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The Logic of Skipped Spawning in Fish

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The logic of skipped spawning in fish

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8 **Abstract**

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

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

27 **Introduction**

28 Observations suggest that 5-30% of mature birds (Cam and Monnat 2000) and as much as
29 20-50% of mature fish (Walsh et al. 1986; Schwalme and Chouinard 1999; Rideout et al.
30 2000) skip reproduction in some populations. These individuals have already undergone the
31 physiological changes associated with maturation, and are potentially capable of spawning.
32 Why should long-lived iteroparous individuals skip reproduction after they have reached
33 sexual maturity?

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

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

49 Skipped spawning can also be analysed on the evolutionary time scale by assessing how –
50 and to what degree – ecological factors may modify the optimal life-history strategy and its
51 consequences on the schedule of reproductive events. Since skipped spawning results from

52 the trade-off between current and future reproductive success, we would expect that factors
53 such as mortality, food intake, and migration costs would influence the optimal life history,
54 and thus the frequency and pattern of skipped spawning.

55 This study explores reproductive strategies in Atlantic cod (*Gadus morhua*) using a
56 flexible life-history model. Cod is iteroparous (capable of repeated spawning), and the
57 Northeast Arctic stock, which is the focus of this study, performs annual migrations from the
58 feeding grounds in the Barents Sea to spawning grounds off Lofoten. The annual migrations
59 entail a direct cost in terms of energy and time. Therefore, the potential benefit of
60 reproduction has to be traded off against migration costs, possibilities for growth, and natural
61 and fisheries-induced mortalities. The trade-offs are mediated mechanistically through
62 allocation of ingested energy toward stores or growth; stored energy determines fecundity if
63 reproduction occurs and survival in the event of low prey availability. In the present model,
64 we focus on this allocation rule, which is dependent on age (in months, thus including
65 seasonal variations), body length, state of the energy stores, and food availability. Each point
66 on the resulting hyper-surface that describes the allocation rule is independent, so that the
67 allocation rule is not artificially constrained but allows any shape to emerge evolutionarily.
68 The optimal allocation rule, which is also the allocation rule supposedly favoured by natural
69 selection, can then be found for various ecological scenarios. Patterns of growth and
70 reproduction (i.e., life-histories) resulting from optimal allocation rules can then be predicted
71 and analysed.

72 Using the outlined model, this paper first focuses on the physiological and ecological
73 conditions determining skipped spawning on the ecological time scale, then turns to
74 ecological factors that affect the evolution of life history strategies and skipped spawning.
75 Finally, we discuss the results obtained in light of the existing biological knowledge on
76 skipped spawning, before highlighting management-oriented issues, namely how exploitation

77 can alter the level of skipped spawning and how skipped spawning may affect stock–recruit
78 relationships.

79 **Model description**

80 Our study is based on a flexible life-history model describing a migratory fish (see
81 Jørgensen and Fiksen, this issue, for a detailed description of the model). The model is
82 parameterised for the Northeast Arctic cod stock and fits well with observed growth in natural
83 stocks experiencing variable environmental conditions. A key assumption of the model is that
84 energy, ingested in a stochastic feeding environment, can be allocated either to growth or to
85 storage. Growth is irreversible and increases somatic structures together with a minimum
86 amount of muscle mass. Energy stores (lipids in the liver and increased white muscle mass)
87 grow reversibly between a minimum and maximum condition factor, and the stored energy
88 can be utilised for metabolic or reproductive purposes. The model considers only females.
89 Northeast Arctic cod males are generally more active at the spawning grounds, and may also
90 suffer a higher mortality when gear that is selective for activity is used. Both effort and
91 success is more related to behaviour for males, which were important reasons to exclude these
92 from the model as data are lacking to parameterise relevant functions.

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

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

102 1999; Clark and Mangel 2000) with four state variables: age (in months, thus including
103 seasonal variations), stored energy (measured on a relative scale between 0 and 1), body
104 length (cm), and food availability. Expected lifetime egg production, discounted by survival
105 probability until spawning, was used as a fitness criterion in the model. Dynamic
106 programming optimizes a life history by maximizing such a fitness criterion backwards
107 through ages, i.e., in our case finding for each age and state combination the allocation rule
108 that maximises the future expected egg production discounted by survival probability starting
109 at the highest age and sequentially progressing towards earlier ages. For each age and state
110 combination, it was also checked whether spawning was preferable or not by calculating
111 fitness for both the spawning and non-spawning option; the cod were then assumed to behave
112 according to the option that maximized fitness. Secondly, the population dynamics of
113 individuals following the previously determined optimal allocation rules were then simulated
114 for 1000 years and subsequently analysed to derive consequences for life-history strategies,
115 i.e., patterns of growth, maturation, and reproduction, with a particular focus on skipped
116 spawning. For the purpose of conciseness, life-history strategies resulting from optimal
117 allocation rules will be referred to as ‘optimal life-history strategies’ throughout the rest of the
118 text.

119 **Investigated fishing mortality scenarios**

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

126 The first scenario is dominated by a spawner fishery that harvests only the mature part of the

127 population, reflecting the stock's exploitation prior to 1930. The optimal energy allocation
128 rule leads to fish maturing late (at 10.2 years, 117 cm, and 20.8 kg) ($F_S = 0.2$, $F_F = 0.1$).
129 The second scenario mimics the contemporary fishing pressure, where a feeder fishery,
130 harvesting all individuals at the feeding grounds, is the strongest cause of fishing mortality.
131 The corresponding optimal energy allocation rule leads to an early maturing population (at 4.9
132 years, 51 cm, and 1.6 kg) ($F_S = 0.3$, $F_F = 0.6$).
133 The third scenario uses interpolated fisheries mortalities between the two scenarios (20% of
134 the way from late maturation towards early maturation). The corresponding optimal life
135 history fits very well with growth data for the Northeast Arctic cod stock during the period
136 1978–2000, with maturation occurring at an intermediate age and size (at 8.1 years, 89 cm,
137 and 8.9 kg) ($F_S = 0.22$, $F_F = 0.20$).
138 The natural mortality was $M = 0.25 \text{ year}^{-1}$ for all scenarios, and there was also an increased
139 mortality during migration and spawning $M_S = 0.1 \text{ year}^{-1}$.

140 **Results**

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

152 **Factors affecting skipped spawning at the ecological time scale**

153 *Energy allocation rules and individual life histories*

154 The model has been described in detail by Jørgensen and Fiksen (this issue). An example
155 of how allocation of energy between growth and reproduction shapes the life history of one
156 individual cod that skipped spawning several times throughout its life is presented graphically
157 in Figure 1 (the example is from our third scenario). Briefly, growth in terms of length was
158 nearly linear with time early in life (Fig. 1a) when most of the energy was allocated to growth
159 (Fig. 1b; values close to 0). Approximately one year prior to the first spawning, ingested
160 energy was diverted to stores (values close to 1 in Fig. 1b) and this energy was spawned as
161 eggs during the first spawning season (Fig. 1d). After first spawning, the individual in this
162 illustration gave priority to growth for another 5-6 months with little allocation to energy
163 stores, before it once again prepared for spawning. The first and second time this individual
164 spawned (at age 8 and 10, respectively), it had nearly full energy stores. That fecundity
165 increased with as much as 40% between these two spawning events is due to the strategy of
166 skipping spawning at age 9 and giving priority to a larger body size. On average, fecundity
167 increased 36% every time this fish skipped spawning (at ages 9, 11, 13, 16, and 18).

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168 *Trends in skipped spawning in relation to age*

169 Spawning was skipped with a stable frequency of around 10% in the early maturing
170 population, and there was no trend with age (Fig. 2a). In the other two scenarios, skipped
171 spawning was most common among young fish, before it stabilised at 25% and 35% for older
172 fish in the scenarios with intermediate and late maturation, respectively.

173 The pattern becomes even clearer when the frequency of skipped spawning is plotted
174 against the number of years since maturation (Fig. 2b). The stochastic environment led to
175 inter-annual variation in age at maturation, and this variation was removed by subtracting age
176 at maturation from the age at which spawning was skipped. In all scenarios, the year

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177 following maturation showed the highest frequency of skipped spawning, with as much as
178 90% skipped spawning in the late-maturing population (scenario 1, grey curve). As the
179 number of years after maturation increased, the frequency of skipped spawning in the early-
180 maturing population (scenario 3) stabilised quickly at the expected level of 10%. For
181 scenarios 1 and 2, the frequency of skipped spawning showed dampened oscillations, i.e., a
182 pattern where spawning was skipped more often every second year, and gradually becoming
183 more uniform with age. The drop at old ages is a terminal effect of the model, where
184 individuals die at the maximum age of 25 years. It can be interpreted as a very strong
185 senescence effect that reduces the value of future reproductions. A gradually increasing
186 mortality rate at high ages would soften this effect, but the overall picture of higher
187 investment in reproduction towards life's end due to senescence would remain. The curves
188 shown in the figure stop when no more individuals were alive.

189 *Effects of condition and food intake on fecundity and skipped spawning*

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

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201 **Life-history evolution in light of ecological conditions**

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

208 *Variation in fishing mortalities*

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

222 *Variation in mean food availability*

223 Skipped spawning showed a complex relationship when food availability was varied (the
224 left-to-right axis in Fig. 5). This is due to two effects working in opposite directions. When
225 food intake was increased (relative food intake above 1.0 in Fig. 5a-d), more energy was

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226 available for growth, fish would be larger at the same age and could mature earlier and at a
227 larger size (Fig. 5c-d). There would be more years when energy stores could be filled to
228 sustain reproduction, so the increased occurrence of skipped spawning must be due to
229 favourable growth conditions and the advantages a larger size has on fecundity (Fig. 5a-b).
230 This is an effect of the increased value of future reproduction. On the other hand, when food
231 intake was decreased, (relative food intake below 1.0 in Fig. 5a-d), growth would be slower so
232 that maturation would take place at a smaller size, and there would not be food or time to fill
233 energy stores sufficiently in all years. As a consequence, skipped spawning would again
234 increase. Maturation would still take place earlier (Fig. 5c), presumably so that individuals
235 can spread the chances of experiencing high enough food availability to sustain migration and
236 spawning over more years. This is probably an effect of the uncertain value of reproduction in
237 any given year.

238 *Variation in natural mortality rate*

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

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

251 *Variation in migration costs*

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

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257 **Effects of skipped spawning on spawning stock biomass**

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

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262 **Discussion**

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

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

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

285 **Evidence of skipped spawning in fish**

286 Bull and Shine (1979) reviewed skipped reproduction among iteroparous animals with a
287 focus on amphibians. Skipped reproduction was most often linked to migration, brooding, or
288 livebearing, and was most common among females. In fish, various studies have identified
289 skipped spawning: Greenland halibut (*Reinhardtius hippoglossoides*; Fedorov 1971; Walsh
290 and Bowering 1981 found reabsorption of oocytes among females attempting to mature for
291 the first time, but no evidence for later skipping), sole (*Solea solea*; Ramsay and Witthames
292 1996), long rough dab (*Hippoglossoides platessoides*; Bagenal 1957), Norway pout
293 (*Trisopterus esmarkii*; Gokhale 1957), winter flounder (*Pleuronectes americanus*; Burton
294 1991, 1994), carp (*Cyprinus carpio*; Ivanov 1971), chub (*Leuciscus cephalus*; Fredrich et al.
295 2003), perch (*Perca fluviatilis*; Holmgren 2003), hake (*Merluccius merluccius*; Hickling
296 1930), and herring (*Clupea harengus*; Engelhard and Heino 2004). For plaice (*Pleuronectes
297 platessa*), skipped spawning was observed in the laboratory (Rijnsdorp 1990) but not in a
298 long-term data set from the North Sea (Rijnsdorp 1989).

299 For Atlantic cod, the discussions of skipped spawning began in the 1930s, with the early

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

318 In our model, 2-35% of the mature population skipped spawning (numbers taken from Fig.
319 4a). This level of occurrence is consistent with observations published more recently: in
320 Newfoundland, Canada, as much as one third of cod females were skipping spawning
321 (Rideout et al. 2000), and it was estimated that on average 32% of potential cod spawners on
322 the Flemish Cap skipped spawning in any given year between 1978 and 1985 (Walsh et al.
323 1986). Growth rates were increasing in the same period (Walsh et al. 1986), meaning that
324 food shortage cannot explain the frequent skipping. Histological examinations of trawl-

325 sampled cod from the Barents Sea just prior to the spawning migration found that up to 57%
326 of potential repeat spawners skipped spawning (Oganesyanyan 1993). In 1987, during the Barents
327 Sea capelin collapse, no Northeast Arctic cod larger than 90 cm were found on the spawning
328 banks although they were present in the population (Marshall et al. 1998). In the Gulf of St.
329 Lawrence, Canada, 20-40% of sexually mature cod had underdeveloped gonads at the time of
330 spawning (Schwalme and Chouinard 1999), indicating that they were skipping reproduction
331 this year.

332 **Phenotypic plasticity and the physiology of skipped spawning**

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

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

346 From a life history perspective, there is at the same time 1) a distinct disadvantage from
347 having a small body size and 2) a clear advantage from being bigger. 1) Small fish have
348 higher weight-specific metabolic rates and swim less economically (Schmidt-Nielsen 1984);
349 they thus have a higher energetic threshold for participating in migration and spawning, and a

350 lower share of the energy invested in reproduction is actually used to produce gametes. 2)
351 Fecundity in fish is roughly proportional to body mass, so a 25% increase in length will
352 double fecundity. Add these two effects on top of each other, and it becomes clear that, for a
353 small migrating fish, growing to a larger size can increase future fecundity to a degree that
354 easily outweighs its current reproductive potential.

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

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

368 **Causes of skipped spawning in relation to physiological and ecological conditions**

369 In the published observations of skipped spawning that linked the phenomenon to ecology
370 or life-history, poor feeding conditions was most often identified or suggested as the likely
371 cause (e.g., Burton and Idler 1987; Rijnsdorp 1990; Rideout et al. 2000). On the basis of the
372 potential for phenotypic plasticity highlighted above, we would expect that skipped spawning
373 would be more frequent in our model when an unfavourable feeding environment had led to
374 poor individual condition, a concept supported by our model results (Fig. 3a). Furthermore,

375 we found that it was favourable for larger cod to spawn even when their energy stores were
376 not full (Fig. 3b), reflecting the benefits that come with a larger body size. The two axes on
377 Figure 3b represent length and energy stores, which were dimensions also in the allocation
378 rule; the area in Figure 3b for which grey and black circles overlap therefore indicate when
379 the two additional dimensions, namely current food availability and age, were necessary to
380 fine-tune the migration and allocation pattern.

381 The clear relationship observed between the frequency of skipped spawning and age means
382 that skipped spawning is also an active component in the life history of fish. If low food
383 availability was the only cause leading to skipped spawning, we would expect the frequency
384 of skipped spawning to be relatively stable across all ages, since all age classes suffer from
385 the same environment (we do not consider here the case where subgroups of the mature
386 population utilise different and unlinked food resources; this might apply for Northeast Arctic
387 cod but is not addressed by this study). Poor condition alone probably explains the frequency
388 of skipped spawning in our second scenario (imitating the evolutionary end-point of
389 contemporary fishing patterns; the high mortality results in an early-maturing population).
390 Spawning was skipped at a frequency of 10%, and did not show any variation with age. This
391 life-history strategy is geared to value current reproduction much higher than potential future
392 spawnings. Only when individual condition was too low to sustain migration, or when the
393 stored energy could offer only a very limited egg production, was the spawning opportunity
394 totally abandoned.

395 Skipped spawning occurred more frequently in our first and second scenarios, where
396 mortality rates were lower. There was also an evident trend with age: skipped spawning was
397 most common in the years following maturation. Similar results have been found in wild cod,
398 where skipped spawning was most common for cod of small size (Oganessian 1993). That
399 skipped spawning got less common with age reflects a temporal trade-off, where early growth

400 and later reproduction are favoured. Young cod can potentially spawn many times in the
401 future, and increasing the fecundity for all these reproductive seasons should be attractive.
402 The decision of whether to spawn or not needs only compare expectations for the current
403 reproductive season with the expected future benefit that comes from a larger size if spawning
404 is skipped. An individual's growth trajectory can thus be roughly divided into three phases:
405 first, only somatic growth takes place up to the age at sexual maturation; second, growth is
406 balanced with reproduction during some years following maturation (mechanistically, growth
407 takes precedence when spawning migrations are skipped more frequently); and third, after
408 that reproduction receives the full focus of energy allocation and the frequency of skipped
409 spawning stabilises.

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

417 The underlying mechanisms become clearer when the frequency of skipped spawning is
418 considered relative to the age at which maturation takes place. The stochastic environment
419 leads to inter-annual variations in age and size at maturation, and this variation overshadowed
420 a distinct pattern in how skipped spawning was distributed relative to maturation. In the first
421 5-10 years after maturation, the frequency of skipped spawning oscillated: a larger proportion
422 of individuals skipped spawning if their age since maturation was an odd number. This
423 corresponds to a life-history strategy with a two-year reproductive cycle during which
424 migration (in order to spawn) and feeding (in order to grow) alternate. With age, these

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

430 **Potential evolutionary consequences of altered ecological conditions on skipped** 431 **spawning**

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

448 Variations in mortality can affect both phenotypic plasticity (through increasing growth
449 rates in response to relieved density dependence) and evolutionary adaptations (since the

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

456 Increased natural mortality will favour earlier maturation and less skipped spawning,
457 because future reproductive effort will be discounted more heavily. The pattern becomes more
458 complicated, however, when mortalities affect only specific parts of the population, as is the
459 case in the stage-selective fisheries harvesting the Northeast Arctic cod stock (Law and Grey
460 1989). Low mortality at the feeding grounds compared to the spawning grounds will, for
461 instance, create a mortality refuge for fish that choose to grow rather than spawn and will
462 favour skipping. The model's prediction of late maturation at a large size resulting from this
463 setting corresponds well with observed maturation patterns for the Northeast Arctic cod stock
464 from the beginning of the 20th century (Jørgensen 1990). Since trawling started in the Barents
465 Sea around 1930, annual harvest has been high, with the total harvest from the Northeast
466 Arctic cod stock exceeding one million metric tons per year in several years between 1950
467 and 1980. With such a high mortality at the feeding grounds, a late-maturing cod will have a
468 low probability of reproducing at all, which will, as our model shows, lead to evolution
469 towards earlier maturation (Law and Grey 1989) and a diminished frequency of skipped
470 spawning.

471 **Consequences of altered exploitation**

472 Our model predicts that exploitation-induced changes in skipped spawning occur on two
473 time scales. On the ecological time scale, exploitation will shift the age distribution of the
474 stock towards younger year classes. The frequency of skipped spawning will therefore

475 increase in the population as a whole, since it is most frequent during the first years after
476 maturation. This is a response at the level of population dynamics (corresponding to a move
477 to the left on the continuous black or grey curve in Fig. 2). On the evolutionary time scale, a
478 high fishing mortality creates a selection pressure towards earlier maturation. Skipped
479 spawning will then become less common as the stock adapts. This is an evolutionary response
480 to high exploitation rates (a move from the grey to the black to the dotted curve in Fig. 2).
481 Thus, our model suggests that high fishing pressures will lead to contrasting short-term and
482 long-term effects of exploitation on skipped spawning.

483 **Implications for estimating and using stock–recruit relationships**

484 The frequency of skipped spawning predicted by our model has consequences for stock–
485 recruit relationships whenever the mature part of the population is used to predict recruitment
486 (Jørgensen and Fiksen this issue). Spawning stock biomass–recruit (SSB–recruit) models
487 commonly assume that all sexually mature biomass contributes equally to the population’s
488 overall egg production. There may be, however, effects of age and experience that modify
489 this, e.g., among first-time spawners (Kjesbu et al. 1996; Trippel 1998; Murawski et al. 2001).
490 Skipped spawning will add on top of this, since its consequences are particularly pronounced
491 for the abundant year classes following maturation. Technically, an inflated value of the SSB
492 will be used inadvertently, since up to 30% of mature individuals may skip spawning in an
493 average year. Moreover, cohorts are affected differently, meaning that cohort abundance and
494 growth history affect skipped spawning in intricate manners. Understanding how these factors
495 influence the part of the population that is actually spawning requires further research;
496 especially observations to see to what degree the predictions from modelling attempts such as
497 the one presented here apply in nature.

498 To prevent these distortions in estimated SSB, some measure of individual condition (e.g.,
499 lipid stores in the liver) could be used, providing a better estimate of the part of the mature

500 population that has actually prepared for spawning. This could improve predictions for
501 recruitment (Marshall et al. 1999). However, a possible pitfall for such a method is the
502 bimodality in gonad or liver weights that can arise when part of a cohort skips spawning
503 (Schwalme and Chouinard 1999). Different population-level measures were tested as
504 predictors of the stock's total egg production using this model (Jørgensen and Fiksen this
505 issue). The population's total liver weight was a good predictor of total egg production,
506 although using the biomass of the part of the population actually engaged in spawning was an
507 even better predictor.

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

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628

629 **Figure captions**

630 **Figure 1.** Growth trajectory and physiology for one individual female cod (*Gadus morhua*)
631 from a life history model for the Northeast Arctic cod, simulated in a stochastic environment.
632 The x -axis shows age and is common for all the graphs. (a) Length (black line, left axis) and
633 weight (grey line, right axis). (b) Allocation of available energy between energy stores (high
634 values) and growth (low values). The line shows gaps because no energy is available for
635 allocation during spawning migrations. (c) Fulton's condition factor (black line). The grey
636 lines represent minimum and maximum condition factors attainable at that length; these
637 increase because body mass is proportional to length to the power of 3.065. (d) Number of
638 eggs spawned (in millions). In preparation of sexual maturation, this individual cod directed
639 all its energy was towards stores approximately one year prior to first spawning.

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

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

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

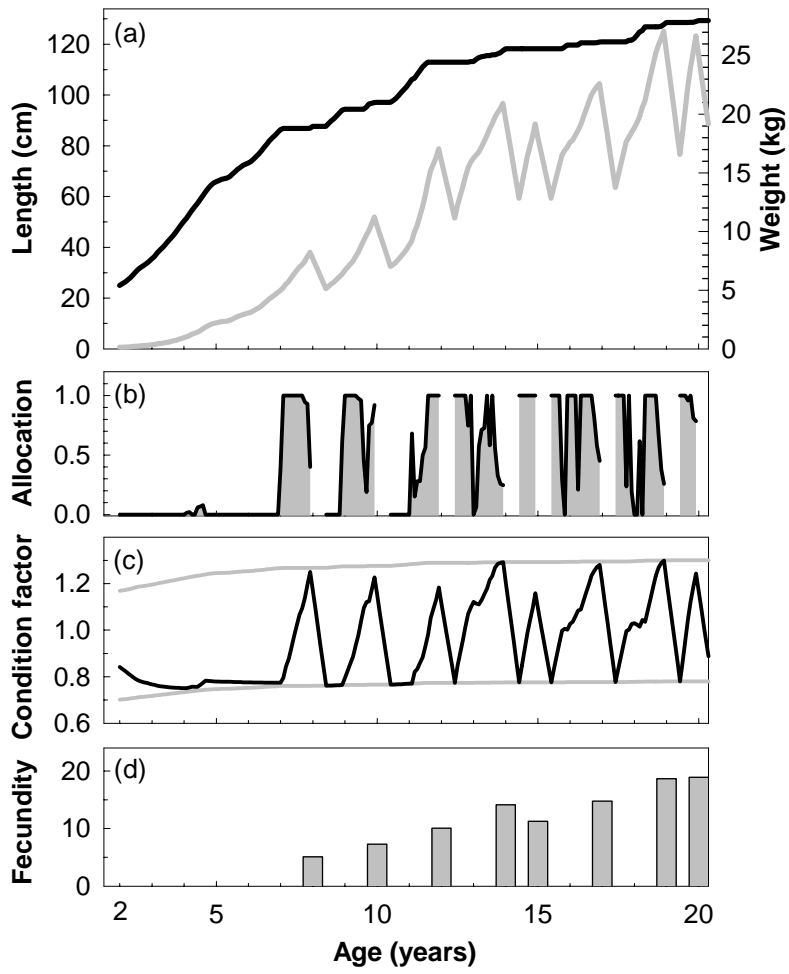
656 **Figure 4.** Effects of varying mortality levels in the spawner and feeder fishery (year^{-1}). At
657 high mortalities in the feeder fishery the population went extinct; this is visible as the area
658 where the values drop to 0. (a) Mean proportion of spawning stock biomass (defined as all
659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

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

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

679 specific parameter combination.

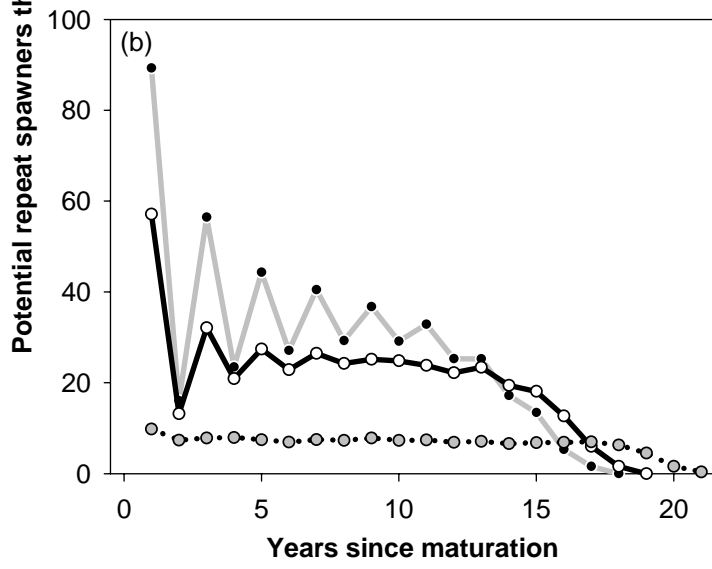
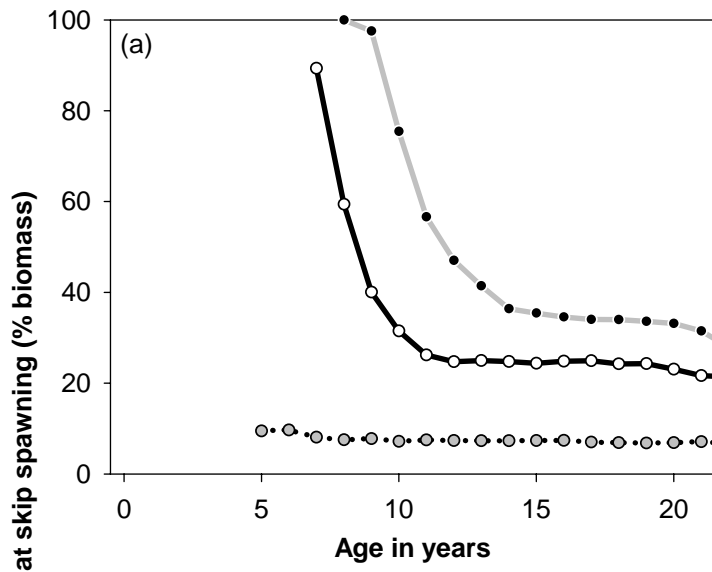
680 **Figure 7.** The proportion of sexually mature biomass that comprises first-time spawners
681 (black), repeat spawners (grey), and that skips spawning (white) for optimal life histories
682 under the three combinations of feeder (F_F) and spawner (F_S) fishery mortalities considered.
683 The values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



685

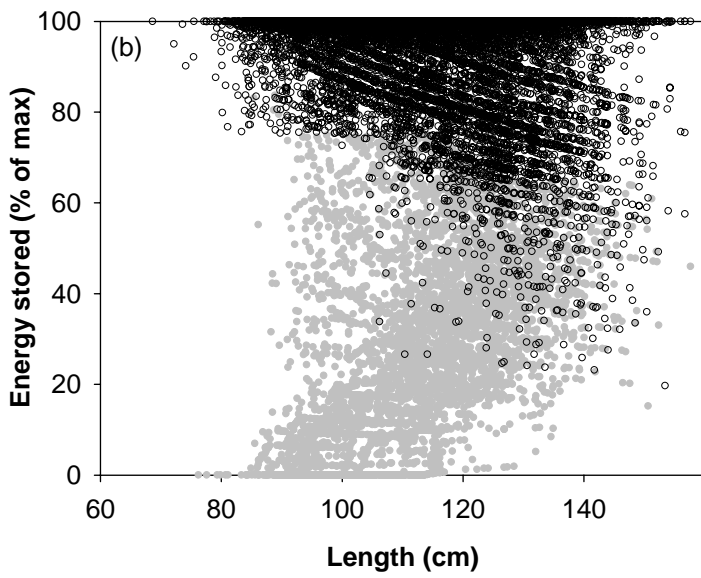
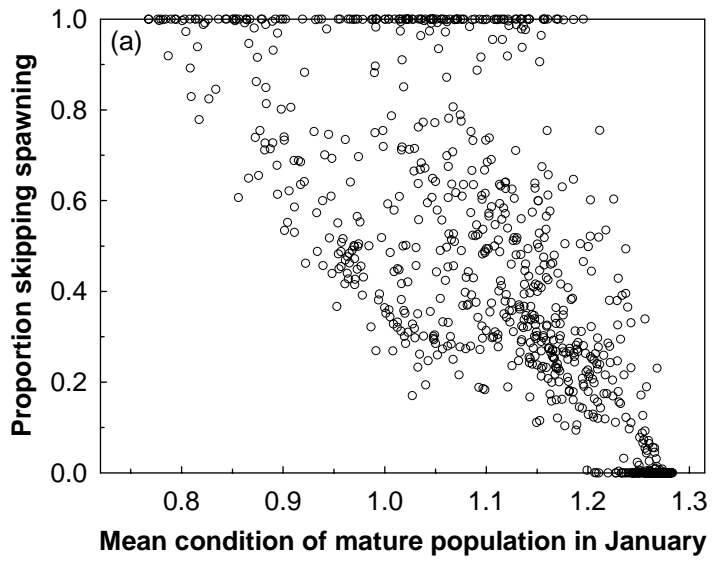
686 Jørgensen et al. The logic of skipped spawning in fish.

687 **Figure 1.**



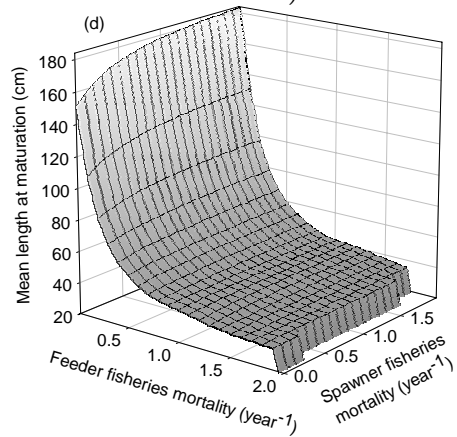
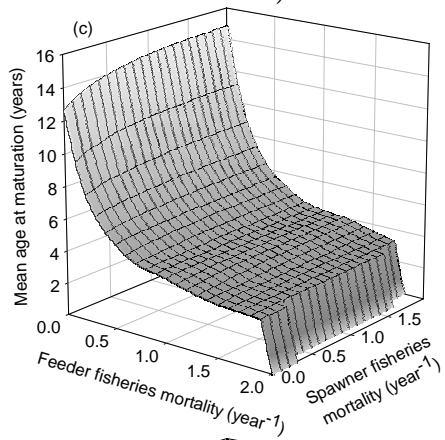
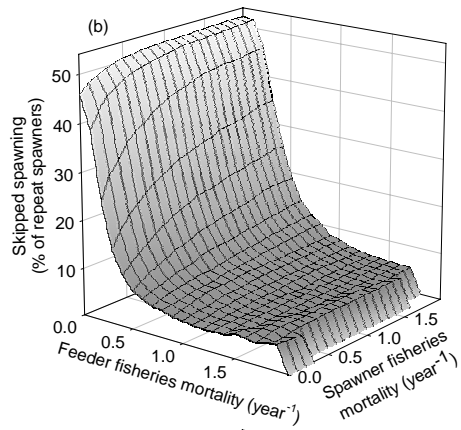
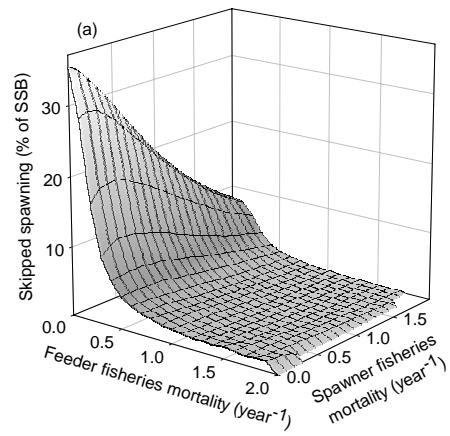
689 Jørgensen et al. The logic of skipped spawning in fish.

690 **Figure 2.**



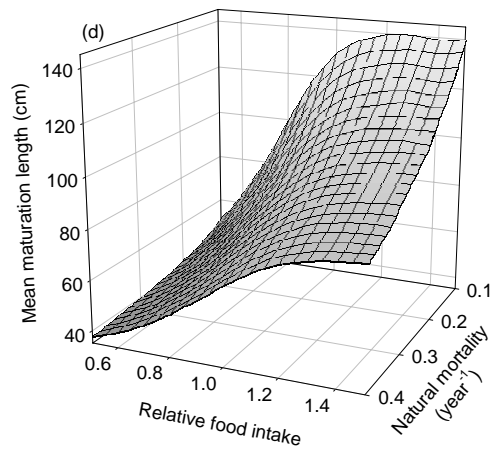
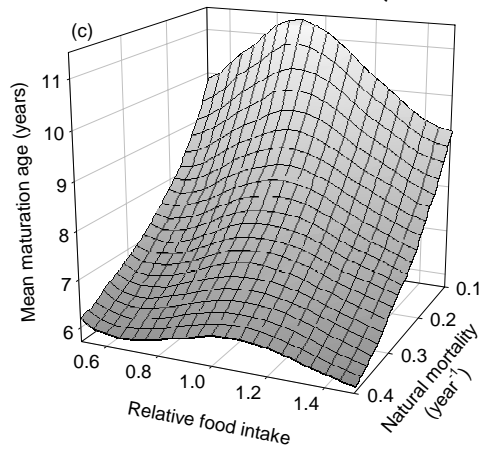
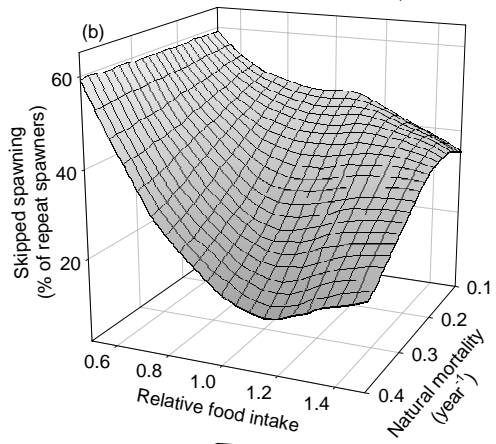
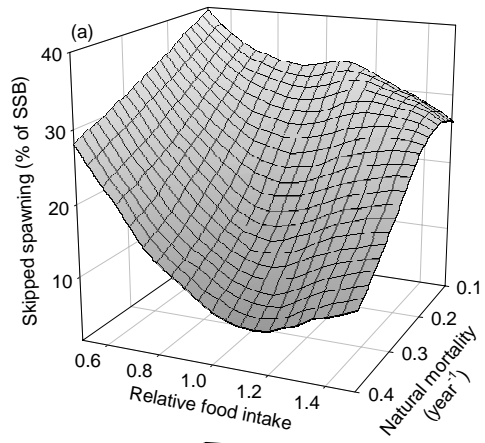
692 Jørgensen et al. The logic of skipped spawning in fish.

693 **Figure 3.**



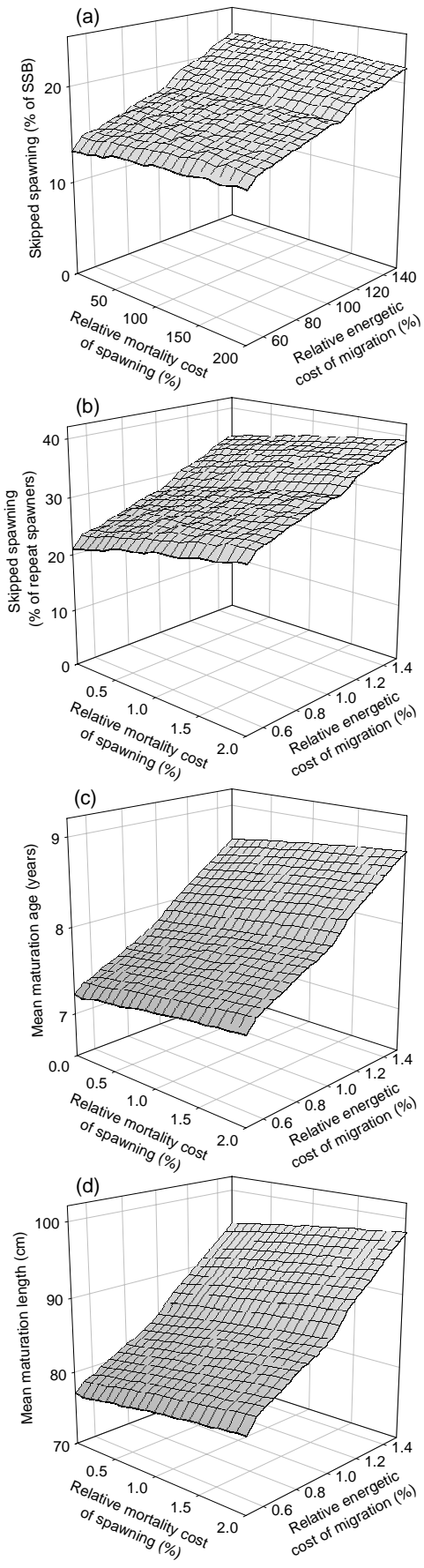
695 Jørgensen et al. The logic of skipped spawning in fish.

696 **Figure 4.**



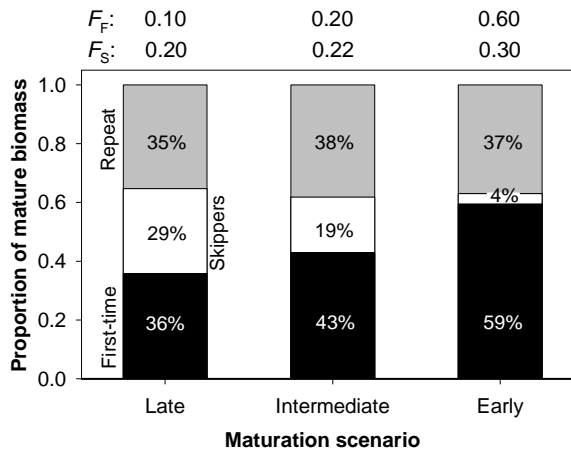
698 Jørgensen et al. The logic of skipped spawning in fish.

699 **Figure 5.**



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

702 **Figure 6.**



703

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

705 **Figure 7.**