for ageing on board. The otoliths were stored in paper envelopes for photography, measurement, and back-calculation when ashore. Further information about vessels and sampling procedure can be found in Skjæraasen et al. (2010). The fish included in the present study constitutes a subsample of the females examined in Skjæraasen et al. (2012), for which we have here calculated individual growth trajectories with the use of otoliths, and combined this with the existing knowledge of reproductive history presented in Skjæraasen et al. (2012).

Between 30 and 40 female fish from each of the four reproductive categories within our 60–82 cm size range were randomly subsampled from the original sample of 693 fish that were examined for reproductive history (Table 1). An initial analysis of size-at-age revealed that all age groups except 6 and 7 were biased compared with population estimates of fish at the same age (Fig. 1a; Table 1), because either the smallest or largest individuals fell outside the sampled size range. Thus, in the following only the 98 fish caught at ages 6 or 7 are included in the analyses. It can be noted that in recent years most females become sexually mature during this age interval, with the percentage of spawning fish increasing from less than 5% as 5-year-olds to 40%–65% as 8-year-olds.

Past and present spawning history

Gonads were first classified macroscopically as either containing developing oocytes for the upcoming spawning period or not. For the former, the presence of developing oocytes was subsequently confirmed by image analysis (Thorsen and Kjesbu 2001). All gonad samples were then subjected to histological analyses using the standard protocols for resin embedding. The presence or absence of POFs, an unequivocal marker of past spawning

(Rideout et al. 2005; Witthames et al. 2010), was used to identify if fish had spawned before. Collectively, this information was used to categorize fish into (i) immatures (no developing oocytes, no POFs), (ii) skipped spawners (no developing oocytes, POFs present), (iii) first-time spawners (developing oocytes (mean oocyte diameter = 558 μm , $n = 28$), no POFs present), and (iv) repeat spawners (developing oocytes (mean oocyte diameter = 590 μm , $n = 33$), POFs present). When characterizing the fish as sexually mature or not, the latter three categories were considered mature, while only the first-time spawners and repeat spawners were characterized as spawning the year of capture. Based on the POFs, the spawning history the previous and upcoming season could be determined for all the fish, with skippers and repeater spawners spawning the year before capture. First year of sexual maturity of skippers and repeat spawners caught at ages 6 and 7 were assumed to be ages 5 and 6, respectively. Further information about the laboratory procedures can be found in (Skjærraasen et al. 2010).

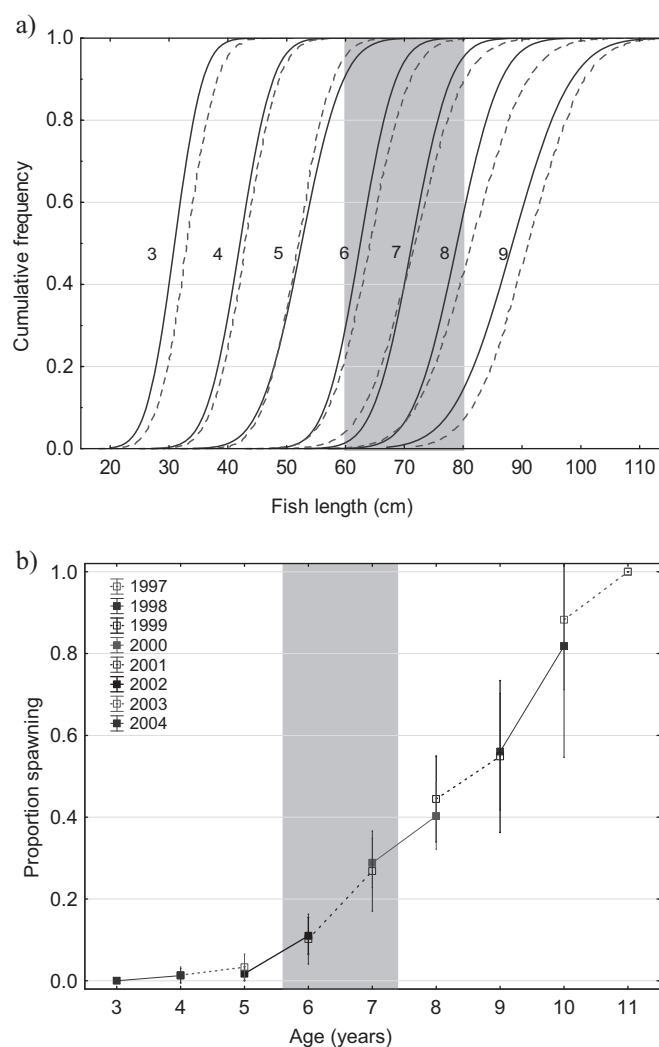
Back-calculation of length

The ageing and annotation of cod otoliths in this study were carried out by highly experienced otolith readers at the Institute of Marine Research (IMR), Bergen, Norway, and the otoliths used here were subject to an extensive embedding, sectioning, and grinding procedure before interpretation (Panfili et al. 2002). The sagittal otoliths were sectioned along the transverse axis and photographed under a stereomicroscope at 10 \times magnification employing a reflected light setting (Høie et al. 2009). Images of 2560 \times 1920 pixel resolution were taken of both otoliths, and since there are no systematic increment or size differences between left and right cod otoliths, the image with the clearest incremental structures was chosen for further analysis. Dark field illumination was used, thus resulting in translucent winter zones appearing as bright zones in the images (Fablet et al. 2011). The otolith sizes at the midpoint of respective annual translucent zones were marked along a transect from the core to the outer distal edge of the otolith, with the transect being approximately perpendicular to the width of the otolith (Li et al. 2008; Fig. 2). Following the recommendations of (Li et al. 2008), a nonlinear scale proportional back-calculation formula ($BCI_i = (O_i/O_c)^{1/\nu} L_c$) was used to estimate fish length (L_i) at previous ages (i) based on the fish size (L_c) and otolith size (O_c) at capture and otolith size-at-age (O_i), where $\nu = 0.63$ is the slope of the $\log(O)$ on $\log(L)$ regression. As an additional analysis independent of back-calculation assumptions, relative otolith increment sizes were used directly after standardization to a mean of 0 and standard deviation of 1 at each age interval. These standardized increments were then used as input in similar analyses as the back-calculated lengths and annual length increment data.

Statistical analyses

Increment data were treated as longitudinal data in mixed effects models (LME) in R 2.15 statistical software (R Core Development Team 2012; Zuur et al. 2009) with reproductive group (immature, first-time, skipper, repeat), maturity status (mature, immature), or spawning status (spawning, not spawning) as fixed factors, fish as random factor, and when stated, age (i), age-at-capture (AC), and years relative to first maturation (YM) as covariate or ordered factor. Model selection was carried out by starting with a full model and sequentially removing insignificant higher-order interactions until the final model with the lowest Akaike information criterion (AIC) was chosen (Zuur et al. 2009). Diagnostic plots were used to check residual patterns before accepting the final model for each analysis. The analysis of size or growth rate at one given period or time interval did not involve repeated data on the same individual and were thus carried out using general linear models (GLM) (StatSoft, Inc. 2012). Treatment contrasts were used in the LME and GLM analyses to determine which of the four reproductive groups differed from each other after applying a

Fig. 1. (a) Fitted normal length distributions of female Northeast Arctic cod from Institute of Marine Research (IMR, Bergen, Norway) winter research surveys for age groups 3–9 (2007 solid line and 2008 dashed line). Shaded area corresponds to length range of fish used in this study. (b) Mean proportion (\pm confidence interval, CI) of female Northeast Arctic cod spawning at age for year classes 1997–2004 based on data from 2007–2008 winter research surveys. Year classes of odd years have open symbols and dashed lines. Shaded area indicate age groups used in this study. Data from the cruises were adjusted by applying an age–sex–length key with weight been given to biological samples (age, maturity, sex, fish mass, etc.), corresponding to catch rate at the trawl station and length group.



Holm–Bonferroni correction for the six possible pairwise tests (R Core Development Team 2012). Graphs were made using Statistica and R statistical software (R Core Development Team 2012; StatSoft, Inc. 2012).

Results

Between-individual differences: big fish mature first

Immature cod caught at ages 6 or 7 had smaller back-calculated length at age 3 than similarly aged cod that had become sexually mature (reproductive status main effect, $P < 0.001$, GLM). Comparing the four different reproductive groups, immatures were significantly smaller at age 3 than the skippers and repeat spawning fish (Fig. 3, treatment contrasts, $P < 0.015$, GLM). The mean estimated size difference at age 3 was about 4 and 5 cm, respectively.

Fig. 2. Image of a transverse section of an otolith of a 6-year-old cod taken under dark field illumination. The core of the otolith is marked by C, and the positions of the following annuli along the distal axis are marked in white by increasing numbers. The last annulus at the outer edge is marked in black. The width of the section (8.0 mm), corresponding to the dorsal-ventral distance, is also indicated.

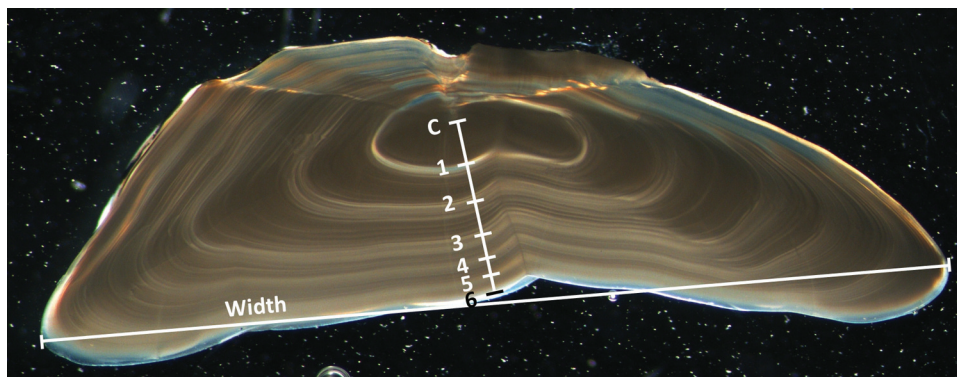
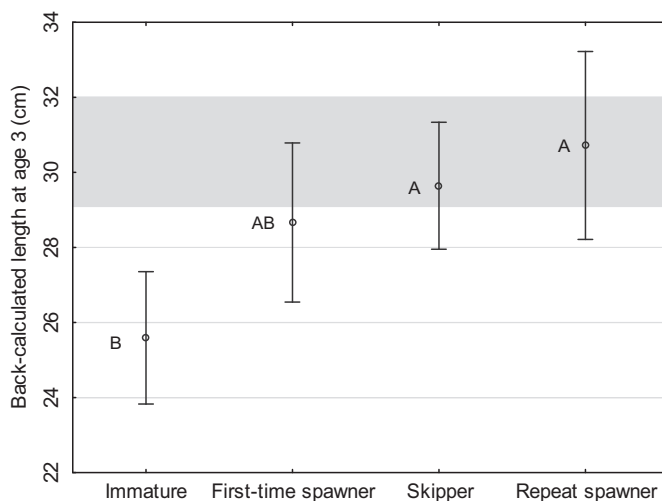


Fig. 3. Predicted mean back-calculated lengths (\pm CI) at age 3 of female cod caught at ages 6 and 7 from GLM model. Different letters next to points represent significantly different means of fish from corresponding spawning groups ($P < 0.05$, GLM analysis). Shaded area represents range of mean sizes of age 3 cod from corresponding year classes 2003–2005 (ICES 2013).



The first-time spawning cod caught at ages 6 and 7 were 3 cm larger at age 3 than cod in the immature group, but this effect was not significant (Fig. 3). Fish caught as 6-year-olds were on average 3.5 cm longer at age 3 than those caught as 7-year-old fish (AC main effect, $P < 0.005$, GLM).

Allocation trade-offs: growth slows down at reproduction

The annual length increment of mature and immature fish differed in the years prior to capture. The immature fish had a lower length growth initially than the mature fish, confirming the results of the previous analysis, but eventually grew faster than the mature fish (maturity status \times age interaction; $P < 0.001$, Fig. 4; Table 2). A nonlinear effect of age revealed that length growth was decreasing and levelling off with age; this happened among reproducing fish but was less pronounced among immature fish (age squared effect, $P < 0.001$, LME; Table 2).

Growth during events of skipped spawning

In the year after first reproduction, skippers grew 2.3 cm more than repeat spawners (Fig. 5, $P < 0.013$, LME). Prior to maturation the skippers did not differ in annual length growth from the two other groups that had matured by ages 6 or 7 ($P > 0.07$, LME). All the mature groups had annual length growth rates below the

Fig. 4. Estimated annual length increment (ALI) at age (cm) of immature (dashed lines) and mature fish (solid lines, including first-time spawners, skippers, and repeat spawners) caught at ages 6 (thin lines) and 7 (thick lines, LME model; Table 2). Numbers next to lines represent number of fish in each category.

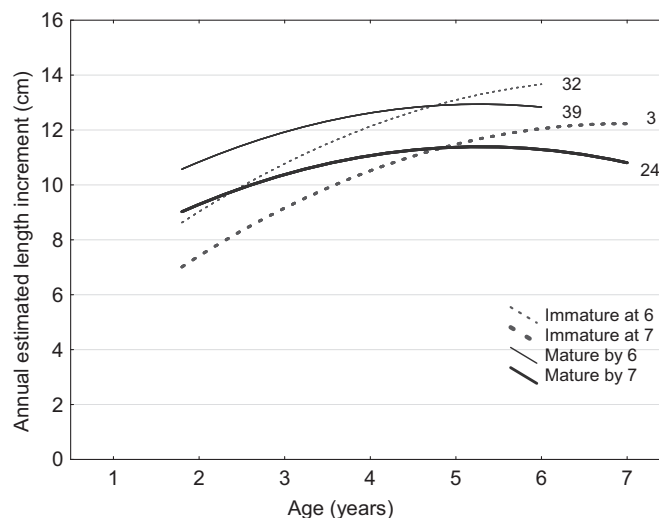


Table 2. Final linear mixed effects model on annual length increment (ALI, cm), with age (years: 4) and age-at-capture (AC, years) as covariates, maturity status at catch (MAT) as a factor (with levels 0 or 1), and fish as random effect.

| | Value | SE | df | t value | p value |
|--------------------------|--------|-------|-----|---------|---------|
| (Intercept) | 21.66 | 1.574 | 416 | 13.76 | 0.0000 |
| (Age 4) | 1.166 | 0.129 | 416 | 9.02 | 0.0000 |
| MAT(1) | 0.527 | 0.246 | 95 | 2.14 | 0.0346 |
| AC | -1.593 | 0.259 | 95 | -6.15 | 0.0000 |
| (Age 4) \times (Age 4) | -0.195 | 0.053 | 416 | -3.71 | 0.0002 |
| (Age 4):MAT(1) | -0.662 | 0.157 | 416 | -4.22 | 0.0000 |

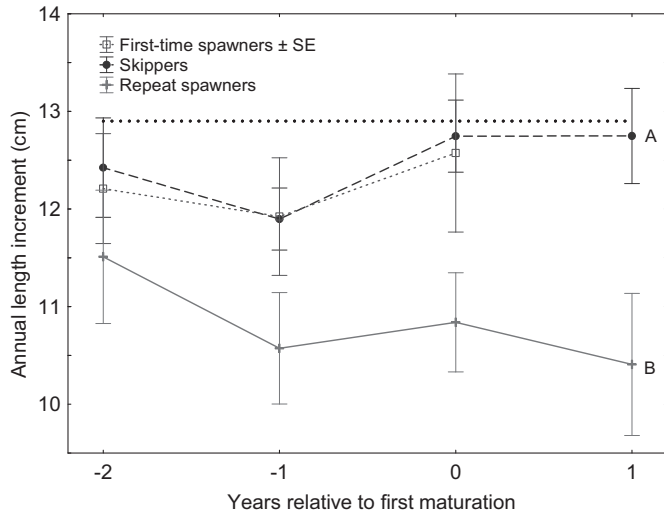
Note: Four years were subtracted to all age values which corresponded to the median age of the data used in the analysis, and MAT(1) represent the added parameter term for fish mature at catch compared with immature fish.

overall average annual growth rates of immatures during the same age interval (Fig. 5).

Using standardized otolith increments yields similar results

The standardized otolith increment growth the last 2 years prior to capture revealed a similar pattern as the back-calculated

Fig. 5. Annual length increment (cm) (\pm SE) of 6- to 7-year-old female cod at time (in years) relative to first maturation. Horizontal dotted line represents mean annual length increment of immature female fish during the three last years prior to capture, short dashed line is for first-time spawners, long dashed line is for skippers, and solid line is for repeat spawners. Different letters next to points at a given time represent significantly different means of fish from corresponding spawning groups ($P < 0.05$, LME and GLM analysis).



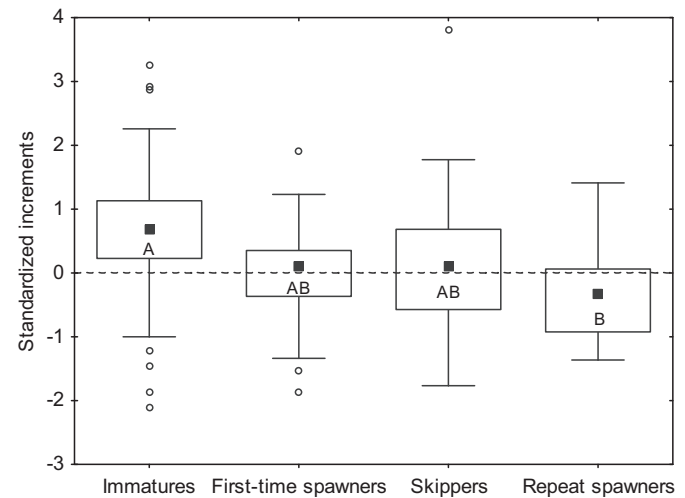
sizes and growth rates. The immature fish had significantly higher growth increments than mature fish ($P < 0.005$, LME), although no significant differences were found between widths of the outer two increments (Fig. 6). Numerically, repeat spawners had the smallest standardized otolith increments among mature fish, but were not significantly different from first-time spawners or skippers.

Discussion

Strategies for when to commence reproduction and with what intensity lie at the core of life-history theory (Lack 1947; Williams 1966), with the key logic revolving around how to best utilize limited resources (Fisher 1930). The key trade-off is that between current and future reproduction; should resources be used for reproduction now or invested in a larger body that perhaps can reproduce more effectively in the future? The mortality rate (Reznick et al. 1990) and environmental conditions (Marshall and Browman 2007) thus become central, as these can be used to predict the likelihood and success of future reproductive events. Not only are fish indeterminate growers with a flexible bauplan that easily can be scaled up (Heino and Kaitala 1999), but fecundity is strongly size-dependent so a larger body usually implies a higher fecundity. At the same time, attaining a large body size comes with costs, both in terms of time, during which injury or fatality may occur, and in terms of resources that need to be allocated towards growth and not reproduction (Enberg et al. 2012).

Fish differ from most terrestrial animals in that there can be large intraspecific variation in body size among reproductive individuals. This has the consequence that it might be easier to detect and quantify the trade-offs that underlie life-history strategies. Two trade-offs were pronounced in our study. First, fast growth early in life increased the probability of becoming sexually mature at any given age. Second, fish that were reproducing grew slower than fish that were immature or skipping spawning. These can both be understood in terms of life-history considerations.

Fig. 6. Boxplot of median standardized increment widths the last 2 years of the four spawning categories of fish caught at ages 6 and 7. Boxes and whiskers represent 25 and 75 percentiles and 1.5 times the interquartile range, respectively. Individual points represent outliers beyond these ranges. Different letters in boxes represent significantly different mean values ($P < 0.05$, LME).



Trade-offs affecting timing of maturation

There are many reasons for why having a minimum body size is advantageous for breeding (Charnov 1982), in addition to the general decline in mortality associated with increased size in marine environments (McGurk 1986). There might be size-dependent competition for mates (Parker 1992), fecundity increases with size (Kjesbu et al. 1998), and migration costs generally decline with size as swimming becomes more efficient (Roff 1988). The latter may have particular relevance for the NEA cod, which undertake a long-range, energetically costly (Jørgensen et al. 2008) migration from the Barents Sea feeding grounds to the Lofoten spawning areas (Bergstad et al. 1987) or even further south along the Norwegian coastline (Godø 1983; Yaragina et al. 2011). Still, empirical quantifications of size-dependent maturation probability (using mean growth rather than back-calculated lengths) have revealed that the larger fish in any given cohort mature first and that the size of 50% maturation probability declines with age (Dieckmann and Heino 2007; Heino et al. 2002b). These trends were also evident in our data, as back-calculated size at age 3 for immature fish were smaller than that for groups that had spawned at least once, and fish that were mature when captured at age 6 had on average grown faster than fish that were mature, but captured at age 7.

Energy allocation trade-offs and skipped spawning

Our results also revealed that growth slowed down when fish began to reproduce. Such energy allocation was previously suggested by Fisher (1930) and has been a central point in several models (Quince et al. 2008; Roff 1983; for cod, see Dunlop et al. 2009; Enberg et al. 2009; Jørgensen and Fiksen 2006). It is not evident that a trade-off between growth and reproduction would have been detected through back-calculation, as it presupposes that the switch of energy allocation coincides with growth zone formation in the otoliths. If spawning occurs in the middle of a growth zone and growth is slowed down for a year prior to spawning, then the growth deceleration will affect two growth zones in the otolith and thus be harder to detect in data. This also implies that effects on growth from changes in energy allocation may be more pronounced than our back-calculation procedure could detect and that the reproductive groups could differ more than was estimated from our data.

It was particularly interesting that skipped spawners grew significantly more than the other groups of fish that had become sexually mature. This tentatively suggests that faster growth and the potential for an increase in future reproductive success may be one factor influencing skipped spawning in fish as a life-history strategy (Jørgensen et al. 2006), although it should be noted that the observed group growth difference may not be sufficient to yield an adaptive advantage. However, skipped spawning may also be linked to energy (Skjæraasen et al. 2012), and it has been shown that fish may skip spawning in years with particularly low food availability (Rideout et al. 2000). This can logically be extended to account for skipped spawning among parasitized or diseased fish, and it is likely that the occurrence of skipping in our dataset was also influenced by the resource situation. If so, it would bring down mean growth for the group of skippers and thus diminish growth differences between those fish skipping spawning as a life-history strategy to increase future fecundity and the other groups of reproductive fish in our study. It would also show up as larger variance in growth among skippers than within the other groups. It should also be mentioned that the cod stock was large in the years we sampled, so there could be density-dependent competition for food and resource shortage at least suffered by some of the fish. A recent study on NEA cod liver size for the last 150 years indicates that this is indeed the case (Kjesbu et al. 2014), although the mean mass-at-age for 4- to 7-year-old NEA cod in these years did not indicate impaired condition (ICES 2013).

Methodological constraints and future studies

To look at fish representative of the population in our study, we only included the age classes 6 and 7. We further made the assumption that skippers and repeat spawners had matured 1 year before they were caught. For the fish caught at age 6, this assumption should hold given the low numbers of females maturing at age 4 (Fig. 1b). In contrast, for skippers and repeat spawners caught at age 7, they could feasibly have matured at age 5. A second minor caveat is whether females matured as 5-year-olds, skipped spawning as 6-year-olds, and then were developing oocytes for spawning when caught as 7-year-olds. Given that POFs are not likely to persist for 2 years (Witthames et al. 2010), these fish would most likely be classified as first-time and not repeat spawners in our analyses. However, given that we focus on either (i) comparing mature and immature fish or (ii) when comparing immature, first-time spawners, repeat spawners, and skippers, we look at growth during the last 2 years, our results or interpretations will not be affected.

An unexpected result of the emerging otolith increment growth patterns in this study was the apparent lack of narrow spawning zones as described in Rollefson (1933). These structures have been used to determine onset of reproduction in NEA cod by use of archived otolith material. In this study, even in cod classified as repeat spawners, most of the otoliths were characterized by relatively similar outer increment widths, resulting in approximately linear, individual back-calculated growth trajectories. Otolith growth has previously been shown to continue even when the somatic growth is reduced or has ceased for some time (Hare and Cowen 1995; Kristoffersen 2007), but the apparent discrepancy between the appearances of otoliths used in this study and those presented by Rollefson (1933) warrant further investigation. Part of the discrepancy could be due to reduced precision in the increment width estimation close to the edge, making the same increments appear more distinct and identifiable if the fish had been older with more increments added to the otolith. Still, the change in otolith zonation is known to be the result of a complex interplay between internal and external environmental factors, and in the case of NEA cod, the period prior to spawning involves major internal biological changes in connection with reproduction itself (Kjesbu et al. 1998), in addition to the changes in ambient environment encountered during the southern migration from the Barents Sea towards the Norwegian coast (Sundby 2000). Multiple

factors are therefore expected to be involved in the zone formation in the otoliths, and further investigations should be aimed at determining the role of spawning per se in altering the otolith zone structure in NEA cod.

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References

- Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* 72(2): 149–177. doi:10.1086/419764.
- Auer, S.K. 2010. Phenotypic plasticity in adult life-history strategies compensates for a poor start in life in Trinidadian guppies (*Poecilia reticulata*). *Am. Nat.* 176(6): 818–829. doi:10.1086/657061. PMID:20973669.
- Auer, S.K., Arendt, J.D., Chandramouli, R., and Reznick, D.N. 2010. Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (*Poecilia reticulata*). *Ecol. Lett.* 13(8): 998–1007. PMID:20545728.
- Bergstad, O.A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. *Fish. Res.* 5: 119–161. doi:10.1016/0165-7836(87)90037-3.
- Charnov, E.L. 1982. The theory of sex allocation. Princeton University Press Princeton, N.J.
- Dieckmann, U., and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Mar. Ecol. Prog. Ser.* 335: 253–269. doi:10.3354/meps335253.
- Dunlop, E.S., Heino, M., and Dieckmann, U. 2009. Eco-genetic modeling of contemporary life-history evolution. *Ecol. Appl.* 19(7): 1815–1834. doi:10.1890/08-1404.1. PMID:19831072.
- Enberg, K., Jørgensen, C., Dunlop, E.S., Heino, M., and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. *Evol. Appl.* 2(3): 394–414. doi:10.1111/j.1752-4571.2009.00077.x.
- Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., and Heino, M. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Mar. Ecol.* 33(1): 1–25. doi:10.1111/j.1439-0485.2011.00460.x.
- Fablet, R., Pecquerie, L., de Pontual, H., Høie, H., Millner, R., Mosegaard, H., and Kooijman, S.A.L.M. 2011. Shedding light on fish otolith biomineralization using a bioenergetic approach. *PLoS ONE*, 6(11): e27055. doi:10.1371/journal.pone.0027055. PMID:22110601.
- Fisher, R.A. 1930. Genetical theory of natural selection. Oxford University Press, Oxford, UK.
- Francis, R.I.C.C., and Campana, S.E. 2004. Inferring age from otolith measurements: a review and a new approach. *Can. J. Fish. Aquat. Sci.* 61(7): 1269–1284. doi:10.1139/f04-063.
- Godø, O.R. 1983. Migration, mingling and homing of North-east Arctic cod from two separated spawning populations. In *Symposium on Reproduction and Recruitment of Arctic Cod*, Leningrad, Russia, 26–30 September 1983. pp. 289–302.
- Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. *Can. J. Fish. Aquat. Sci.* 52(9): 1909–1922. doi:10.1139/f95-783.
- Heino, M., and Kaitala, V. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *J. Evol. Biol.* 12: 423–429. doi:10.1046/j.1420-9101.1999.00044.x.
- Heino, M., Dieckmann, U., and Godø, O.R. 2002a. Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56(4): 669–678. doi:10.1554/0014-3820(2002)056[0669:MPRNF]2.0.CO;2. PMID:12038525.
- Heino, M., Dieckmann, U., and Godø, O.R. 2002b. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. *ICES J. Mar. Sci.* 59: 14.
- Høie, H., Millner, R.S., McCully, S., Nedreaas, K.H., Pilling, G.M., and Skadal, J. 2009. Latitudinal differences in the timing of otolith growth: a comparison between the Barents Sea and southern North Sea. *Fish. Res.* 96(2–3): 319–322. doi:10.1016/j.fishres.2008.12.007.
- ICES. 2013. Report of the Arctic Fisheries Working Group (AFWG). ICES CM 2013/ACOM:05.
- Jørgensen, C., and Fiksen, Ø. 2006. State-dependent energy allocation in cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 63(1): 186–199. doi:10.1139/f05-209.
- Jørgensen, C., and Fiksen, Ø. 2010. Modelling fishing-induced adaptations and consequences for natural mortality. *Can. J. Fish. Aquat. Sci.* 67(7): 1086–1097. doi:10.1139/F10-049.
- Jørgensen, C., Ernande, B., Fiksen, Ø., and Dieckmann, U. 2006. The logic of skipped spawning in fish. *Can. J. Fish. Aquat. Sci.* 63(1): 200–211. doi:10.1139/f05-210.
- Jørgensen, C., Dunlop, E.S., Opdal, A.F., and Fiksen, Ø. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology*, 89(12): 3436–3448. doi:10.1890/07-1469.1. PMID:19137949.
- Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Walker, M.G. 1998. Temporal

- variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *J. Sea Res.* **40**(3–4): 303–321. doi:10.1016/S1385-1101(98)00029-X.
- Kjesbu, O., Opdal, A.F., Korsbrette, K., Devine, J.A., and Skjæraasen, J.E. 2014. Making use of Johan Hjort's "unknown" legacy: reconstruction of a 150-year coastal time-series on northeast Arctic cod (*Gadus morhua*) liver data reveals long-term trends in energy allocation patterns. *ICES J. Mar. Sci.* doi:10.1093/icesjms/fsu030. [In press.]
- Koedijk, R.M., Folkvord, A., Foss, A., Pittman, K., Stefansson, S.O., Handeland, S., and Imsland, A.K. 2010. The influence of first-feeding diet on the Atlantic cod *Gadus morhua* phenotype: survival, development and long-term consequences for growth. *J. Fish Biol.* **77**(1): 1–19. doi:10.1111/j.1095-8649.2010.02652.x. PMID:20646135.
- Kozłowski, J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. *Proc. R. Soc. Ser. B Biol. Sci.* **263**(1370): 559–566. doi:10.1098/rspb.1996.0084.
- Kristoffersen, J.B. 2007. Growth rate and relative otolith size in populations of adult Müller's pearlyside *Maurollicus muelleri*. *J. Fish Biol.* **71**(5): 1317–1330. doi:10.1111/j.1095-8649.2007.01593.x.
- Lack, D. 1947. The significance of clutch size. *Ibis*, **89**: 302–352. doi:10.1111/j.1474-919X.1947.tb04155.x.
- Lea, E. 1910. 1. Contributions to the methodics in herring-investigations. *Publ. Circ. ICES*, **53**(s1): 7–33. doi:10.1093/icesjms/s1.53.7.
- Li, L., Høie, H., Geffen, A.J., Heegaard, E., Skadal, J., and Folkvord, A. 2008. Back-calculation of previous fish size using individually tagged and marked Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **65**(11): 2496–2508. doi:10.1139/F08-157.
- Marshall, C.T., and Browman, H.I. 2007. Disentangling the causes of maturation trends in exploited fish populations. *Mar. Ecol. Prog. Ser.* **335**: 249–251.
- McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: Role of spatial patchiness. *Mar. Ecol. Prog. Ser.* **34**(3): 227–242. doi:10.3354/meps034227.
- Metcalfe, N.B., and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**(5): 254–260. doi:10.1016/S0169-5347(01)02124-3. PMID:11301155.
- Panfili, J., Troadec, H., Pontual, H.d., and Wright, P.J. 2002. Manual of fish sclerochronology. Ifremer-IRD coedition, Brest, France.
- Parker, G.A. 1992. The evolution of sexual size dimorphism in fish. *J. Fish Biol.* **41**: 1–20. doi:10.1111/j.1095-8649.1992.tb03864.x.
- Pedersen, T., and Jobling, M. 1989. Growth rates of large, sexually mature cod, *Gadus morhua*, in relation to condition and temperature during an annual cycle. *Aquaculture*, **81**: 161–168. doi:10.1016/0044-8486(89)90242-1.
- Quince, C., Abrams, P.A., Shuter, B.J., and Lester, N.P. 2008. Biphase growth in fish I: theoretical foundations. *J. Theor. Biol.* **254**(2): 197–206. doi:10.1016/j.jtbi.2008.05.029. PMID:18606423.
- R Core Development Team. 2012. R: A language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from <http://www.R-project.org/>.
- Reznick, D. 1982. The impact of predation on life-history evolution in Trinidadian guppies — genetic basis of observed life-history patterns. *Evolution*, **36**(6): 1236–1250. doi:10.2307/2408156.
- Reznick, D.A., Bryga, H., and Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. *Nature*, **346**: 357–359. doi:10.1038/346357a0.
- Reznick, D., Nunney, L., and Tessier, A. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol.* **15**(10): 421–425. doi:10.1016/S0169-5347(00)01941-8. PMID:10998520.
- Ricklefs, R.E., and Wikelski, M. 2002. The physiology/life-history nexus. *Trends Ecol. Evol.* **17**(10): 462–468. doi:10.1016/S0169-5347(02)02578-8.
- Rideout, R.M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: more common than you might think. *Mar. Coast. Fish. Dyn. Manage. Ecosyst. Sci.* **3**: 176–189. doi:10.1080/19425120.2011.556943.
- Rideout, R.M., Burton, M.P.M., and Rose, G.A. 2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. *J. Fish Biol.* **57**(6): 1429–1440. doi:10.1111/j.1095-8649.2000.tb02222.x.
- Rideout, R.M., Rose, G.A., and Burton, M.P. 2005. Skipped spawning in female iteroparous fishes. *Fish Fish.* **6**: 50–72. doi:10.1111/j.1467-2679.2005.00174.x.
- Roff, D.A. 1983. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* **40**(9): 1395–1404. doi:10.1139/f83-161.
- Roff, D.A. 1988. The evolution of migration and some life history parameters in marine fishes. *Environ. Biol. Fishes.* **22**: 133–146. doi:10.1007/BF00001543.
- Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.
- Rollefsen, G. 1933. The otoliths of cod. *Fiskeridir. Skr. Ser. HavUnders.* **4**(3): 1–14.
- Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. *ICES J. Mar. Sci.* **56**: 303–319. doi:10.1006/jmsc.1999.0458.
- Skjæraasen, J.E., Kennedy, J., Thorsen, A., Fonn, M., Strand, B.N., Mayer, I., and Kjesbu, O.S. 2009. Mechanisms regulating oocyte recruitment and skipped spawning in Northeast Arctic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **66**(9): 1582–1596. doi:10.1139/F09-102.
- Skjæraasen, J.E., Nash, R.D.M., Kennedy, J., Thorsen, A., Nilsen, T., and Kjesbu, O.S. 2010. Liver energy, atresia and oocyte stage influence fecundity regulation in Northeast Arctic cod. *Mar. Ecol. Prog. Ser.* **404**: 173–183. doi:10.3354/meps08486.
- Skjæraasen, J.E., Nash, R.D., Korsbrette, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K.H., Thorsen, A., Witthames, P.R., Geffen, A.J., Høie, H., and Kjesbu, O.S. 2012. Frequent skipped spawning in the world's largest cod population. *Proc. Natl. Acad. Sci. U.S.A.* **109**(23): 8995–8999. doi:10.1073/pnas.1200223109. PMID:22615381.
- StatSoft, Inc. 2012. STATISTICA (data analysis software system) [online]. Version 12. Available from <http://www.statsoft.com>.
- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, **85**: 277–298.
- Thorsen, A., and 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. doi:10.1016/S1385-1101(01)00090-9.
- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690. doi:10.1086/282461.
- Witthames, P.R., Thorsen, A., and Kjesbu, O.S. 2010. The fate of vitellogenic follicles in experimentally monitored Atlantic cod *Gadus morhua* (L.): application to stock assessment. *Fish. Res.* **104**(1–3): 27–37. doi:10.1016/j.fishres.2009.11.008.
- Yaragina, N.A. 2010. Biological parameters of immature, ripening, and non-reproductive, mature northeast Arctic cod in 1984–2006. *ICES J. Mar. Sci.* **67**(9): 2033–2041. doi:10.1093/icesjms/fsq059.
- Yaragina, N.A., Aglen, A., and Sokolov, K.M. 2011. Cod. In *The Barents Sea ecosystem, resources, management. Half a century of Russian–Norwegian cooperation.* Edited by T. Jakobsen and V.K. Ozhigin. Tapir Academic Press, Trondheim, Norway. pp. 225–270.
- Zera, A.J., and Harshman, L.G. 2001. The physiology of life history trade-offs in animals. *Annu. Rev. Ecol. Syst.* **32**: 95–126. doi:10.1146/annurev.ecolsys.32.081501.114006.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.