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The logic of skipped spawning in fish

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Abstract

That sexually mature fish skip reproduction has been documented in many species, especially in response to poor condition. We present results from an energy-allocation life-history model that shed light on the underlying logic of skipped spawning, based on the Northeast Arctic stock of Atlantic cod (*Gadus morhua*). The model predicts that skipped spawning is a regular phenomenon, with up to 30% of the sexually mature biomass skipping spawning. Spawning should be skipped if the expected future gain in reproductive output, discounted by survival, more than balances the expected reproductive success the current year. Skipped spawning was most common 1) among potential second-time spawners and 2) early in life, 3) when fishing mortality at the spawning grounds was high, 4) when fishing mortality at the feeding grounds was low, 5) when natural mortality was low, and 6) when the energetic and mortality costs associated with migration and spawning were high. Cod skipped spawning more often both when food availability was increased (opportunities for better growth) and decreased (too little energy for gonad development), and this pattern interacted with mortality rate. We conclude that skipped spawning may be more widespread than appreciated, and highlight potential consequences for the understanding of stock-recruitment relationships.

Keywords: Skipped spawning, life history theory, iteropary, reproductive effort, *Gadus morhua*.

Introduction

Observations suggest that 5-30% of mature birds (Cam and Monnat 2000) and as much as 20-50% of mature fish (Walsh et al. 1986; Schwalme and Chouinard 1999; Rideout et al. 2000) skip reproduction in some populations. These individuals have already undergone the physiological changes associated with maturation, and are potentially capable of spawning. Why should long-lived iteroparous individuals skip reproduction after they have reached sexual maturity?

To understand skipped spawning it is essential to appreciate how the life-long trade-off between reproduction, growth, and survival affects an organism's life history. These trade-offs involve differentially allocating available resources to growth, egg production, and energy storage for future actions. The onset of reproduction has to be timed relative to growth potential and survival probability, and any deviation from the optimal age and size at maturation can lead to great reductions in fitness (Roff 2002).

Skipped reproduction can be analysed on two separate time scales. On the ecological time scale, skipped spawning is due to phenotypic plasticity of life history strategies in response to physiological and ecological factors. For instance, it has been documented for several fish species that reproduction is skipped more often when individual condition is poor (e.g., Rijnsdorp 1990; Kjesbu et al. 1991; Rideout et al. 2000). In such cases, the time and energy required for reproduction is better channelled into growth and survival in order to increase future success rather than exacerbating already low energy reserves in order to spawn in the current year. This paper furthermore presents results that spawning is skipped more often also by young or small fish, and interprets this in a life history perspective.

Skipped spawning can also be analysed on the evolutionary time scale by assessing how – and to what degree – ecological factors may modify the optimal life-history strategy and its consequences on the schedule of reproductive events. Since skipped spawning results from the trade-off between current and future reproductive success, we would expect that factors such as mortality, food intake, and migration costs would influence the optimal life history, and thus 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 iteroparous (capable of repeated spawning), and the Northeast Arctic stock, which is the focus 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. Therefore, the potential benefit of reproduction has to be traded off against migration costs, possibilities for growth, and natural and fisheries-induced mortalities. The trade-offs are mediated mechanistically through allocation of ingested energy toward stores or growth; stored energy determines fecundity if reproduction occurs and survival in the event of low prey availability. In the present model, we focus on this allocation rule, which is dependent on age (in months, thus including seasonal variations), body length, state of the energy stores, and food availability. Each point on the resulting hyper-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 ecological scenarios. Patterns of growth and reproduction (i.e., life-histories) resulting from optimal allocation rules can then be predicted and analysed.

Using the outlined model, this paper first focuses on the physiological and ecological conditions determining skipped spawning on the ecological time scale, then turns to ecological factors that affect the evolution of life history strategies and skipped spawning. Finally, we discuss the results obtained in light of the existing biological knowledge on skipped spawning, before highlighting management-oriented issues, namely how exploitation can alter the level of skipped spawning and how skipped spawning may affect stock–recruit relationships.

Model description

Our study is based on a flexible life-history model describing a migratory fish (see Jørgensen and Fiksen, this issue, for a detailed description of the model). The model is parameterised 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. 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 utilised for metabolic or reproductive purposes. The model considers only females. Northeast Arctic cod males are generally more active at the spawning grounds, and may also suffer a higher mortality when gear that is selective for activity is used. Both effort and success is more related to behaviour for males, which were important reasons to exclude these from the model as data are lacking to parameterise relevant functions.

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 and spawning grounds.

Life-history strategies, as determined by the optimal allocation rules between growth and energy stores, were investigated as follows. Firstly, optimal allocation rules between growth and energy stores were calculated using dynamic programming (Houston and McNamara

1999; Clark and Mangel 2000) with 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. Expected lifetime egg production, discounted by survival probability until spawning, was used as a fitness criterion in the model. Dynamic programming optimizes a life history by maximizing such a fitness criterion backwards through ages, i.e., in our case finding for each age and state combination the allocation rule that maximises the future expected egg production discounted by survival probability starting at the highest age and sequentially progressing towards earlier ages. For each age and state combination, it was also checked whether spawning was preferable or not by calculating fitness for both the spawning and non-spawning option; the cod were then assumed to behave according to the option that maximized fitness. Secondly, the population dynamics of individuals following the previously determined optimal allocation rules were then simulated for 1000 years and subsequently analysed to derive consequences for life-history strategies, i.e., patterns of growth, maturation, and reproduction, with a particular focus on skipped spawning. For the purpose of conciseness, life-history strategies resulting from optimal allocation rules will be referred to as ‘optimal life-history strategies’ throughout the rest of the text.

Investigated fishing mortality scenarios

Three scenarios were used in our investigation of skipped spawning at the ecological time scale, corresponding to different combinations of fisheries mortalities calculated from historical and present data for the Northeast Arctic cod stock (O. R. Godø, Institute of Marine Research, P. O. Box 1870 Nordnes, 5817 Bergen). Values of annual mortality rates for the spawner fishery (F_S) in the Lofoten area that harvests only spawning individuals, and for the Barents Sea feeder fishery (F_F) that harvests all individuals, are given in brackets.

The first scenario is dominated by a spawner fishery that harvests only the mature part of the population, reflecting the stock's exploitation prior to 1930. The optimal energy allocation rule leads to fish maturing late (at 10.2 years, 117 cm, and 20.8 kg) (F_S = 0.2, F_F = 0.1).

The second scenario mimics the contemporary fishing pressure, where a feeder fishery, harvesting all individuals at the feeding grounds, is the strongest cause of fishing mortality. The corresponding optimal energy allocation rule leads to an early maturing population (at 4.9 years, 51 cm, and 1.6 kg) (F_S = 0.3, F_F = 0.6).

The third scenario uses interpolated fisheries mortalities between the two scenarios (20% of the way from late maturation towards early maturation). The corresponding optimal life history fits very well with growth data for the Northeast Arctic cod stock during the period 1978–2000, with maturation occurring at an intermediate age and size (at 8.1 years, 89 cm, and 8.9 kg) (F_S = 0.22, F_F = 0.20).

The natural mortality was $M = 0.25$ year^{-1} for all scenarios, and there was also an increased mortality during migration and spawning $M_S = 0.1$ year^{-1}.

Results

In this section, we first illustrate how energy allocation rules translate into individual life histories. In a second step, we focus on skipped spawning and its pattern with age and other physiological and ecological conditions. This analysis takes place on the ecological time scale, using life histories that are optimal for the three specific fishing mortality scenarios previously defined. In a third step, we then zoom out to the evolutionary time scale. Tweaking the ecological parameters of the model one at a time, we present how the resulting optimal life histories and related levels of skipped spawning would change. It appears from these first steps that skipped spawning is a frequent phenomenon over the wide range of parameters tested, with up to 30% of the mature population and up to 60% of potential repeat spawners skipping spawning. In light of these general results, we finally investigate the significance of skipped spawning for effective spawning stock biomass and stock–recruit relationships.

Factors affecting skipped spawning at the ecological time scale

Energy allocation rules and individual life histories

The model has been described in detail by Jørgensen and Fiksen (this issue). An example of how allocation of energy between growth and reproduction shapes the life history of one individual cod that skipped spawning several times throughout its life is presented graphically in Figure 1 (the example is from our third scenario). Briefly, growth in terms of length was nearly linear with time early in life (Fig. 1a) when most of the energy was allocated to growth (Fig. 1b; values close to 0). Approximately one year prior to the first spawning, ingested energy was diverted to stores (values close to 1 in Fig. 1b) and this energy was spawned as eggs during the first spawning season (Fig. 1d). After first spawning, the individual in this illustration gave priority to growth for another 5-6 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. That fecundity increased with as much as 40% between these two spawning events is due to the strategy of skipping spawning at age 9 and giving priority to a larger body size. On average, fecundity increased 36% every time this fish skipped spawning (at ages 9, 11, 13, 16, and 18).

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Trends in skipped spawning in relation to age

Spawning was skipped with a stable frequency of around 10% in the early maturing population, and there was no trend with age (Fig. 2a). 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.

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The pattern becomes even clearer when the frequency of skipped spawning is plotted against the number of years since maturation (Fig. 2b). 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 showed the highest frequency of skipped spawning, with as much as 90% skipped spawning in the late-maturing population (scenario 1, grey curve). As the number of years after maturation increased, the frequency of skipped spawning in the early-maturing population (scenario 3) stabilised quickly at the expected level of 10%. For scenarios 1 and 2, the frequency of skipped spawning showed dampened oscillations, i.e., a pattern where spawning was skipped more often every second year, and gradually becoming more uniform with age. The drop at old ages is a terminal effect of the model, where individuals die at the maximum age of 25 years. It can be interpreted as a very strong senescence effect that reduces the value of future reproductions. A gradually increasing mortality rate at high ages would soften this effect, but the overall picture of higher investment in reproduction towards life's end due to senescence would remain. The curves shown in the figure stop when no more individuals were alive.

Effects of condition and food intake on fecundity and skipped spawning

The optimised life-history strategies were flexible enough to respond to variations in food availability. Population fecundity increased when food was abundant; the direct effect on fecundity is mediated through changes in condition factor, where more stored energy allows for more eggs being spawned (Jørgensen and Fiksen this issue). An indirect effect could also be observed: skipped spawning became less frequent as the average condition factor of the mature population increased, thus explaining a substantial part of the population level fecundity increase with food availability (Fig. 3a). Smaller cod needed full energy stores in order to spawn (Fig. 3b), whereas larger cod spawned also when less energy was stored. The stratification of points is due to the discretisation of the feeding environment in the model (Fig. 3b; points not conforming to this pattern are first-time spawners or correspond to spawning events that take place after spawning has been skipped).

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Life-history evolution in light of ecological conditions

The following results present optimal life histories (i.e., the life history strategy supposedly favoured by natural selection) under various ecological conditions. For each parameter combination, the optimal life-long pattern of energy allocation was found, and the resulting life history strategies were determined by simulating the corresponding population dynamics. Each point on the surfaces in Figures 4-6 thus represents the life history that is realised at the predicted evolutionary end-point under that specific combination of parameters.

Variation in fishing mortalities

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Mortalities that affected only parts of the population had a strong impact on the optimal life-history strategy. Mortality on the feeding grounds had a much more pronounced effect than mortality on the spawning grounds (Fig. 4). Characteristically, the two types of mortality also had mostly opposite effects (Fig. 4b-d). The proportion of potential repeat spawners that skipped spawning depended primarily on the feeder-fishery mortality (Fig. 4b). The seemingly contradicting picture in Figure 4a is due to demographic reasons, since first-time spawners make up a larger fraction in populations where sexually mature individuals are strongly harvested. As a result, there would be a smaller proportion of repeat spawners, and consequently also a smaller proportion of mature fish that skipped spawning. Age and length at maturation decreased strongly with increasing feeder-fishery mortality (Fig. 4c-d). Under high mortalities on the feeding grounds, the optimal life history implied maturation at 3-5 years of age and at lengths around 30-50 cm. When fishing was confined to the spawning grounds, mean age and size at maturation were 12-15 years and 150-180 cm, respectively.

Variation in mean food availability

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Skipped spawning showed a complex relationship when food availability was varied (the left-to-right axis in Fig. 5). This is due to two effects working in opposite directions. When food intake was increased (relative food intake above 1.0 in Fig. 5a-d), more energy was available for growth, fish would be larger at the same age and could mature earlier and at a larger size (Fig. 5c-d). There would be more years when energy stores could be filled to sustain reproduction, so the increased occurrence of skipped spawning must be due to favourable growth conditions and the advantages a larger size has on fecundity (Fig. 5a-b). This is an effect of the increased value of future reproduction. On the other hand, when food intake was decreased, (relative food intake below 1.0 in Fig. 5a-d), growth would be slower so that maturation would take place at a smaller size, and there would not be food or time to fill energy stores sufficiently in all years. As a consequence, skipped spawning would again increase. Maturation would still take place earlier (Fig. 5c), presumably so that individuals can spread the chances of experiencing high enough food availability to sustain migration and spawning over more years. This is probably an effect of the uncertain value of reproduction in any given year.

Variation in natural mortality rate

Varying the natural mortality rate markedly affected both skipped spawning and maturation dynamics (the back-to-front axis in Fig. 5). The general trend was that increasing natural mortality rate favoured early reproduction, resulting in early maturation at correspondingly smaller size, as well as less frequent skipping of spawning. The effect of natural mortality is similar but not identical to the effect of the feeder fisheries mortality; both apply to immature and mature fish at the feeding grounds, but the natural mortality also applies to mature fish at the spawning grounds. Natural mortality is thus not stage-selective in the same way the feeder fisheries mortality is.

The model, as would be expected from the central role of mortality in life history evolution, is sensitive to the exact numerical estimate of this parameter. For the purpose of studying skipped spawning, however, natural mortality changed the overall level but not so much the general or age-related trends.

Variation in migration costs

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Not surprisingly, increasing the energetic cost of migration led to a linearly increasing number of skipped spawnings, and the age and length at maturation also increased linearly (Fig. 6a-d). This was due to a higher energetic cost for participating in reproduction, favouring a larger size and fuller energy stores. Increasing the level of mortality associated with spawning and migration had similar but less pronounced effects (Fig. 6a-d).

Effects of skipped spawning on spawning stock biomass

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With earlier maturation, fewer potential repeat spawners would skip, but a larger proportion of the sexually mature biomass would be first-time spawners. The proportion of the sexually mature biomass that was made up of repeat spawners was more or less constant between the three scenarios (Fig. 7).

Discussion

Every year, cod in the Barents Sea are confronted with the choice of whether or not to migrate towards the spawning grounds. In principle, the decision rule is simple: if an individual skips spawning, the loss in fecundity this year has to be outweighed by the chances of increased egg production in the future, discounted by the survival probability up to that point (Houston and McNamara 1999; Clark and Mangel 2000; Roff 2002). Skipping spawning will thus be beneficial if it has a sufficiently strong effect of increasing future fecundity or reducing mortality. Our study has shown, however, that applying this rule is not straightforward due to the multiplicity of physiological and ecological factors affecting this balance. To improve our understanding, we will in the following provide some background on 1) the evidence of skipped spawning in nature and 2) the individual plasticity in female cod reproduction as the physiological basis for skipped spawning. Then, we will examine 3) the causes of skipped spawning in relationship with physiological and ecological conditions, and

4) how evolution resulting from alterations in ecological conditions may affect skipped spawning. Finally, we will discuss 5) how skipped spawning may change on different time scales as a result of human exploitation, and 6) how skipped spawning may bias estimates of stock-recruit relationships.

Our model allows for plasticity in energy allocation in response to age, size, energy stores and food availability, and thus for flexible life-history strategies. Based on the growth and maturation patterns presented in this paper and in Jørgensen and Fiksen (this issue), we conclude that our model's ability to capture complex growth phenomena and trade-offs, together with its flexible response to variations in various conditions within a lifetime, make it suitable for interpreting complex life-history phenomena, such as skipped spawning.

Evidence of skipped spawning in fish

Bull and Shine (1979) reviewed skipped reproduction among iteroparous animals with a focus on amphibians. Skipped reproduction was most often linked to migration, brooding, or livebearing, and was most common among females. In fish, various studies have identified skipped spawning: Greenland halibut (*Reinhardtius hippoglossoides*; Fedorov 1971; Walsh and Bowering 1981 found reabsorption of oocytes among females attempting to mature for the first time, but no evidence for later skipping), sole (*Solea solea*; Ramsay and Witthames 1996), long rough dab (*Hippoglossoides platessoides*; Bagenal 1957), Norway pout (*Trisopterus esmarkii*; Gokhale 1957), winter flounder (*Pleuronectes americanus*; Burton 1991, 1994), carp (*Cyprinus carpio*; Ivanov 1971), chub (*Leuciscus cephalus*; Fredrich et al. 2003), perch (*Perca fluviatilis*; Holmgren 2003), hake (*Merluccius merluccius*; Hickling 1930), and herring (*Clupea harengus*; Engelhard and Heino 2004). For plaice (*Pleuronectes platessa*), skipped spawning was observed in the laboratory (Rijnsdorp 1990) but not in a long-term data set from the North Sea (Rijnsdorp 1989).

For Atlantic cod, the discussions of skipped spawning began in the 1930s, with the early descriptions portraying a rather contradictory picture. Summarising Russian surveys from the Barents Sea, Messiatzeva (1932) stated that ‘no more than 10-15% of the fish migrate annually to spawn. The cod does not spawn every year, but apparently only 2 or 3 times in the course of its whole existence’. The background data needed to support this statement were not given and have, to our knowledge, not been published. Sivertsen (1935) refuted these claims, suggesting that the problem stemmed from the inclusion of immature age classes, which naturally would explain the low participation in spawning. References were also made in the older literature to adolescent cod, or ‘gjelltorsk’ (which means sterile cod) – large cod with seemingly underdeveloped gonads. Iversen (1934) recorded the gonadal status for cod larger than 70 cm in the Barents Sea. In one location near Bear Island, the proportion of gjelltorsk increased from around 10% in December (prior to the spawning migration) to around 55% in February (when spawning cod should be in Lofoten further south). At some locations, more than 80% of cod larger than 70 cm were recorded as gjelltorsk in February (Iversen 1934, their Fig. 8). It seems plausible that at least some of these cod were skipping spawning. At the same time, Rollefsen (1933) argued that these cod were only late-maturing individuals that had not yet reached sexual maturity. Since the 1930s, the issue of skipped reproduction in cod has received little and scattered attention, and it is not a part of managerial considerations today.

In our model, 2-35% of the mature population skipped spawning (numbers taken from Fig. 4a). 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 on average 32% of potential cod spawners on the Flemish Cap skipped spawning in any given year between 1978 and 1985 (Walsh et al. 1986). Growth rates were increasing in the same period (Walsh et al. 1986), meaning that food shortage cannot explain the frequent skipping. Histological examinations of trawlsampled cod from the Barents Sea just prior to the spawning migration found that up to 57% of potential repeat spawners skipped spawning (Oganesyan 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.

Phenotypic plasticity and the physiology of skipped spawning

For fish, the physiology and histology of skipped spawning were recently reviewed by Rideout et al. (2005). They argued that methodological problems in identifying the post-mature non-reproductive state have lead fisheries science to underestimate its frequency, and thus also its importance for recruitment. Especially, the timing of sampling is important, because signals that may identify skipped spawning are weak or non-existing during parts of the annual cycle.

Atlantic cod females initiate gonad development up to seven months prior to spawning (Burton et al. 1997). During that period, impaired or non-improving feeding conditions may render reproduction less attractive; accordingly, energy temporarily invested in gonads can later be resorbed through atresia (Kjesbu et al. 1991). In laboratory experiments on Atlantic cod, females in poor condition either underwent atresia, or skipped gonad development altogether (Kjesbu et al. 1991; Burton et al. 1997). In flatfish, experimental food deprivation induced skipped spawning (Burton and Idler 1987; Rijnsdorp 1990).

From a life history perspective, there is at the same time 1) a distinct disadvantage from having a small body size and 2) a clear advantage from being bigger. 1) Small fish have higher weight-specific metabolic rates and swim less economically (Schmidt-Nielsen 1984); they thus have a higher energetic threshold for participating in migration and spawning, and a lower share of the energy invested in reproduction is actually used to produce gametes. 2) Fecundity in fish is roughly proportional to body mass, so a 25% increase in length will double fecundity. Add these two effects on top of each other, and it becomes clear that, for a small migrating fish, growing to a larger size can increase future fecundity to a degree that easily outweighs its current reproductive potential.

It is here worth mentioning that our model does not distinguish between the two physiological mechanisms underlying skipped spawning, that is atresia and skipped gonad development. In the model, skipped spawning occurs when an individual skips a spawning migration after their first successful reproduction. In reality, this will cover both atresia and cod that skip gonad maturation altogether.

The interpretation of poor individual condition at the beginning of a spawning season is ambiguous, both in the model and in nature: it can be either a cause for or an effect of skipped spawning. If, for some reason resulting from an individual’s life-history strategy, spawning should be skipped in a certain year, the best option may very well be to give priority to somatic growth and keep energy reserves at a moderate level. This would be recorded as a low condition factor, but the poor condition would be an effect of skipped spawning, and thus hard to separate from poor condition stemming from low food availability which could lead to skipped spawning.

Causes of skipped spawning in relation to physiological and ecological conditions

In the published observations of skipped spawning that linked the phenomenon to ecology or life-history, poor feeding conditions was most often identified or suggested as the likely cause (e.g., Burton and Idler 1987; Rijnsdorp 1990; Rideout et al. 2000). On the basis of the potential for phenotypic plasticity highlighted above, we would expect that skipped spawning would be more frequent in our model when an unfavourable feeding environment had led to poor individual condition, a concept supported by our model results (Fig. 3a). Furthermore, we found that it was favourable for larger cod to spawn even when their energy stores were not full (Fig. 3b), reflecting the benefits that come with a larger body size. The two axes on Figure 3b represent length and energy stores, which were dimensions also in the allocation rule; the area in Figure 3b for which grey and black circles overlap therefore indicate when the two additional dimensions, namely current food availability and age, were necessary to fine-tune the migration and allocation pattern.

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. If low food availability 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 case where subgroups of the mature population utilise different and unlinked food resources; this might apply for Northeast Arctic cod but is not addressed by this study). Poor condition alone probably explains the frequency of skipped spawning in our second scenario (imitating the evolutionary end-point of contemporary fishing patterns; the high mortality results in an early-maturing population). Spawning was skipped at a frequency of 10%, and did not show any variation with age. This life-history strategy is geared to value current reproduction much higher than potential future spawnings. Only when individual condition was too low to sustain migration, or when the stored energy could offer only a very limited egg production, was the spawning opportunity totally abandoned.

Skipped spawning occurred more frequently in our first and second scenarios, where mortality rates were lower. There was also an evident trend with age: skipped spawning was most common in the years following maturation. Similar results have been found in wild cod, where skipped spawning was most common for cod of small size (Oganesyan 1993). That skipped spawning got less common with age reflects a temporal trade-off, where early growth and later reproduction are favoured. Young cod can potentially spawn many times in the future, and increasing the fecundity for all these reproductive seasons should be attractive. The decision of whether to spawn or not needs only compare expectations for the current reproductive season with the expected future benefit that comes from a larger size if spawning is skipped. An individual’s growth trajectory can thus be roughly divided into three phases: first, only somatic growth takes place up to the age at sexual maturation; second, growth is balanced with reproduction during some years following maturation (mechanistically, growth takes precedence when spawning migrations are skipped more frequently); and third, after that reproduction receives the full focus of energy allocation and the frequency of skipped spawning stabilises.

The link between skipped spawning and growth has also been demonstrated in perch (Holmgren 2003); to our knowledge the only work on fish that demonstrates a clear life-history trade-off between reproduction and growth after sexual maturation. By back-calculating individual growth from otolith patterns, Holmgren (2003) found that growth was highest in the years when spawning was skipped. This indicates that skipped spawning was not a response to poor food availability, but that spawning could be skipped to redistribute energy towards accelerated growth.

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. 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. With age, these oscillations were dampened. The stochastic environment made this age pattern more diffuse with time, which partly explains the dampening. In short, there seems to be two superimposed effects that together can explain the observed age pattern: indeterminate growth causes skipped spawning to be more frequent during the first years after maturation, and a two-year reproductive cycle creates the oscillating pattern.

Potential evolutionary consequences of altered ecological conditions on skipped spawning

A long and energy-costly migration makes skipped spawning an attractive option, because the saved energy can, if invested in growth, lead to a large increase in future fecundity. As we can observe from the model, the frequency of skipped spawning increases when the energetic costs of migration are higher. The situation is less clear when it comes to the long-term mean food intake, and we can formulate two competing hypotheses. First, we would expect that the potential for a high food intake at the feeding grounds would favour skipped spawning: then the expected gain in future fecundity will rise, making growth an attractive way to spend time and energy. A detail along these lines not included in the model is that cod is normally feasting on migrating capelin on its way toward its spawning areas on the Finnmark coast in northern Norway. This migration overlaps in time with the spawning period of cod, and the concurrent abundance of highly nutritious capelin would thus favour skipped spawning because growth conditions are especially generous this time of year. Second, we might also hypothesise that a lower food intake would result in fewer years with full replenishment of the energy stores; also resulting in more skipped spawning but for other reasons. The results of our model are influenced by both these hypotheses, as can be seen in the increasing occurrence of skipped spawning both when food intake was reduced and increased.

Variations in mortality can affect both phenotypic plasticity (through increasing growth rates in response to relieved density dependence) and evolutionary adaptations (since the balance between current and future reproduction has to be rescaled depending on the expected survival probability). Accordingly, there are ongoing discussions about how to best separate observed life-history changes in response to altered fishing pressure into those accounted for by plasticity and those due to genetic change (Heino and Godø 2002; Heino et al. 2002; Olsen et al. 2004). Because there is no density-dependent growth in our model, we discuss the effects of mortality here in this section on evolutionary change.

Increased natural mortality will favour earlier maturation and less skipped spawning, because future reproductive effort will be discounted more heavily. The pattern becomes more complicated, however, when mortalities affect only specific parts of the population, as is the case in the stage-selective fisheries harvesting the Northeast Arctic cod stock (Law and Grey 1989). Low mortality at the feeding grounds compared to the spawning grounds will, for instance, create a mortality refuge for fish that choose to grow rather than spawn and will favour skipping. The model's prediction of late maturation at a large size resulting from this setting corresponds well with observed maturation patterns for the Northeast Arctic cod stock from the beginning of the 20th century (Jørgensen 1990). Since trawling started in the Barents Sea around 1930, annual harvest has been high, with the total harvest from the Northeast Arctic cod stock exceeding one million metric tons per year in several years between 1950 and 1980. With such a high mortality at the feeding grounds, a late-maturing cod will have a low probability of reproducing at all, which will, as our model shows, lead to evolution towards earlier maturation (Law and Grey 1989) and a diminished frequency of skipped spawning.

Consequences of altered exploitation

Our model predicts that exploitation-induced changes in skipped spawning occur on two time scales. On the ecological time scale, exploitation will shift the age distribution of the stock towards younger year classes. The frequency of skipped spawning will therefore increase in the population as a whole, since it is most frequent during the first years after maturation. This is a response at the level of population dynamics (corresponding to a move to the left on the continuous black or grey curve in Fig. 2). On the evolutionary time scale, a high fishing mortality creates a selection pressure towards earlier maturation. Skipped spawning will then become less common as the stock adapts. This is an evolutionary response to high exploitation rates (a move from the grey to the black to the dotted curve in Fig. 2). Thus, our model suggests that high fishing pressures will lead to contrasting short-term and long-term effects of exploitation on skipped spawning.

Implications for estimating and using stock–recruit relationships

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 (Jørgensen and Fiksen this issue). Spawning stock biomass–recruit (SSB–recruit) models commonly 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; 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. Moreover, cohorts are affected differently, meaning that cohort abundance and growth history affect skipped spawning in intricate manners. Understanding how these factors influence the part of the population that is actually spawning requires further research; especially observations to see to what degree the predictions from modelling attempts such as the one presented here apply in nature.

To prevent these distortions in estimated SSB, some measure of individual condition (e.g., lipid stores in the liver) could be used, providing a better estimate of the part of the mature population that has actually prepared for spawning. This could improve predictions for recruitment (Marshall et al. 1999). However, a possible pitfall for such a method is the bimodality in gonad or liver weights that can arise when part of a cohort skips spawning (Schwalme and Chouinard 1999). Different population-level measures were tested as predictors of the stock's total egg production using this model (Jørgensen and Fiksen this issue). The population's total liver weight was a good predictor of total egg production, although using the biomass of the part of the population actually engaged in spawning was an even better predictor.

In conclusion, using the age distribution of a stock can increase the explanatory power in both SSB–egg production and SSB–recruit relationships. For such improvements to be realised, the age-specific rates of reproductive success stemming from fecundity, breeding pattern, and egg quality have to be included in predictive models – as well as the age-specific frequencies of skipped spawning. This study supports the view that skipped spawning is such a common phenomenon that it can hardly be neglected in models addressing recruitment. For example, the reproductive potential of exploited cod stocks is often heavily dependent on one or a few strong year-classes. However, a large proportion of such a strong year-class will reach sexual maturity in the same year, and thus the same large proportion will be likely to skip spawning the following year. Understanding such swings in reproductive potential can be particularly important during recovery periods, when recruitment is crucial. Further theoretical, experimental, and field research is clearly needed to fully understand the mechanisms regulating the frequency of skipped spawning, and to further assess its implications for individual cod and cod stocks as a whole.

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Figure captions

Figure 1. Growth trajectory and physiology for one individual female cod (*Gadus morhua*) from a life history model for the Northeast Arctic cod, simulated in a stochastic environment. The *x*-axis shows age and is common for all the graphs. (a) Length (black line, left axis) and weight (grey line, right axis). (b) Allocation of available energy between energy stores (high values) and growth (low values). 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 attainable at that length; these increase because body mass is proportional to length to the power of 3.065. (d) Number of eggs spawned (in millions). In preparation of sexual maturation, this individual cod directed all its energy was towards stores approximately one year prior to first spawning.

Figure 2. The proportion of potential repeat spawners that skip spawning (by biomass) for Northeast Arctic cod (*Gadus morhua*). (a) Plotted by age (age class). (b) Plotted against the number of years since maturation. In this representation, the variation stemming from differences in age at maturation is removed. The three curves represent different combinations of spawner (F_S) and feeder (F_F) fishery mortalities giving rise to populations with different maturation strategies: a late-maturing population ($F_S = 0.2$, $F_F = 0.1$; grey solid line), an early-maturing population ($F_S = 0.3$, $F_F = 0.6$; dotted black line), and a population described by a set of parameters providing good fit to growth data for the present Northeast Arctic cod stock, implying intermediate maturation ($F_S = 0.22$, $F_F = 0.20$; black solid line). Each population was simulated for 1000 years in a stochastic environment.

Figure 3. (a) The relationship between average condition in the mature part of the population in January and the frequency of potential repeat spawners that skip spawning. (b) The effect of stored energy on skipped spawning. The amount of stored energy, expressed as a fraction of the maximum storage, is plotted against length for all mature individuals. Open

black circles denote spawning individuals; filled grey circles indicate individuals that skipped spawning. The results are from a simulation of population dynamics for 1000 years.

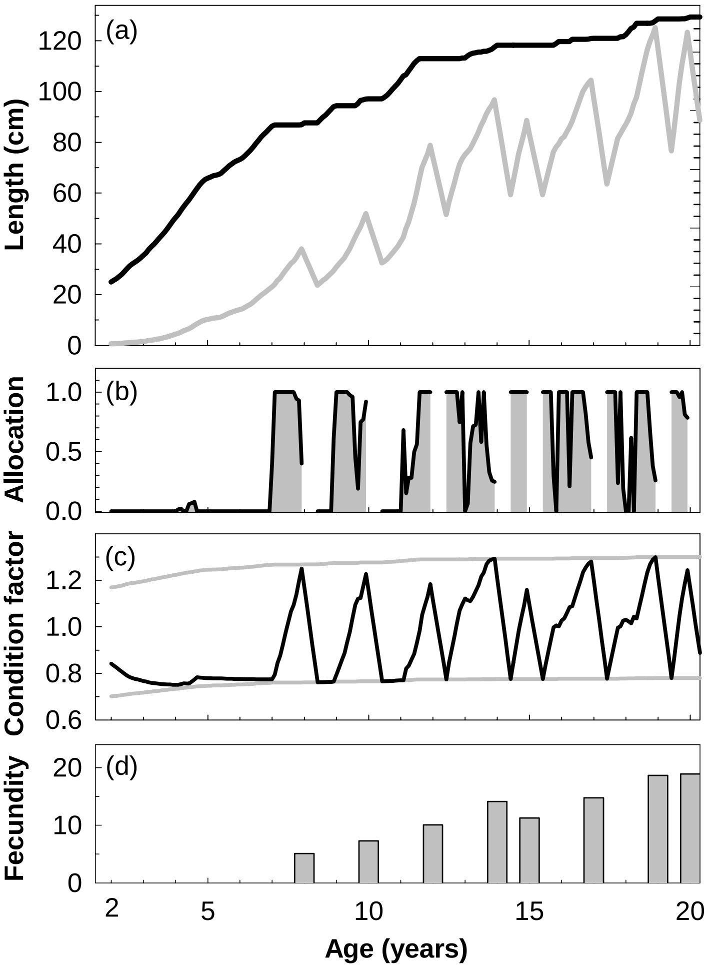
Figure 4. Effects of varying mortality levels in the spawner and feeder fishery (year^{-1}). At high mortalities in the feeder fishery the population went extinct; this is visible as the area where the values drop to 0. (a) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (b) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (c) Mean age at maturation (years). (d) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that specific parameter combination.

Figure 5. Effects of varying mean food availability (relative to the intermediate maturation scenario) and natural mortality (year^{-1}). (a) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (b) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (c) Mean age at maturation (years). (d) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that specific parameter combination.

Figure 6. Effects of the costs of migration in terms of energy and mortality rate on skipped spawning and maturation. The energy required for migration was varied within ±50% of the level used for the intermediate maturation scenario; the additional mortality during the spawning migration was varied within ±100%. (a) Mean proportion of spawning stock biomass (defined as all sexually mature individuals) that skips spawning. (b) The mean proportion of skipped spawning among potential repeat spawners (by biomass). (c) Mean age at maturation (years). (d) Mean length at maturation (cm). For every grid point, a population was simulated for 1000 years with an energy allocation strategy that was optimised for that

specific parameter combination.

Figure 7. The proportion of sexually mature biomass that comprises first-time spawners (black), repeat spawners (grey), and that skips spawning (white) for optimal life histories under the three combinations of feeder (F_F) and spawner (F_S) fishery mortalities considered. The values are mean over 1000 years of population simulation.


(a)
Length (cm)
0
20
40
60
80
100
120
Weight (kg)
0
5
10
15
20
25
(b)
Allocation
0.0
0.5
1.0
(c)
Condition factor
0.6
0.8
1.0
1.2
(d)
Fecundity
0
10
20
2
5
10
15
20
Age (years)

685

Figure 1.

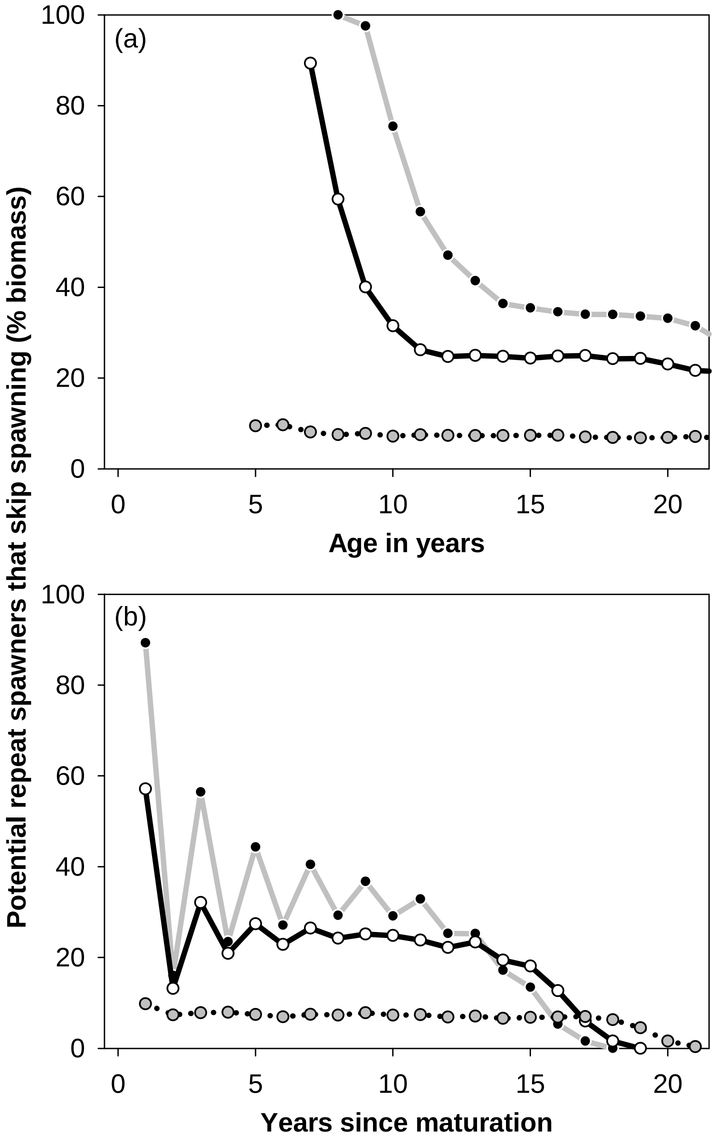

(a)
(b)
Potential repeat spawners that skip spawning (% biomass)
Age in years
Years since maturation
0
20
40
60
80
100
0
5
10
15
20

Figure 2.

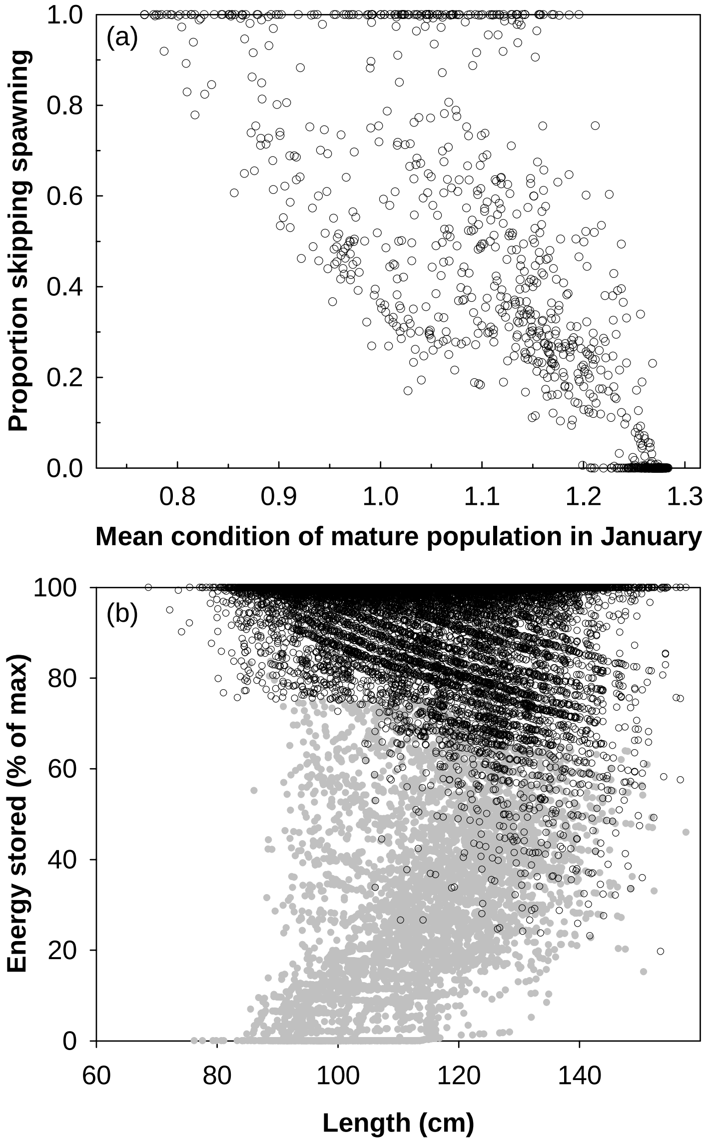

(a)
Proportion skipping spawning
1.0
0.8
0.6
0.4
0.2
0.0
0.8
0.9
1.0
1.1
1.2
1.3
Mean condition of mature population in January
(b)
Energy stored (% of max)
100
80
60
40
20
0
60
80
100
120
140
Length (cm)

Figure 3.

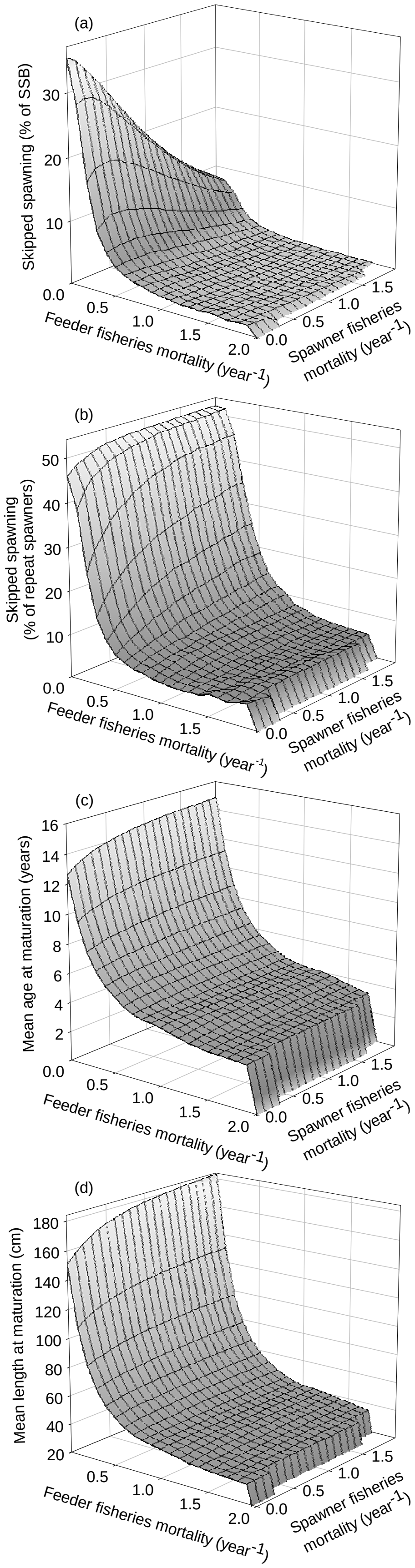
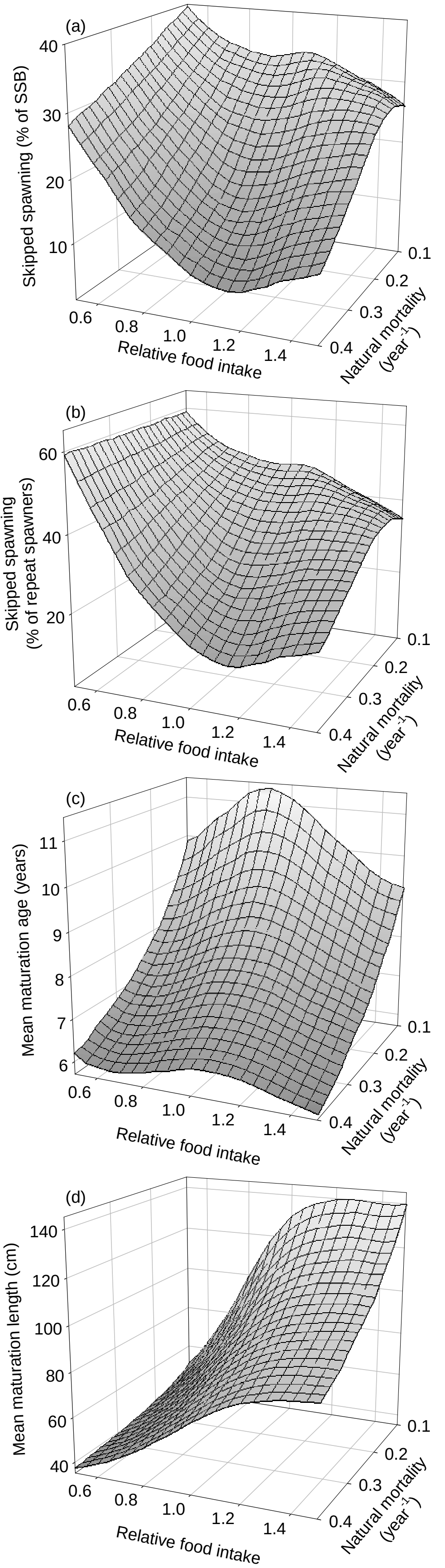

(a)
Skipped spawning (% of SSB)
0.0
10
20
30
0.5
1.0
1.5
2.0
Feeder fisheries mortality (year-1)
0.0
0.5
1.0
1.5
Spawner fisheries mortality (year-1)
(b)
Skipped spawning (% of repeat spawners)
0.0
10
20
30
40
50
0.5
1.0
1.5
Feeder fisheries mortality (year-1)
0.0
0.5
1.0
1.5
Spawner fisheries mortality (year-1)
(c)
Mean age at maturation (years)
0.0
2
4
6
8
10
12
14
16
0.5
1.0
1.5
2.0
Feeder fisheries mortality (year-1)
0.0
0.5
1.0
1.5
Spawner fisheries mortality (year-1)
(d)
Mean length at maturation (cm)
20
40
60
80
100
120
140
160
180
0.5
1.0
1.5
2.0
Feeder fisheries mortality (year-1)
0.0
0.5
1.0
1.5
Spawner fisheries mortality (year-1)

Figure 4.


(a)
Skipped spawning (% of SSB)
40
30
20
10
0.6
0.8
1.0
1.2
1.4
Relative food intake
0.1
0.2
0.3
0.4
Natural mortality
(year^{-1})
(b)
Skipped spawning
(% of repeat spawners)
60
40
20
0.6
0.8
1.0
1.2
1.4
Relative food intake
0.1
0.2
0.3
0.4
Natural mortality
(year^{-1})
(c)
Mean maturation age (years)
11
10
9
8
7
6
0.6
0.8
1.0
1.2
1.4
Relative food intake
0.1
0.2
0.3
0.4
Natural mortality
(year^{-1})
(d)
Mean maturation length (cm)
140
120
100
80
60
40
0.6
0.8
1.0
1.2
1.4
Relative food intake
0.1
0.2
0.3
0.4
Natural mortality
(year^{-1})

Jørgensen et al. The logic of skipped spawning in fish.

Figure 5.

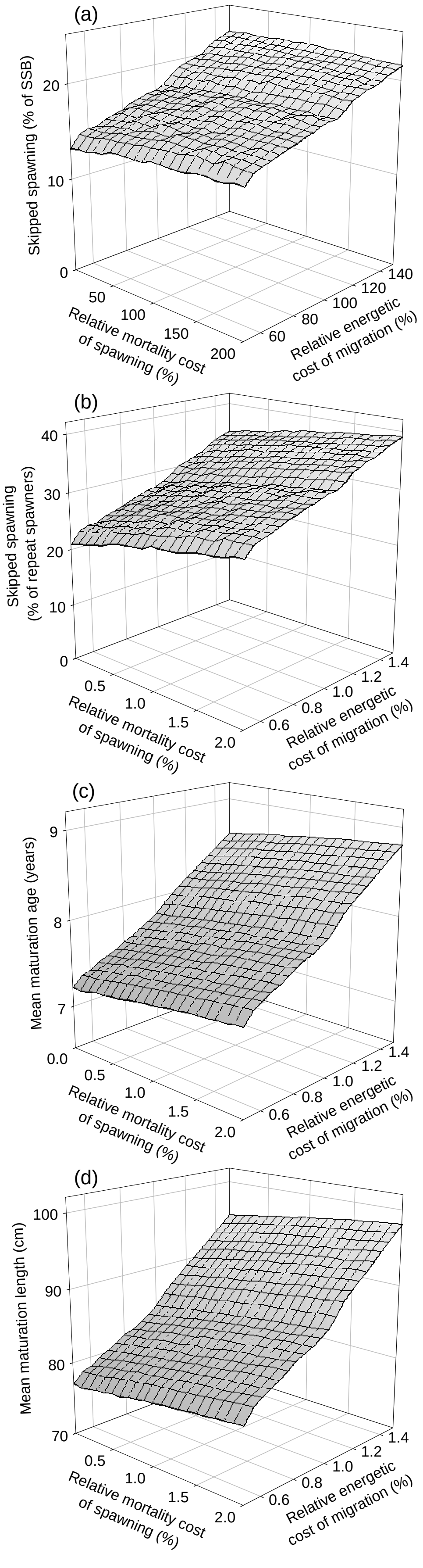

(a)
Skipped spawning (% of SSB)
0
10
20
50
100
150
200
Relative mortality cost of spawning (%)
60
80
100
120
140
Relative energetic cost of migration (%)
(b)
Skipped spawning (% of repeat spawners)
0
10
20
30
40
0.5
1.0
1.5
2.0
Relative mortality cost of spawning (%)
0.6
0.8
1.0
1.2
1.4
Relative energetic cost of migration (%)
(c)
Mean maturation age (years)
0.0
7
8
9
0.5
1.0
1.5
2.0
Relative mortality cost of spawning (%)
0.6
0.8
1.0
1.2
1.4
Relative energetic cost of migration (%)
(d)
Mean maturation length (cm)
70
80
90
100
0.5
1.0
1.5
2.0
Relative mortality cost of spawning (%)
0.6
0.8
1.0
1.2
1.4
Relative energetic cost of migration (%)

Figure 6.

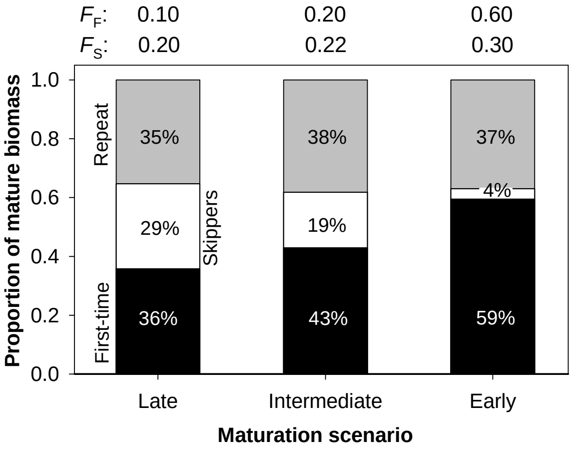

F_F: 0.10 0.20 0.60
F_S: 0.20 0.22 0.30
Proportion of mature biomass
1.0
0.8
0.6
0.4
0.2
0.0
Repeat
Skippers
First-time
35%
29%
36%
38%
19%
43%
37%
4%
59%
Late
Intermediate
Early
Maturation scenario

Figure 7.