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## **Skipped spawning is common for the Northeast Arctic cod in a life-history energy allocation model**

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### **Abstract**

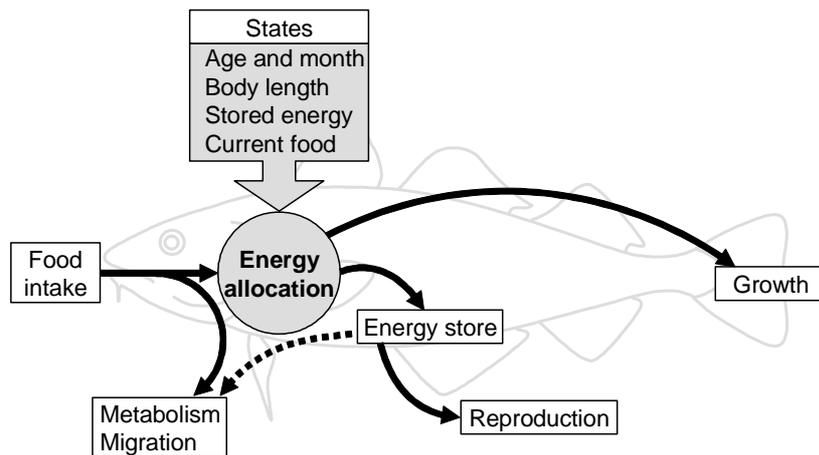
*That iteroparous fish reproduce every year after they have become sexually mature is a common assumption in fisheries science. Experimental and field studies suggest, however, that mature fish commonly skip spawning, often but not only in relation with failing food resources. This study presents a life-history model based on optimal energy allocation for the Northeast Arctic cod. Ingested energy can either be allocated to growth or to storage for the next spawning period. This trade-off embodies life-long patterns of growth, maturation, and reproduction. The allocation decision was optimised based on five individual states: age, length, size of energy stores, month of the year, and the current food availability. The model showed that skipped spawning was partly related to periods of low food intake (there was not sufficient energy to spawn), but that it also played a central role in life-history: spawning should be omitted because of the benefits that come from growth to a larger size. Skipped spawning was most common in the years just following maturation. The influence of several parameters was tested, and skipped spawning was more common when: 1) juvenile mortality was high; 2) mortality at the spawning grounds was low; 3) the energetic cost of migration was high; and 4) food intake was low.*

### **Introduction**

Why should long-lived iteroparous individuals skip reproduction after they have reached sexual maturity? These individuals have already undergone the physiological changes associated with maturation, and are thus, in principle, prepared for repeated and successful reproduction. To understand such patterns of reproduction it is essential to appreciate how the life-long trade-off between reproduction, growth, and survival affects an organism's life history. From the organism's point of view, these trade-offs require strategies for differentially allocating available resources to changes in size, fecundity, and energy stored for future actions.

Reproduction is more often skipped when individual condition is poor. In fish, this has been documented for several species (Bagenal, 1957; Rijnsdorp, 1990; Kjesbu et al., 1991; Rideout et al., 2000). Instead of exacerbating already low energy reserves, the time and energy required for reproduction should be channelled to increase future successes.

Additional factors may modify the optimal life-history strategy. Since skipped spawning results from the trade-off between current and future reproduction, we would expect that factors such as mortality, food intake, and migration costs would trigger evolution of life



**Figure 1.** Schematic overview over a life-history energy allocation model for the Northeast Arctic cod. The energy allocation decision and the states influencing are shaded in grey, and black arrows indicate energy flow. The dotted line indicates that energy stores are drained in periods when food intake cannot sustain metabolic demands.

history strategies, and thus influence the frequency and pattern of skipped spawning.

This study explores reproductive strategies in Atlantic cod (*Gadus morhua*) using a flexible life-history model. Cod is a repeat spawner, and the Northeast Arctic stock, which is the object of this study, performs annual migrations from the feeding grounds in the Barents Sea to spawning grounds off Lofoten. The annual migrations entail a direct cost in terms of energy and time. In the present model, we focus on this allocation rule, which is dependent on age, time of year, body length, state of the energy stores, and food availability. Each point on the resulting five-dimensional surface that describes the allocation rule is independent, so that the allocation rule is not artificially constrained but allows any shape to emerge evolutionarily. The optimal allocation rule, which is also the allocation rule supposedly favoured by natural selection, can then be found for various environmental scenarios. On this basis, patterns of growth and reproduction can be predicted and analyzed.

Using the model thus outlined, this paper first focuses on the mechanisms of skipped spawning, then turns to factors that affect life-history strategies in an evolutionary perspective.

### Model description

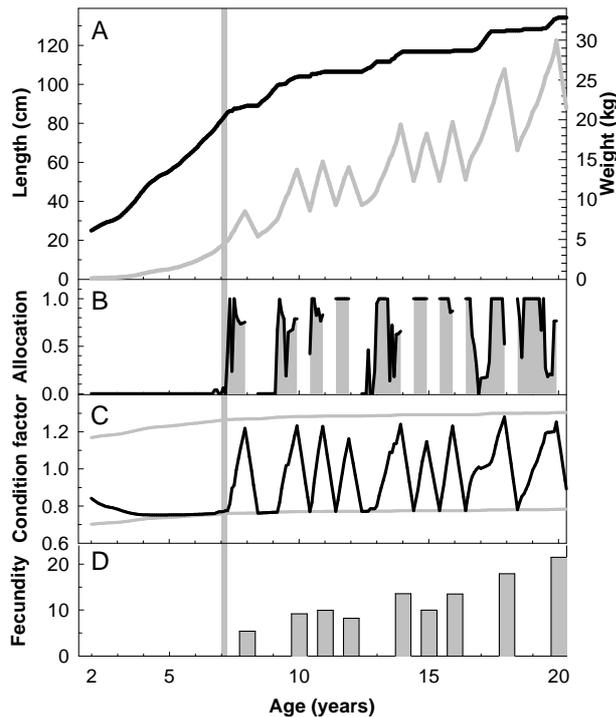
Our study is based on a flexible life-history model describing a migratory fish (a detailed description of the model will be found in Jørgensen and Fiksen, In prep.). The model is parameterized for the Northeast Arctic cod stock and fits well with observed growth in natural stocks experiencing variable environmental conditions. A key assumption of the model is that energy, ingested in a stochastic feeding environment, can be allocated either to growth or to storage (Fig. 1). Growth is irreversible and

increases somatic structures together with a minimum amount of muscle mass. Energy stores (lipids in the liver and increased white muscle mass) grow reversibly between a minimum and maximum condition factor, and the stored energy can be utilized for metabolic or reproductive purposes.

Eggs are spawned in one batch in March, and reproduction requires migrations to the spawning grounds. Migration is costly in terms of energy (increased metabolic rate during the migration), time (cod eat little during migration and spawning and thus forego opportunities for growth), and mortality (natural mortality increases during migration and spawning). In addition to natural mortality, fishing mortality can occur on the feeding ( $Z_F$ ) and spawning ( $Z_S$ ) grounds due to human fisheries.

Optimal life-history strategies were calculated using dynamic optimization (Houston and McNamara, 1999; Clark and Mangel, 2000), using four state variables: age (in months, thus including seasonal variations), stored energy (measured on a relative scale between 0 and 1), body length (cm), and food availability. The optimal allocation strategies were then simulated and population dynamics for 1.000 years analyzed to derive consequences for individual and population patterns of growth, maturation, and reproduction.

Three scenarios were used in our investigation of skipped spawning: 1) a moderate spawner fishery and a light fishery at the feeding grounds ( $Z_S=0.1$ ,  $Z_F=0.05$ ), resembling the fishing regime at the beginning of the 20<sup>th</sup> century and resulting in a life history with **late maturation**; 2) a high spawner fishery and an intense fishery on the feeding grounds ( $Z_S=0.3$ ,  $Z_F=0.5$ ), resembling contemporary fishing and resulting in **early maturation**; and



**Figure 2.** Growth trajectory and physiology of a cod individual from the population with intermediate maturation. The vertical grey line indicates the time at which energy is diverted towards stores prior to first spawning. (A) Length (black line, left axis) and weight (grey line, right axis). (B) Proportion of available energy that is allocated to energy stores (the remainder is diverted to growth). The line shows gaps because no energy is available for allocation during spawning migrations. (C) Fulton's condition factor (black line). The grey lines represent minimum and maximum condition factors specific to body length at age; these increase because growth in body mass is proportional to length to the power of 3.065. (D) Number of eggs spawned (in millions).

3) fisheries mortalities in between these two scenarios ( $Z_S=0.14$ ,  $Z_F=0.15$ ), resulting in **intermediate maturation** and a life history that resembles growth in the Northeast Arctic cod stock between 1978 and 2000 (ICES, 2003).

## Results

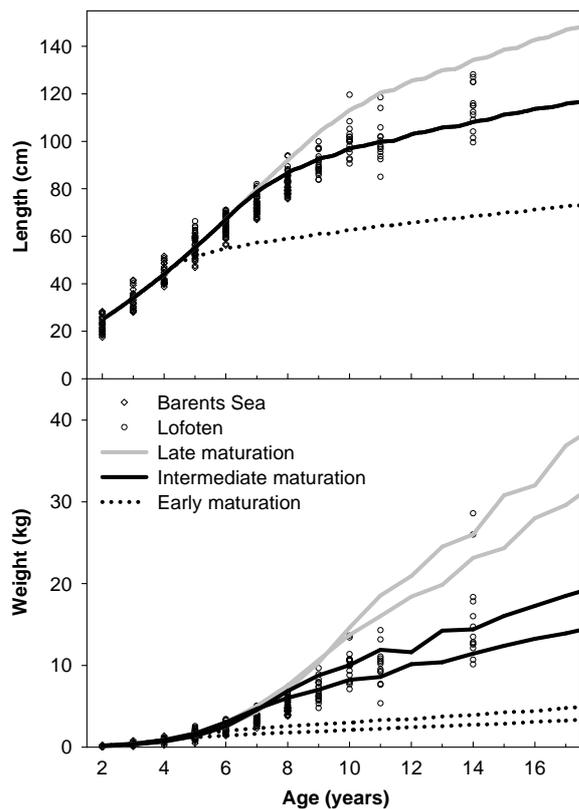
An example of how allocation of energy between growth and reproduction shapes the life history of one individual cod from our third scenario is presented graphically in Figure 2. Briefly, length growth (Fig. 2A) was nearly linear with time early in life and most of the energy was allocated to growth (Fig. 2B; values close to 0). Approximately one year prior to the first spawning, ingested energy was diverted to stores (values close to 1 in Fig. 2B; highlighted by the grey vertical line) and this energy was released as eggs during the first spawning season (Fig. 2D). After first spawning, the individual in this illustration gave priority to growth for another 7-8 months, with little allocation to energy stores, before it once again prepared for spawning. The first and second time this individual spawned (at age 8 and 10, respectively), it had nearly full energy stores. Therefore, the 70% increase in fecundity observed between these two spawning events is entirely due to the strategy of skipping spawning at age 9 and giving priority to a larger body size. A similar jump in fecundity occurred when the

individual skipped spawning at age 13. The variation in fecundity between years seen at ages 14-16 is due to the stochastic food availability.

Population dynamics were simulated for individuals that each follow allocation strategies resulting in patterns of growth and reproduction as described above, and results for the three scenarios are shown in Figure 3. Growth for the intermediate scenario corresponds well with field observations for the Northeast Arctic cod stock over the period 1978-2000 (Fig. 3), both in terms of length- and weight-at-age.

The frequency of potential repeat spawners that skip spawning is plotted separately for each cohort and for each of the three scenarios in Figure 4A. After maturation, there was no trend with age in the early maturing population, where spawning was skipped with a stable frequency of around 10%. In the other two scenarios, skipped spawning was most common among young fish, before it stabilised at 25% and 35% for older fish in the scenarios with intermediate and late maturation, respectively.

The pattern becomes even clearer when the frequency of skipped spawning is plotted against the number of years since maturation (Fig. 4B). The stochastic environment led to inter-annual variation in age at maturation, and this variation was removed by subtracting age at maturation from the age at which spawning was skipped. In all scenarios, the year following maturation



**Figure 3.** Growth in an energy allocation model parameterised for the Northeast Arctic cod (*Gadus morhua*) stock. Observed length and weight at age from the Barents Sea (diamonds, immature fish) and the Lofoten archipelago (circles, mature fish) from the period 1978-2000 is plotted for comparison; the category 12+ is plotted at age 14. The three scenarios presented are: a late maturing population with a life history strategy that was optimal before 1930 (grey line), an early maturing population that with an optimal life history for the contemporary fishing regime (dotted line), and an intermediate population that best describes growth pattern in the present Northeast Arctic cod stock. A) Length at age. B) Weight at age. The two lines for each scenario is mean weight in January (before spawning) and May (spent).

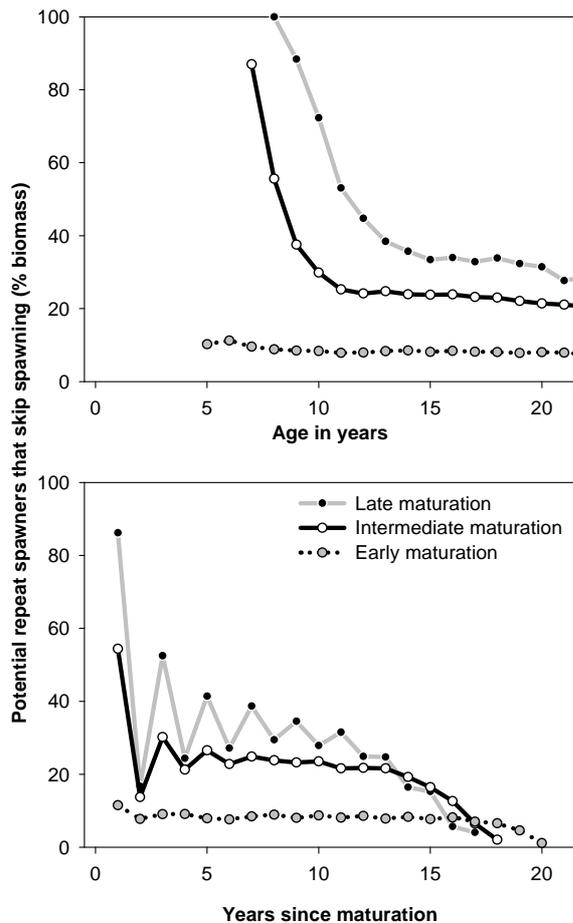
showed the highest frequency of skipped spawning; in the late-maturing population almost 90 % skipped spawning in the year following maturation. As the number of years after maturation increased, the frequency of skipped spawning in the early-maturing population stabilized quickly at the expected level of 10 %. For the other two scenarios, the frequency of skipped spawning showed dampened oscillations, i.e., a pattern where spawning was skipped more often every second year, and becoming more uniform with age.

Figure 5 shows how the mature part of the population was distributed between first-time spawners, skipped spawners, and repeat spawners for each of the three scenarios. The proportion of repeat spawners that actually reproduced was more or less constant between the three scenarios. With earlier maturation, the spawning part of the population would consist of a larger fraction of first-time spawners. At the same time, fewer potential repeat spawners would skip spawning.

## Discussion

In our model, around 30 % of the mature population skipped spawning. This level of occurrence is consistent with observations published more recently: in Newfoundland, Canada, as much as one third of cod females

were skipping spawning (Rideout et al., 2000), and it was estimated that as much as two thirds of potential cod spawners on the Flemish Cap skipped spawning in any given year between 1978 and 1985 (Walsh et al., cited as unpublished in Rideout et al., 2000). Histological examinations of trawl-sampled cod from the Barents Sea just prior to the spawning migration found that up to 57% of potential repeat spawners skipped spawning (Oganessian, 1993). In 1987, during the Barents Sea capelin collapse, no Northeast Arctic cod larger than 90 cm were found on the spawning banks although they were present in the population (Marshall et al., 1998). In the Gulf of St. Lawrence, Canada, 20-40 % of sexually mature cod had underdeveloped gonads at the time of spawning (Schwalme and Chouinard, 1999), indicating that they were skipping reproduction this year. Skipped spawning has also been documented for Greenland halibut *Reinhardtius hippoglossoides* (Fedorov, 1971; but not in Walsh and Bowering, 1981), sole *Solea solea* (Ramsay and Witthames, 1996), long rough dab *Hippoglossoides platessoides* (Bagenal, 1957), whiting *Gadus merlangus* (Gokhale, 1957), winter flounder *Pleuronectes americanus* (Burton, 1994, 1991), carp *Cyprinus carpio* (Ivanov, 1971), chub *Leuciscus cephalus* (Fredrich et al., 2003), perch *Perca fluviatilis*



**Figure 4.** (A) Frequency of skipped spawning for each cohort (age class). Cohorts prior to maturation are not shown. (B) Frequency of skipped spawning plotted against the number of years since maturation. In this representation, the variation stemming from differences in age at maturation is removed. In both panels, the frequency of skipped spawning was weighed according to the varying size of cohorts. The three lines represent different combinations of fishery mortalities giving rise to populations with different maturation strategies: a late-maturing population (spawner fishery is the most important source of mortality; grey solid line), an early-maturing population (feeder fishery most important; dotted black line), and a population described by a set of parameters providing a good fit to growth data for the present Northeast Arctic cod stock, implying intermediate maturation (combination of spawner and feeder fishery; black solid line). Each population was simulated for 1000 years in a stochastic environment.

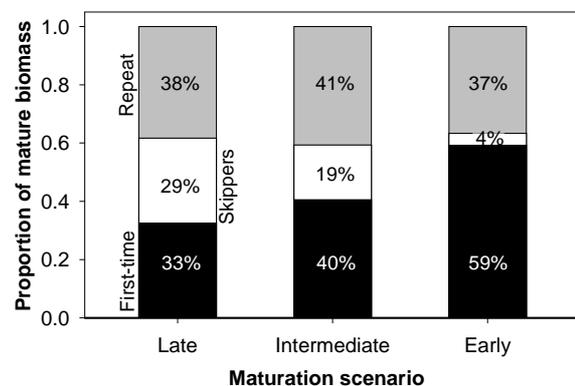
(Holmgren, 2003), and herring *Clupea harengus* (G. Engelhard, pers. comm.).

Surprisingly, our model showed that skipped spawning was not merely a response to poor feeding environment. The clear relationship observed between the frequency of skipped spawning and age means that skipped spawning is also an active component in the life history of fish, a finding that requires further investigation.

Every year, cod in the Barents Sea is confronted with the option to migrate towards the spawning grounds or not. In principle, the decision rule is simple: if an individual skips migration, the loss in fecundity this year has to be balanced by the chances of increased fecundity in the future, discounted by the survival probability up to that point (Roff, 2002).

If poor environmental condition was the only cause leading to skipped spawning, we would expect the frequency of skipped spawning to be relatively stable across all ages, since all age classes suffer from the same environment (we do not consider here the special case where subgroups of the mature population utilize different and unlinked food resources). If, on the

other hand, skipped spawning was an active choice in life history, then we would expect some pattern with age or size where skipped spawning would evidently be more common at some ages or sizes than could be explained by environmental influences alone. Poor condition alone probably explains the frequency of



**Figure 5.** The proportion of the sexually mature biomass that are first-time spawners (black), repeat spawners (grey), and that skip spawning (white) for the three maturation scenarios considered. The values are mean over 1000 years of population simulation.

skipped spawning in our second scenario (imitating the evolutionary end-point of contemporary fishing patterns and resulting in an early-maturing population). Spawning was skipped at a frequency of 10 %, and did not show any variation with age. Both the early age at maturation and the absence of an age pattern for skipped spawning suggest that this life-history strategy is geared to value current reproduction much higher than potential future spawnings; an interpretation consistent with the high mortality rates. Only when the condition of individuals was really too low to sustain migration, or when the stored energy could offer only a very limited egg production, was the spawning opportunity totally abandoned.

In our first and third scenarios, skipped spawning occurred more frequently. A lower mortality rate would always increase the value of future reproductions, and this would elevate the threshold below which poor condition is a sufficient reason to abandon spawning. But, in these two scenarios there was also an evident trend with age: skipped spawning was most common in the years following maturation (Fig. 4A). Similar results have also been found in wild cod, where skipped spawning was most common for cod of small size (Oganessian, 1993). That skipped spawning got less common with age reflects a temporal trade-off, where early growth and later reproduction are favoured. One reason that young cod should be especially prone to skip reproduction is that they have a larger future residual component in fitness: they can spawn many times in the future and increasing the fecundity for all these reproductive seasons should be attractive.

The underlying mechanisms become clearer when the frequency of skipped spawning is considered relative to the age at which maturation takes place. The stochastic environment leads to inter-annual variations in age and size at maturation, and this variation overshadowed a distinct pattern in how skipped spawning was distributed relative to maturation. In the first 5-10 years after maturation, the frequency of skipped spawning oscillated: a larger proportion of individuals skipped spawning if their age since maturation was an odd number (Fig. 4B). This corresponds to a life-history strategy with a two-year reproductive cycle during which migration (in order to spawn) and feeding (in order to grow) alternate (see also Fig. 2, where energy was

allocated to growth when spawning was skipped at age 9 and 13).

The frequency of skipped spawning predicted by our model has consequences for stock–recruit relationships whenever the mature part of the population is used to predict recruitment. Spawning stock biomass–recruit (SSB–recruit) models often assume that all sexually mature biomass contributes equally to the population’s overall egg production. There may be, however, effects of age and experience that modify this, e.g. among first-time spawners (Kjesbu et al., 1996; Marshall et al., 1998; Trippel, 1998; Murawski et al., 2001). Skipped spawning will add on top of this, since its consequences are particularly pronounced for the abundant year classes following maturation. Technically, an inflated value of the SSB will be used inadvertently, since up to 30 % of mature individuals may skip spawning in an average year (Fig. 5).

Marshall et al. (1998) were not able to confirm the proportionality assumption between spawning stock biomass and egg production for the Northeast Arctic cod stock: egg production was significantly lower at low stock sizes than would be expected by proportionality. This Allee effect can be explained by age-specific reproductive rates. If low stock size results from high fishing mortality, the stocks’ age distribution will be shifted toward younger year classes. Laboratory experiments on Atlantic cod have shown that first-time spawners are reproductively inferior, exhibiting lower fecundity and producing fewer batches with smaller eggs, which in turn results in lower fertilization and hatching rates (Kjesbu et al., 1996; Marshall et al., 1998; Trippel, 1998). This means that not all SSB contributes equally to stock recruitment. First, in terms of fecundity, a younger SSB will spawn fewer eggs per biomass. This Allee effect will explain the observed drop in egg production at low stock sizes. Second, effects resulting from the quality of spawned eggs will be superimposed on this pattern through decreased juvenile survival (Murawski et al., 2001; Aanes, 2003).

The high frequencies of skipped spawning demonstrated in this study are expected to cause another Allee effect by contributing to age-dependent variation in reproductive rates. Skipped spawning was most frequent in the years just following maturation (Fig. 4). When stock size is low as a result of heavy exploitation, these young year classes will

contribute proportionally more to biomass in the mature population. Skipped spawning will therefore be more common in the population as a whole, and this will, in turn, create an Allee effect.

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