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Size-selective fishing gear and life history evolution in the Northeast Arctic cod

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Abstract:

Industrial fishing has been identified as a cause for life history changes in many harvested stocks, mainly because of the intense fishing mortality and its size-selectivity. Because these changes are potentially evolutionary, we investigate evolutionarily stable life-histories and yield in an energy-allocation state-dependent model for Northeast Arctic cod Gadus morhua. We focus on the evolutionary effects of size-selective fishing because regulation of gear selectivity may be an efficient management tool. Trawling, which harvests fish above a certain size, leads to early maturation except when fishing is low and confined to mature fish. Gillnets, where small and large fish escape, lead to late maturation for low to moderate harvest rates, but when harvest rates increase maturation age suddenly drops. This is because bell-shaped selectivity has two size-refuges, for fish that are below and above the harvestable size-classes. Depending on the harvest rate it either pays to grow through the harvestable slot and mature above it, or mature small below it. Sustainable yield on the evolutionary time-scale is highest when fishing is done by trawling, but only for a small parameter region. Fishing with gillnets is better able to withstand life-history evolution, and maintains yield over a wider range of fishing intensities.

Keywords: energy allocation • evolutionary modeling • fisheries management • fishing-induced changes • life history evolution

Introduction

Exploitation of living resources can lead to evolutionary changes in harvested populations of plants (Law and Salick 2005) and mammals (Coltman et al. 2003), but because of the grand scale of commercial fishing most examples come from fish. The reviews by e.g., Jørgensen et al. (2007), Kuparinen and Merilä (2007), Fenberg and Roy (2008), and Hutchings and Fraser (2008) list phenotypic evidence of morphology and life history traits that changed over time in wild 22 populations. Because these changes cannot be totally explained by environmental factors, part of

23   the change is thought to represent contemporary evolution. The rates of change are furthermore

24   rapid, and in general comparable to those observed in breeding programs (Reznick and

25   Ghalambor 2001, Jørgensen et al. 2007). In a comparative study of anthropogenic causes for

26   contemporary evolution, harvesting was found to result in quicker evolutionary change than

27   other human influences (Darimont et al. 2009). Heritable changes in a number of behavioral and

28   life history traits have also been observed in populations harvested experimentally (Conover and

29   Munch 2002, Walsh et al. 2006, Biro and Post 2008). The problem of fishing-induced evolution

30   requires attention because it might be widespread, as most commercially harvested fish stocks

31   experience intense exploitation rates, with fishing mortality being up to four times higher than

32   the natural mortality (Mertz and Myers 1998). In general, theoretical models predict less of an

33   evolutionary response to harvesting if fishing mortality is lower (Law and Grey 1989, Ernande et

34   al. 2004, Brown et al. 2008). This prediction is supported also by fisheries data, for example in

35   Pink salmon where phenotypic change that could not be explained by environment was slower in

36   regions with lower fishing mortality or less selective gear (Ricker 1981).

37   Although there is general agreement that the world's fishing fleets are vastly oversized

38   for a sustainable harvest practice, it has turned out difficult to down-regulate this overcapacity.

39   The reason is a fundamental conflict between the short-term rewards that motivate individual

40   players in the fishing industry versus the long-term goals of sustainability that would insure the

41   viability of the very same industry. Any management solution has to acknowledge and address

42   this trade-off (the following description of the state of fisheries management draws on Clark

43   2006). Catch quotas are often negotiated higher than advised because of lobbying by the fishing

44   industry looking to capitalize quickly on investments in infrastructure and vessels, or small-scale

45   fishermen eager to cover their expenses while competing with other fishermen for the same

46   shared resource. A similar fate befalls effort control regulations, where technology creep leads to

47   increasing ability to catch fish although the numbers of vessels or days at sea remain constant.

48   The attempts by politicians and managers of more drastic methods, such as buyback programs to

49   take vessels out of the fishery, have also failed. Fishermen are like other business owners, and

50   either expect such buyback programs to take place and expand beforehand, or sell only the most

51   inefficient boats so that there are only minor effects on overall fleet capacity. Individually owned

52   quotas that give fishermen a long-term perspective have been proposed as a promising option to

53   break the trade-off between short-term profit and long-term sustainability (see Costello et al.

54   2008). Under such regulations it becomes profitable for a fisherman to spare some fish since he

55   has ownership of a fixed share of future harvest. Such individually transferable quotas (ITQs)

56   avoid the tragedy of the commons but run into other problems because the public basically

57   abandons ownership of a natural resource for free; at least the question of compensation remains

58   largely unresolved. Given the immense difficulties in controlling effort and reducing harvest

59   pressure, it seems that general advice of the type 'reduce fishing mortality to one quarter to

60   lessen the evolutionary impact' is unlikely to be effectively implemented in the near future. An

61   alternative avenue may be to manage fishing gear and its size-selectivity (Law and Rowell 1993,

62   Law 2000).

63   Most kinds of fishing gear do not catch all fish with equal probability but are selective for

64   certain types of fish in one way or another. Often, this selectivity is based on body size. For

65   example, small fish may slip through gillnets and large fish avoid getting caught, while fish with

66   a girth close to the mesh size are most effectively harvested (Hamley 1975). For trawls, sorting

67   grids and mesh size in the codend let small fish escape while larger fish are harvested. The

68   pattern of size-selectivity may have large consequences for fishing-induced evolution, because

69   the fish that survive and can pass on their genes to the next generation differ between gear types.

70   For example, it has often been stated that if only fish above a certain size threshold are harvested,

71   then it would become optimal to grow slower (Miller 1957) and mature earlier (Law and Grey

72   1989). These qualitative expectations have been confirmed by theoretical models (e.g., Favro et

73   al. 1979, Law and Grey 1989, Ernande et al. 2004, Gårdmark and Dieckmann 2006) and found in

74   harvesting experiments (Edley and Law 1988, Conover and Munch 2002). The most

75   comprehensive experiment to date is on Atlantic silversides *Menidia menidia* (Conover and

76   Munch 2002, Walsh et al. 2006). In that study, harvesting of the largest individuals, which is

77   analogous to trawling, led to heritable changes towards smaller fish, slower growth, reduced

78   fecundity, poorer viability of larvae, and diminished yield. Because of the potential for

79   detrimental evolutionary effects caused by trawling-like size-selectivity, several authors have

80   suggested that the bell-shaped selectivity curves of gillnets may be better from a sustainability

81   perspective (Law and Rowell 1993, Law 2007). With a bell-shaped selectivity curve, fish that

82   survive as they grow through the sizes vulnerable to the fishery may successfully reproduce,

83   potentially repeatedly and at a large size. This may weaken selection toward early maturation,

84   and thus lead to less of an evolutionary response compared to trawling (Law 2007).

85   Because there already is a tradition for mesh-size and gear-type regulation in fisheries

86   management as well as routines for enforcement, it seems worthwhile considering gear

87   regulation as a tool to manage evolutionary trait changes generated by fishing practices. This

88   raises the question: what would a desirable harvesting regime look like from the perspective of

89   an evolutionarily concerned fisheries manager? Ultimately, the goals of management are to be

90   decided through a democratic and political process during which the views of the public,

91   stakeholders, and interest groups are duly heard and considered (Jørgensen et al. 2007). From a

92 biological perspective and for the sake of illustration, however, it can be worthwhile to focus on

93 two relatively conservative aims initially. The first one is that the harvesting practice leads to

94 little evolutionary change relative to the pre-harvesting situation. Currently, little is known about

95 the potential consequences of fishing-induced evolution, but because life history traits are

96 affected and these are central to population dynamics, many stock characteristics such as

97 productivity, yield, and resilience might be altered. In general, the manager's tasks of predicting

98 stock development and planning harvesting schemes would be easier if stock properties stayed as

99 constant as possible. It might therefore be good for a manager to have a stock that undergoes

100 little evolutionary change, so that sensitivity to environmental factors and responses to

101 harvesting can be known or learnt from the stock's past behavior. Ecosystem relationships are

102 also more likely to remain the same if the changes in stock characteristics are small. A second

103 property that our evolutionary concerned manager might desire is that her choice of gear type is

104 robust to excess harvesting, as the overall harvest rate has proven difficult to control as discussed

105 above. By expecting that harvest rates might be higher than planned, she should choose a gear

106 type that has minor consequences for the evolutionary outcome if harvest levels were to increase.

107   To our knowledge, the potential evolutionary outcome of a fishery with a bell-shaped

108 selectivity curves has not yet been investigated. We therefore chose to study the effects of gear

109 type and its size-selectivity on expected evolutionary trait changes. The life history model we use

110 is designed for the Northeast Arctic stock of Atlantic cod *Gadus morhua* and is rich in ecological

111 and physiological detail (Jørgensen and Fiksen 2006). Primarily we contrast different types of

112 gillnets and trawls in search of evolutionarily desirable harvesting practices.

Model description

Life history model

The life history model we used finds the lifelong pattern of energy allocation between growth and reproduction that would maximize lifetime expected fecundity. The allocation decision depends on the individual's state, that is, its age (in months, thus also including seasonal patterns), body length (in cm), level of stored energy (percent of full energy stores), and the current state of the feeding environment that undergoes autocorrelated temporal variability (a graphical overview of the model is given in Figure 1). As such, the model explicitly includes phenotypically plastic response to the internal (age, body length, level of stored energy) and the external (food availability) environment. The model optimizes the state-dependent energy allocation, with the result that age and size at maturation, growth rates, skipped spawning, and the level of energy stored are emergent properties arising from the optimal pattern of energy allocation. The description below is based on Jørgensen and Fiksen (2006) which is referred to for further details. The model has previously been used to investigate the potential for fishing-induced evolution to cause changes in life history traits and skipped spawning (Jørgensen et al. 2006) and in migration distance and large-scale geographical distribution (Jørgensen et al. 2008). Although selection from size-selective fishing gear has been quantified in earlier studies (e.g., Law and Rowell 1993) this is to our knowledge the first paper to systematically investigate the potential evolutionary consequences of size-selectivity harvesting on fish life histories.

Each month the individuals receive an amount of food that is stochastic and autocorrelated in time. Food intake scales allometrically with length L [cm] as $L^{2.41}$ (based on Jobling 1988), and after energy to cover metabolic rate and basic activity has been spent, the

135   remainder is available for allocation between somatic growth and storage as lipids and proteins

136   for future reproduction.

137   The Northeast Arctic cod stock uses the Barents Sea as feeding area but spawns along the

138   Norwegian coast, with the main spawning taking place in Lofoten after a migration of around

139   800 km. We assume it takes five months in total to migrate south to the spawning area, spawn

140   (cod may produce up to 20 batches of eggs that each needs to mature; Kjesbu et al. 1996), and to

141   migrate back north again. The energetic cost of migration is taken from the energy stores, and

142   during spawning and migration cod only eat enough to cover their standard metabolism. The

143   weight-specific energetic cost of migration decreases with fish size (see Ware 1978 and

144   Alexander 2003 for general treatments of size-dependent swimming costs in fish). What is left of

145   their energy stores after migration is used to produce eggs that are spawned. We model only

146   females to avoid the problems of sexual selection and frequency-dependent competition among

147   males.

148   Natural mortality $M(L)$ is negatively size-dependent so that it is highest for small fish and

149   then stabilizes at 0.25 year^{-1} for larger fish. Fishing takes place both at the spawning grounds

150   (where there are only mature fish) and at the feeding grounds (where immature fish are all year

151   round and mature fish the seven months they are not migrating or spawning). Life history theory

152   has shown that these two types of fishery act in opposite directions on age at maturation (Law

153   and Grey 1989): while the feeder fishery favors early-maturing fish that manage to reproduce

154   while still alive, a high mortality on the spawning grounds favor fish that are large when they

155   risk that mortality to reproduce and therefore selects for late maturation. Studies have shown that

156   maturation is much more sensitive to the mortality in the feeder fishery than the harvest rate at

157   the spawning grounds (Law and Grey 1989, Jørgensen et al. 2006).

158   **Evolutionary modeling approach**

159   Optimal energy allocation patterns, i.e., energy allocation patterns that maximize individual

160   fitness and thus result in optimal emergent life history strategies, were found using state-

161   dependent dynamic programming (Houston and McNamara 1999, Clark and Mangel 2000). As

162   fitness measure we used the expected lifetime reproductive success R_0, i.e. the expected number

163   of offspring produced in a lifetime. Theoretical studies have shown that evolution optimizes R_0

164   as long as density dependence affecting the population acts only multiplicatively on the expected

165   lifetime production of offspring (Mylius and Diekmann 1995), which is the case in our model

166   (see section below on yield calculation). We therefore maximize reproductive value V, which at

167   birth corresponds to R_0 (Houston and McNamara 1999). For each age, reproductive value V has a

168   future component that the individual can achieve if it survives, and this expected residual

169   reproductive value depends on the new state the individual is in. Every year, the individual can

170   also add to its reproductive value by reproducing. The algorithm finds the optimal allocation

171   pattern by iterating backwards, starting at the maximum age of 25 years at which all individuals

172   die and have no residual reproductive value. The model then compares the fitness consequences

173   of all allocation values α between reproduction and growth and stores the allocation value that

174   maximizes fitness. This is repeated for all lengths L, sizes of energy store E, and environmental

175   food availability F, before the model moves one time-step backwards and repeats the process,

176   assuming that energy allocation is optimal for the remainder of its life. The logic can be

177   condensed to the dynamic programming equation, which can be written as:

178    $$V(A,L,E,F) = \max_{\alpha} \left[B(E) + S \sum_{F'} P(F' \mid F) \cdot V(A+1, L', E', F') \right].$$

179   Here the left-hand side is the reproductive value for a given state-combination, and it is found by

180   choosing the allocation α that maximizes fitness. Fitness is expressed within the square brackets,

181   and it consists of *i*) the current fecundity *B* which is a function of the energy available for

182   reproduction, and *ii*) the residual fitness if the individual survives (with probability *S*). The

183   residual fitness depends on the new state at age *A*+1 (one month older) when the individual has

184   grown to length *L′* and its energy store is *E′* (these state changes follow from α). The summation

185   over *F′* finds the expected fitness over the possible levels of the feeding environment. Since *F* is

186   autocorrelated in time, the conditional probability $P(F′|F)$ gives the probability of having food

187   availability *F′* in the next month if the current level is *F*.

188   Optimization approaches rely on a static fitness measure, which is valid for populations

189   experiencing simple density-dependent processes but means that frequency-dependent

190   consequences on fitness cannot be included. Examples of such effects that need to be ignored are

191   density dependence acting on growth, or mate competition based on relative size structure. The

192   environmental influence is modeled as fluctuating and autocorrelated, but the environmental

193   variance is constant over time.

194   The advantage of using state-dependent dynamic programming over other evolutionary

195   modeling approaches, like optimality models (Stearns 1992) or selection gradient approaches

196   (Abrams 2001) such as quantitative genetics (Lande 1976) or adaptive dynamics (Dieckmann

197   and Law 1996), is that state dependence can be incorporated in great detail and that individual-

198   level processes can be relatively complex. As such, the methodology needs to make fewer

199   assumptions about how phenotypic plasticity should be constrained. The biological complexity

200   of state-dependent strategies and phenotypic plasticity that dynamic programming models can

201   deal with is generally out of reach for the other approaches. One limitation is that, although it is

202   fully accounted for, the selection gradient cannot be computed explicitly.

203   When the optimal energy allocation pattern has been found for a given fishing regime, we

204   simulate the population dynamics of this life history strategy using a state-structured population

205   model in discrete time to record the emergent life history traits and long-term yield. The results

206   we show are recorded during such forward simulations of optimal life history strategies.

207   The details of the model including the dynamic programming equation were published in

208   Jørgensen and Fiksen (2006), and we refer the reader to that paper for further details on the

209   physiological and ecological mechanisms included.

210   **Genetic assumptions**

211   The methodology we use finds phenotypes that optimize individual fitness given selection

212   pressures generated by the ecological setting, which here originates from fishing and its size-

213   selectivity but also from natural mortality, physiological constraints and environmental

214   stochasticity. These optimal phenotypes are evolutionarily stable strategies. As such, they are

215   evolutionary endpoints resulting from long-term evolution as dictated by selection pressures

216   only. The underlying genetic assumptions of the model are thus according to the streetcar theory

217   of evolution (Hammerstein 1996): there are no genetic constraints that delimit the long term

218   evolutionary outcome. In other words, traits are heritable and genetic correlations do not prevent

219   evolution to proceed (note that ecological and physiological constraints are specified in the

220   model processes, though). The modeling approach does not rely on any particular value for

221   heritability for the traits in question, as the heritability parameter would only scale the rate at

222   which the optimal phenotype is approached but not change the long-term evolutionary endpoint

223   itself. It is worthwhile highlighting here that the model actually finds optimal phenotypically

224   plastic (or state-dependent) phenotypes and therefore incorporates explicitly both plasticity and

225   evolution by considering the long-term evolution of plastic responses or multidimensional

226   reaction norms.

227   **Gear selectivity**

228   In previous versions of this model, fishing mortality affected all individuals equally, regardless

229   of their size or other individual states. The addition in this paper is that we introduce fishing

230   selectivity curves $U(L)$ that depend on an individual's length L and take values between 0 (the

231   fish is unaffected by the fishery) and 1 (the fish is maximally selected by the fishery). The

232   fishing mortality $F(L)$ an individual of length L experiences is thus $F(L)=U(L){\cdot}f_{max}$, where f_{max} is

233   the maximum annual harvest [year^{-1}] when selectivity $U(L)=1$. Total mortality is $Z(L) = M(L) +$

234    $F(L)$ and monthly survival probability $P(L)$ is then $P(L) = e^{-Z(L)/12}$. The results we present use

235   different values of f_{max} for the feeder fishery and the spawner fishery, as indicated on the graphs.

236   The focus is on drawing the management 'map' of how a choice of fisheries mortalities in the

237   two fisheries might affect the evolutionary outcome in the longer term.

238   Because we use optimization, the methodology constrains us to use a fixed fishing

239   intensity and size-selectivity while we find the optimal life history response to it. An inherent

240   assumption is therefore that the fishing fleet continues to use the same gear while fish evolve life

241   histories that allow them to escape the fishing mortality. This can result in a realized fishing

242   mortality that is much lower than f_{max} as life histories evolve to sizes that are less vulnerable to

243   the fishery. Alternative approaches could have been to determine a fixed total allowable catch or

244   a harvest control rule with a given size-selectivity, and study the consequences of that

245   management regime. In an optimization framework that would require an iterative procedure that

246   first finds the optimal life history strategy, then simulates the catch resulting from this strategy,

247   before modifying the fishing regime and repeating these steps in the next iteration, this until

248   convergence. Such studies are better tackled through models where ecology and evolution take

249   place on the same time-scale such as selection gradient approaches (Abrams 2001) or individual-

250   based evolutionary models (Strand et al. 2002), although these models cannot include as much

251   individual detail. We amend this by showing the fisheries yield that results from a given optimal

252   life history, so that it becomes easier to interpret the evolutionary endpoint of a given harvest

253   regime together with the long-term fisheries yield it would result in.

254   Size-selectivity curves for Atlantic cod have been determined for trawls and gillnets by

255   Huse et al. (2000). Their findings agree with earlier studies where gillnets show bell-shaped

256   selectivity curves as fish with a certain girth are captured with a higher probability than smaller

257   fish that can slip through or larger fish that don't get far enough through the mesh to get stuck

258   (reviewed by Hamley 1975). We modeled gillnet selectivity U_G as a Gaussian function around a

259   size of maximum selectivity L_{max}:

260
$$U_G(L) = \exp\left(\frac{-(L - L_{max})^2}{2\sigma^2} \right) \ .$$

261   Huse et al. (2000) found that the width parameter σ of the selectivity curves was 14% of the

262   mean for the three mesh sizes they investigated. A mesh size regulation implemented in a real

263   fishery would probably catch a wider size-range of fish than what was obtained in one scientific

264   study (Huse et al. 2000), because of differences between boats, variable fishing practices, and

265   variation in location and timing of fishing. We thus chose to double the width of the selectivity

266   curve, such that $\sigma = 0.28 \cdot L_{max}$. This makes the size-selectivity curves more similar to the

267   empirical examples shown in Hilborn and Minte-Vera (2008). The conclusions and the

268   qualitative results are the same if a narrower selectivity curve is used, but the quantitative

269   predictions change somewhat. For cod, longlines (hook and bait) have a similar bell-shaped size-

270   selectivity to gillnets (Huse et al. 2000).

271   In trawls, small fish can escape through the mesh in the codend or through specially

272   designed sorting grids, whereas fish larger than a certain size are retained (Millar and Fryer

273   1999) resulting in sigmoid selectivity curves. To facilitate comparison, we modeled the trawl

274   selectivity curve U_T as the left half of the same Gaussian function as gillnets up to a size of L_{max},

275   from which on selectivity was kept at 1:

276
$$U_T(L) = \begin{cases} U_G(L), & L < L_{max} \\ 1, & L \geq L_{max} \end{cases}.$$

277   We are aware of the tradition in fisheries science of using logistic functions for sigmoid

278   selectivity curves. However for the sake of comparison, we preferred to keep the formulation of

279   the selectivity curves as similar as possible for gillnet and trawl.

280   For both types of fishing gear, we show results for L_{max} of 70 cm, 90 cm, and 110 cm;

281   selectivity curves for gillnet and trawl with these parameters are shown in Figure 2. The main

282   aim of this study is to contrast the effects of gillnetting and trawling on fishing-induced life

283   history evolution and its consequences for yield. To achieve this comparison, we applied the

284   same fishing size-selectivity, either sigmoid or bell-shaped, at both the spawning and the feeding

285   grounds. In contrast, the existing fishery for Northeast Arctic cod is dominated by trawling at the

286   feeding grounds and longlines and gillnets at the spawning grounds. Therefore, we also ran the

287   model with sigmoid selectivity, $U_T(L)$, at the feeding grounds and bell-shaped selectivity, $U_G(L)$,

288   at the spawning grounds, both with $L_{max} = 90$ cm, to see how a fishery with mixed gear types

289   compares to fishing with only one gear type.

290 **Yield calculations**

291 The population dynamics of individuals following the optimal life history strategies were

292 simulated in a structured population model. Population size was regulated by a Beverton-Holt

293 density-dependent function for recruit survival, which on its general form can be written as:

294 $$N_2(t+2) = \frac{\lambda B(t)}{1 + \gamma B(t)} \ .$$

295 Here $N_2(t+2)$ is the number of recruits introduced into the structured population model at age 2 at

296 time $t+2$, and $B(t)$ is the population's total egg production at time t. The two parameters λ and γ

297 determine the strength of density dependence, where λ is the recruit survival at low population

298 densities and the ratio λ/γ is the asymptotic recruitment level. By choosing parameters so that

299 $\lambda = \gamma$ the asymptotic recruitment level becomes $\lambda/\gamma = 1$, implying that abundance N is scaled

300 relative to this asymptotic level.

301 We used two versions of Beverton-Holt parameters in the population dynamics

302 simulations, corresponding to different assumptions about how recruitment density dependence

303 may change with population size. First, we assumed that the Beverton-Holt relationship

304 remained constant whatever population size ($\lambda = \gamma = 5.45 \cdot 10^{-7}$; Fig. A1a). This would correspond

305 to the situation where recruitment density dependence is regulated by purely external factors

306 such as habitat availability, or by food (prey) abundance and predation that depend on static

307 populations which do not respond to the size of our focal population (Walters and Korman

308 1999). In a second scenario, we assumed that the Beverton-Holt density dependent recruitment

309 curve had constant curvature around the equilibrium population biomass. This would correspond

310 to the assumption that density dependence is felt in the same way by individuals whatever the

311 size of their population. This would occur if prey and predator populations were changing in size

312   with our focal species, or if range contractions (or expansions) led to constant strength of

313   predator-prey interactions as our focal population becomes smaller (or larger). This scenario was

314   implemented using a calibrating procedure. First, the population dynamics was run with a

315   constant recruitment $\overline{N}_2 = 0.6$. We then recorded the annual egg production in the population

316   over time to estimate its mean $\overline{B}$. The value of λ ($=\gamma$) that would let the Beverton-Holt curve go

317   through the point ($\overline{B}$, $\overline{N}_2$) was then found by solving:

318    $$\overline{N}_2 = \frac{\lambda\overline{B}}{1 + \lambda\overline{B}} \, ,$$

319   which, when rearranged, gives

320    $$\lambda = \frac{\overline{N}_2}{(1 - \overline{N}_2)\overline{B}} \, .$$

321   This value of λ was then used for the population dynamics simulations. Examples of this

322   rescaling are shown in Figure A1b.

Results

324   Our results depict the long-term effects of fishing-induced life history evolution on the stock as a

325   function of fishing on all fish, i.e. immature and mature individuals (the feeder fishery), versus

326   fishing only on mature fish (the spawner fishery). The results will be shown as 3D-surfaces

327   representing age at maturation emerging from optimal energy allocation strategies as a function

328   of maximum fishing mortality f_{max} in the feeder fishery (on the left-to-right axis) and in the

329   spawner fishery (on the front-to-back axis). Age at maturation was chosen because this central

330   life history trait is linked to population dynamics, stock productivity, and the stock's size-

331   structure. It is also the trait for which most empirical evidence suggesting fishing-induced

332   evolution has been analyzed and published (Jørgensen et al. 2007). We also show similar 3D-

333   surfaces for yield. For a stock like the Northeast Arctic cod, where the mature component of the

334   population is geographically separated for parts of the year and the two fisheries can be managed

335   relatively independently, the surfaces represent a decision landscape for our evolutionarily

336   concerned fisheries manager. In fish stocks where fishing intensity cannot be distributed between

337   mature and immature individuals, the manager should look along the diagonal line where the

338   fishing intensity is the same in the spawner and the feeder fishery.

339   We first illustrate the general effect of size-selectivity on evolution of maturation age

340   (Fig. 3). If fishing is un-selective for size (fish of all sizes are harvested with equal probability),

341   then the optimal age at maturation decreases strongly as mortality goes up in the feeder fishery,

342   while it increases slightly as the mortality in the spawner fishery becomes more intense (Fig. 3a).

343   This result agrees with the general prediction from life history theory (see also Law and Grey

344   1989, Ernande et al. 2004, and Jørgensen et al. 2006). This is in contrast to maturation evolution

345   if the fishery is based purely on trawling, where almost all combinations of harvest rates lead to

346   early maturation (Fig. 3b; sigmoid size-selectivity, $L_{max} = 70$ cm). The only exception is when

347   there is no or little fishing in the feeder fishery and just some fishing at the spawning grounds. If

348   the fish were harvested by gillnets, yet another situation occurs (Fig. 3c; bell-shaped size-

349   selectivity, $L_{max} = 90$ cm). Now there are two plateaus for optimal age at maturation depending

350   on the exploitation rate in the feeder fishery: when feeder fishery mortality is light to moderate

351   then late maturation is optimal, whereas there is a sudden drop to early maturation if harvest

352   rates become more intense at the feeding grounds. The spawner fishery has a weak effect of

353   raising age at maturation.

354   The evolutionary outcome for age at maturation in a gillnet fishery depends on its mesh

355   size, which corresponds to the fish length for which selectivity is maximal, L_{max} (Fig. 4a-c).

356 Common for the different mesh sizes is that age at maturation is most sensitive to the fishing

357 mortality in the feeder fishery. Below a threshold value for the intensity of the feeder fishery, the

358 optimal life history matures late (at ~12.8 years irrespective of mesh size). This threshold fishing

359 mortality declines from ~1.4 year^{-1} to ~0.8 year^{-1} to ~0.4 year^{-1} as the mesh size goes up from 70

360 to 90 to 110 cm, respectively. A stock adapted to a fishery with smaller mesh sizes can thus

361 withstand higher fishing rates before selection leads to early maturation ages. On the other hand,

362 if fishing were so intense that it exceeded this threshold and caused evolution toward earlier

363 maturation, then a smaller mesh size would lead to a larger drop in maturation age. This is seen

364 as the level of the rightmost plateau which increases with mesh size in the panels of Figure 4a-c,

365 where age at maturation is ~5.7 years when L_{max} is 70 cm (Fig. 4a), 7.0 years when L_{max} is 90 cm

366 (Fig. 4b), and 8.3 years when L_{max} is 110 cm (Fig. 4c).

367 The outcome is different when fishing is conducted with a gear type that has a sigmoid

368 size-selectivity, for example trawls (Fig. 4d-f). Except when fishing is confined to the spawning

369 grounds and is conducted at low intensities, it is optimal for the cod to mature below the sizes at

370 which vulnerability to harvesting is maximal. The age and corresponding sizes are: 5.6 years and

371 55 cm when L_{max} is 70 cm (Fig. 4d), 7.0 years and 72 cm when L_{max} is 90 cm (Fig. 4e), and 8.3

372 years and 88 cm when L_{max} is 110 cm (Fig. 4f).

373 The long-term equilibrium yield depends on the fisheries selectivity first because it

374 determines which fish are caught, and second because the harvesting regime leads to life history

375 evolution that changes size distributions and population dynamics and thereby which fish are

376 available for the fishery. Whatever the scenario considered for Beverton-Holt density-dependent

377 recruitment (Fig. 7 and 8), maximum yield obtained with sigmoid size-selectivity is higher than

378 with bell-shaped size-selectivity. However, high levels of yield for trawl selectivity are limited to

379 a sharp peak around a small range of harvest rates in the spawner fishery only. Harvesting in the

380 feeder fishery or at higher intensities in the spawner fishery leads to smaller yield than with

381 gillnet selectivity.

382 In one of our scenarios for yield, we rescaled the Beverton-Holt recruitment curve for

383 each optimal life history strategy so that the equilibrium population always produced the same

384 number of recruits (see Fig. A1b in the online appendix). Under these conditions, the stock did

385 not go extinct even at the highest exploitation rates (Fig. 5). In this case, yield when fishing is

386 done by gillnets appears insensitive to the harvest rate in the spawner fishery and shows a dome-

387 shaped relationship with harvest rate in the feeder fishery, peaking at $f_{max} \approx 1.5$ year^{-1} when L_{max}

388 is 70 cm, $f_{max} \approx 0.8$ year^{-1} 90 cm, and $f_{max} \approx 0.4$ year^{-1} when L_{max} is 110 cm.

389 When the Beverton-Holt stock recruitment curve was kept constant, harvest could bring

390 about stock extinction (Fig. A2 in the online appendix). This happens with bell-shaped

391 selectivity when the feeder fishery is intense ($f_{max} > 1.0$ year^{-1}; Fig. A2a,b) and with sigmoid

392 size-selectivity even when fishing is kept at low levels ($f_{max} > 0.2$ year^{-1} in the feeder fishery and

393 $f_{max} > 0.5$ year^{-1} in the spawner fishery; Fig. A2d,e). When mesh size is large (L_{max}=110 cm; Fig.

394 A2c,f), fishing does not lead to extinction as the stock is able to evolve life histories that mature

395 and reproduce sufficiently at sizes smaller than those vulnerable to fishing, regardless of whether

396 size-selectivity is bell-shaped or sigmoid. Otherwise, the surfaces that depict yield (Fig. A2) have

397 the same qualitative characteristics as with a rescaled Beverton-Holt curve (Fig. 5). The main

398 quantitative differences are that for bell-shaped size-selectivity, the maximum yield is obtained

399 at lower fishing intensities, and for sigmoid size-selectivity, the peak of high levels of yield

400 extends over a narrower range of harvest rates in the spawner fishery.

401   Finally, we ran the model with mixed gear types to better reflect how the fishery really

402   operates nowadays. We used bell-shaped size-selectivity curves in Lofoten, as fishing for the

403   spawning fish is done mostly with longlines and gillnets that both have similar size-selectivity

404   (Huse et al. 2000). For the feeder fishery in the Barents Sea, mostly done by trawling, we used

405   sigmoid size-selectivity. Both selectivity curves had a maximum selectivity size of $L_{max} = 90$ cm.

406   The resulting optimal age at maturation is similar to that when only sigmoid selectivity curves

407   (trawling) were used in both fisheries, except for very low harvest rates in the feeder fishery (Fig.

408   A3).

Discussion

410   In this paper we used a life history optimization model for fish to investigate how the size-

411   selectivity of fishing gear may affect fishing-induced evolution. We focused on two outcomes.

412   First, we assessed the degree of expected life history evolution in a given harvest regime,

413   quantified as the mean age at maturation emerging from the optimal state-dependent energy

414   allocation pattern that would result from long-term evolution as dictated by selective pressures.

415   Since we used state-dependent optimization, the energy allocation strategy that maximizes

416   lifetime reproductive value corresponds to the evolutionarily stable strategies in the environment

417   set by fishing, and the methodology includes phenotypic plasticity. Second, we quantified the

418   effects of fishing-induced evolution on the long-term equilibrium yield. The harvesting strategy

419   that maximizes long-term equilibrium yield after life-history evolution has been called the

420   evolutionarily stable optimal harvesting strategy (ESOHS, Law and Grey 1989). Instead of

421   focusing only on the single harvesting regime that optimizes yield, we show results for varying

422   fishing mortalities in both the feeder and the spawner fishery to paint decision landscapes for

423   how a harvesting strategy would affect long-term outcomes.

Maturation evolution under bell-shaped versus sigmoid size-selectivity

Our results show that whether fishing gear has bell-shaped or sigmoid size-selectivity has surprisingly strong effects on the qualitative outcomes both in terms of expected evolution of life history traits and in terms of the resulting fisheries yield. The ages and sizes at maturation that are optimal at intense fishing rates with gillnets are evolutionarily favored at even low harvest rates when trawling. It is also interesting how the gradual response in maturation age seen under random harvest disappears when fishing is size-selective, leading to a few life history outcomes that cover wide regions of parameter space and with sharp transitions between them. This can be explained by keeping in mind that fitness is defined as the expected lifetime reproductive success, which depends on the fecundity at age and the survival probability until that age.

With sigmoid size-selectivity when trawling, all fish above a certain size suffer reduced survival, which quickly erodes the advantages of maturing large with high fecundity. Even at low fishing intensities, fish that mature at sizes below the vulnerable ones have high survival until maturation, and will also survive better for the consecutive spawning seasons if they do not grow into the harvestable size classes. There is a size-refuge for small fish, which quickly becomes the best option even at low harvest intensities.

In the case of bell-shaped size-selectivity, such as with gillnets, the situation is more complex because there are size refugia for both small and large fish, while fish of intermediate size are harvested. Under intense fishing, few fish would survive as they grow through the harvestable size slot. Because the larger size-refuge is then practically unreachable due to the high fishing pressure, the optimal solution is to mature at sizes below those vulnerable, i.e. in the smaller size-refuge, as for trawling. If fishing is less intense, however, it can still pay to grow large and mature in the large size-refuge, although there is some probability of dying on the way.

447 By maturing large, fecundity will increase but survival until maturation will be reduced.

448 Depending on which effect is strongest, the expected lifetime reproductive success can be higher

449 if maturation takes place at sizes either above or below the harvestable size slot. This explains

450 the two plateaus for late and early maturation seen in optimal strategies with gillnet harvesting.

451 Also, the transition between late and early maturation is so sudden in terms of increasing harvest

452 rates because the optimal strategy is either to mature before or after the harvestable slot, but not

453 in the middle of it.

454 **Ecological advantages of bell-shaped selectivity**

455 Bell-shaped size-selectivity curves retain some of the older and larger fish in the population. The

456 fraction retained and its size composition depends on harvest rate and the exact shape and width

457 of the size-selectivity curve. There are, as Law (2007) pointed out, both good ecological and

458 good evolutionary reasons to prefer bell-shaped over sigmoid size-selectivity curves (see also

459 Berkeley et al. 2004b, Birkeland and Dayton 2005). As an example of a beneficial ecological

460 effect, a diverse age-structure has been shown to lead to enhanced recruitment in Icelandic cod

461 (Marteinsdottir and Thorarinsson 1998). In our model, the main ecological advantages of larger

462 fish are that they have higher fecundity because of sheer size, and they also have more cost-

463 effective migration to and from the spawning sites. We did not specifically implement parental

464 effects, which have the potential to add further advantages to a diverse stock structure. One

465 example of such an effect is the increased viability of larvae spawned by large or old mothers in

466 rockfish (Berkeley et al. 2004a). Similar correlations between parent size and offspring traits

467 were found also in the artificial harvesting experiment reported in Walsh et al. (2006).

468   Another interesting feature of a broad age- or size-distribution in the population is that it

469 buffers the population dynamical effects of environmental factors such as climate (Brander

470 2008). Ottersen et al. (2006) studied recruitment as a proxy for population dynamics of the

471 Northeast Arctic cod, together with regional climate indices such as the North Atlantic

472 Oscillation and sea temperature through a transect in the Barents Sea. Their main finding was

473 that the correlation between recruitment and climate grew stronger over time, in parallel with the

474 truncation of the population's age- and size-structure. As the fish matured earlier, they became

475 more tightly tied to climate. Along similar lines, Hsieh et al. (2008) reported that the

476 geographical ranges of fished species fluctuated more with climate than unfished species, and

477 they related this tightened coupling to the truncated population structure caused by fishing. For

478 the Northeast Arctic cod, one possible mechanism can be the long spawning migration, which is

479 relatively cheaper in energetic terms for larger fish. With a similar model as here but allowing

480 migration distance to vary, Jørgensen et al. (2009) showed that because a population adapted to

481 fishing will contain more early-maturing and smaller fish, the optimal migration distances are

482 shorter, and they will spawn along a reduced geographical range compared to the pristine pre-

483 fishing state. Because fish then would sample the environment over a narrower geographical

484 range, one could expect that spawning areas that are particularly good in a given year may not be

485 visited and that the population as a whole does not buffer climatic variation to the same degree as

486 before. Any such effect where large or old individuals have beneficial consequences for

487 population dynamics and recruitment would be preserved better with a bell-shaped size-

488 selectivity curve whereby some large fish are retained, compared to sigmoid size-selectivity

489 curves where also the big ones are fished out.

490 **Fishing at the spawning grounds**

491 The standard prediction from life history models without size-selective harvesting mortality is

492 that mortality at the spawning grounds, which removes only mature fish, will increase age at

493   maturation. This can be seen in the scenario with un-selective harvest (Fig. 3a) and has been

494   shown also in other studies (Law and Grey 1989, Ernande et al. 2004, Gårdmark and Dieckmann

495   2006, Jørgensen et al. 2006). The underlying life history logic is that because fecundity increases

496   with size, it becomes profitable to have large gonads when one accepts the extra mortality

497   associated with spawning. Conversely, if mortality at the spawning grounds is lower than

498   elsewhere, it would select for earlier maturation as spawning then offers a refuge from

499   harvesting.

500   With size-selective harvesting, this result holds also under the bell-shaped size-selectivity

501   typical for a gillnet fishery: although the effect is weaker, optimal maturation age goes up as the

502   spawner fishery is increased (most easily seen in the sharp transition phase between the two

503   plateaus in Fig. 4a-c). In contrast, under sigmoid size-selectivity, optimal age at maturation

504   increases with increasing harvest mortality at the spawning grounds only up to a certain point,

505   from which it suddenly drops to early maturation. The sigmoid size-selectivity creates a size-

506   refuge for small fish also at the spawning grounds, and this refuge becomes more important as

507   harvest rates go up. With little selection for early maturation in the feeder fishery and low

508   harvest rates at the spawning grounds, the benefit of maturing large still outweighs early

509   maturation (left corner of panels in Fig. 4d-f). However, increasing harvest rates in both the

510   feeder and spawner fishery removes this size-advantage, consequently leading to early

511   maturation below the harvestable size.

512   **Effects of size-selectivity on evolutionary stable yield**

513   The model predicts that trawling can give the highest yield if it selects also small fish. High yield

514   results from the same harvest rates that cause late maturation, but even a minor increase in

515   harvest intensity causes early maturation to become optimal (Fig. 4c-f, 5, A2). Thus, high

516   evolutionarily stable yield is only achieved if three conditions are met: harvest rates have to be

517   very low, mainly confined to the spawning grounds, and strictly controlled. Each of these three

518   conditions are hard to meet with current fisheries management, meaning that the optimal solution

519   is likely impossible in practice. If excess harvesting happens intermittently, it may be sufficient

520   to cause maturation evolution and long-term loss of yield.

521   Gillnets produce more stable outcomes with respect to variation in fishing rates so that

522   larger regions of parameter space give good yield (Fig. 5; see also Fig. A2). From a management

523   perspective this means that a gillnet fishery is more robust to errors in the realized fishing

524   mortality. Such errors can stem from uncertainty in stock assessments, politicized quota setting,

525   or poor enforcement of management regulations. The stock's sensitivity to evolution may also

526   vary with factors that were not included in the model. The major problem with a fishery based on

527   gear types with bell-shaped size-selectivity is that if harvest rates become too high in the feeder

528   fishery, then early maturation can become optimal, resulting also in a drop in the evolutionarily

529   stable yield.

530   **Comparing stock-recruitment curves**

531   The two alternatives we investigated for the stock–recruitment relationship represent different

532   scenarios for how the ecosystem will respond to changes in population abundance and

533   demography. It is probably unlikely that the stock–recruitment curve stays exactly the same as

534   the stock undergoes large changes (first scenario). It is probably also unlikely that the ecosystem

535   fully compensates so that the curves becomes steeper as egg production diminishes, but with the

536   same carrying capacity (second scenario). The ecosystem response will likely lie somewhere in

537   between our two scenarios, so that they bracket the potential outcomes (although at least in

538   theory, the stock–recruitment curve could also become less steep as adaptations take place). The

539   major difference between the two scenarios is that a constant stock-recruitment relationship

540   causes stock extinction at intense harvest levels.

541   Beyond stock extinction, the qualitative differences between the stock-recruitment

542   mechanisms are minor and discrepancies are mostly quantitative. Studying yield consequences of

543   fishing-induced changes is extremely difficult because it relies on critical assumptions about

544   density dependence and how the rest of the ecosystem will react to harvest-induced changes in

545   stock structure and life history traits (e.g., Abrams and Matsuda 2005, Gårdmark et al. 2003). For

546   instance, we omitted other types of density dependence than the Beverton-Holt recruit survival,

547   and many are known to act in the wild (e.g. on growth, Lorenzen and Enberg 2002; see also

548   Enberg et al. this volume and the role of size-dependent growth in Arlinghaus et al. this volume).

549   The predictions we report for yield must therefore be interpreted with caution. Fully frequency-

550   dependent models are better suited to include several sources of density dependence, and we

551   look forward to studies that address effects on yield in further detail.

552   **Robust management**

553   If our evolutionarily concerned fisheries manager could manage gear size-selectivity, she would

554   probably choose bell-shaped size-selectivity. One reason is that sigmoid size-selectivity easily

555   leads to stock extinction or extremely low yield, depending on the stock-recruitment scenario, as

556   soon as harvest rates increase to moderate levels. In contrast, population dynamics is much more

557   robust under gillnet selectivity, which yields favorable outcomes over a larger area of parameter

558   space.

559   However, when implementing a gillnet fishery, our manager is faced with a trade-off

560   with respect to the choice of mesh size. For small mesh size, the population is evolutionarily

561   relatively insensitive to harvest rates, and only with extreme fishing rates at the feeding grounds

562 will it become optimal for cod to mature early. Yield is also high across many combinations of

563 harvest rates on the feeding and spawning grounds. However, small mesh size also means that if

564 harvest rates are so high as to lead to evolution, then the resulting life history strategy matures at

565 a very early age. When mesh size is large, the late maturation plateau shrinks, evolution toward

566 the early maturation plateau may take place at lower fishing intensities, but the early maturation

567 plateau corresponds to a later maturation age. By choosing larger mesh sizes, the manager thus

568 needs to exercise more caution in controlling the applied harvest rates, but she risks less of a

569 reduction in maturation age if she fails. The optimal level of this trade-off depends on how

570 important it is for management to prevent evolution and to what degree the fisheries management

571 institution can influence quotas and control the fishing fleet.

572 **Comparison with current fishing regime**

573 Currently, Northeast Arctic cod is mostly fished by trawlers in the Barents Sea, represented by

574 the feeder fishery in our model, with a harvest rate around 0.5 year^{-1}. The potential to market

575 fresh fish year round concentrates effort on the feeder fishery rather than the spawner fishery,

576 where fish are only present for a few months. In contrast, the spawner fishery consists mostly of

577 long-liners and gill-netters. Our model predicts that with these gear types, any harvest rate above

578 0.2 year^{-1} in the feeder fishery has the potential to cause early maturing fish, regardless of the

579 mortality in the spawner fishery. Maturation ages have indeed declined in the Northeast Arctic

580 cod (Jørgensen 1990), and the observed temporal trend can be related to changes in the

581 probabilistic maturation reaction norm (Heino et al. 2002), which suggests that its cause is

582 evolutionary. The observed changes in the stock are consistent with the predictions from our

583 model, although we cannot assess evolutionary rates because optimization methods find

584 evolutionary endpoints but do not answer whether these endpoints are attainable or at what rates

585   they may be attained. On this issue, it is worth noting that the rate of change of maturation age in

586   Northeast Arctic cod is comparable to observed rates in many other stocks thought to undergo

587   fishing-induced evolution (quantified in the online appendix of Jørgensen et al. 2007). It would

588   be interesting to look into what gear types have been used in these fisheries, how the use of gear

589   and its selectivity have changed over time, what evolutionary outcomes one could expect, and

590   finally compare those predicted outcomes to the observed life history changes for these stocks.

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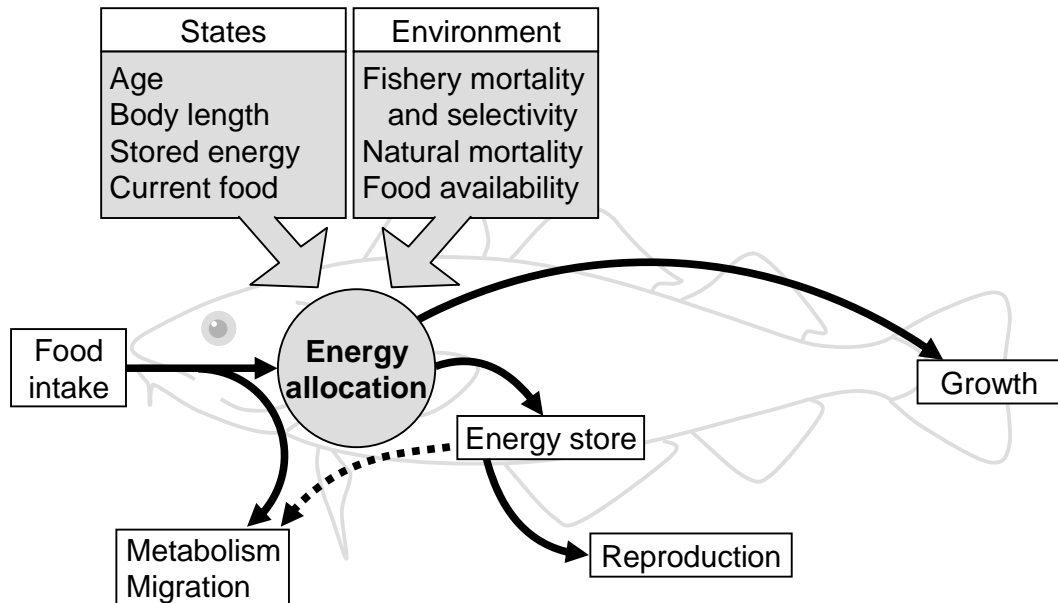
Figures

Figure 1. Graphical representation of the life-history energy-allocation model, parameterized for the Northeast Arctic cod (*Gadus morhua*). The central process is energy allocation toward growth or stores/reproduction. The energy allocation can take independent values depending on the individuals state (age, size, level of energy stored, and current food availability). The model is then solved with different forcing, here with focus on changing the size-selectivity and intensity of the fishing mortality. Black arrows denote energy flow. In periods when food intake is insufficient for metabolic demands, energy requirements can be met by stores (dotted line). The figure is modified from Jørgensen and Fiksen (2006).
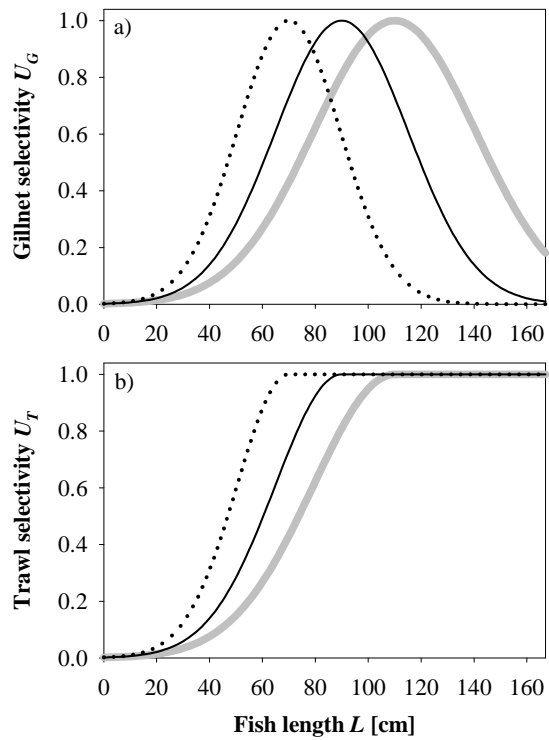
Figure 2. Size-selectivity curves used to impose selection on Northeast Arctic cod life histories. At maximum selectivity, fish of that size are harvested at the rate specified by the parameter f_{max}. a) Bell-shaped size-selectivity curves for gillnets. The peaks of the Gaussian functions are at 70 cm (dotted line), 90 cm (thin black line), and 110 cm (thick grey line). In each case the standard deviation is 28% of the mean. b) Sigmoid trawl selectivity was modeled based on the same probability distributions as for gillnets, but with maximum selectivity for all fish lengths larger than the peak.
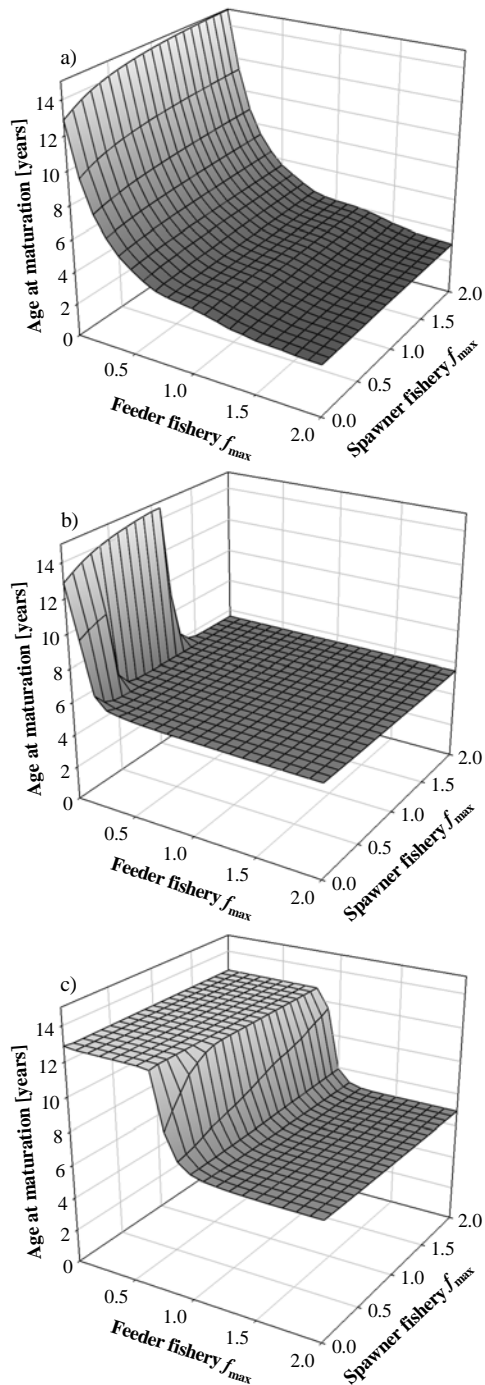
Figure 3. The effects of size-selective fishing gear on optimal age at maturation in the Northeast Arctic cod *Gadus morhua*. The left-to-right axis is the fishing mortality f_{max} [year^{-1}] in the feeder fishery at the sizes where selectivity is 1, and the front-to-back axis is the fishing mortality f_{max} [year^{-1}] at the spawning grounds. a) Unselective fishing mortality; all sizes have the same probability of being caught (selectivity U is always 1). b) Sigmoid trawl selectivity, where the size-selectivity of the fishery increases with the fish' body size (here at maximum from $L_{max} = 70$ cm onwards). c) Bell-shaped size-selectivity is typical for gillnets (here with maximum selectivity at $L_{max} = 90$ cm).

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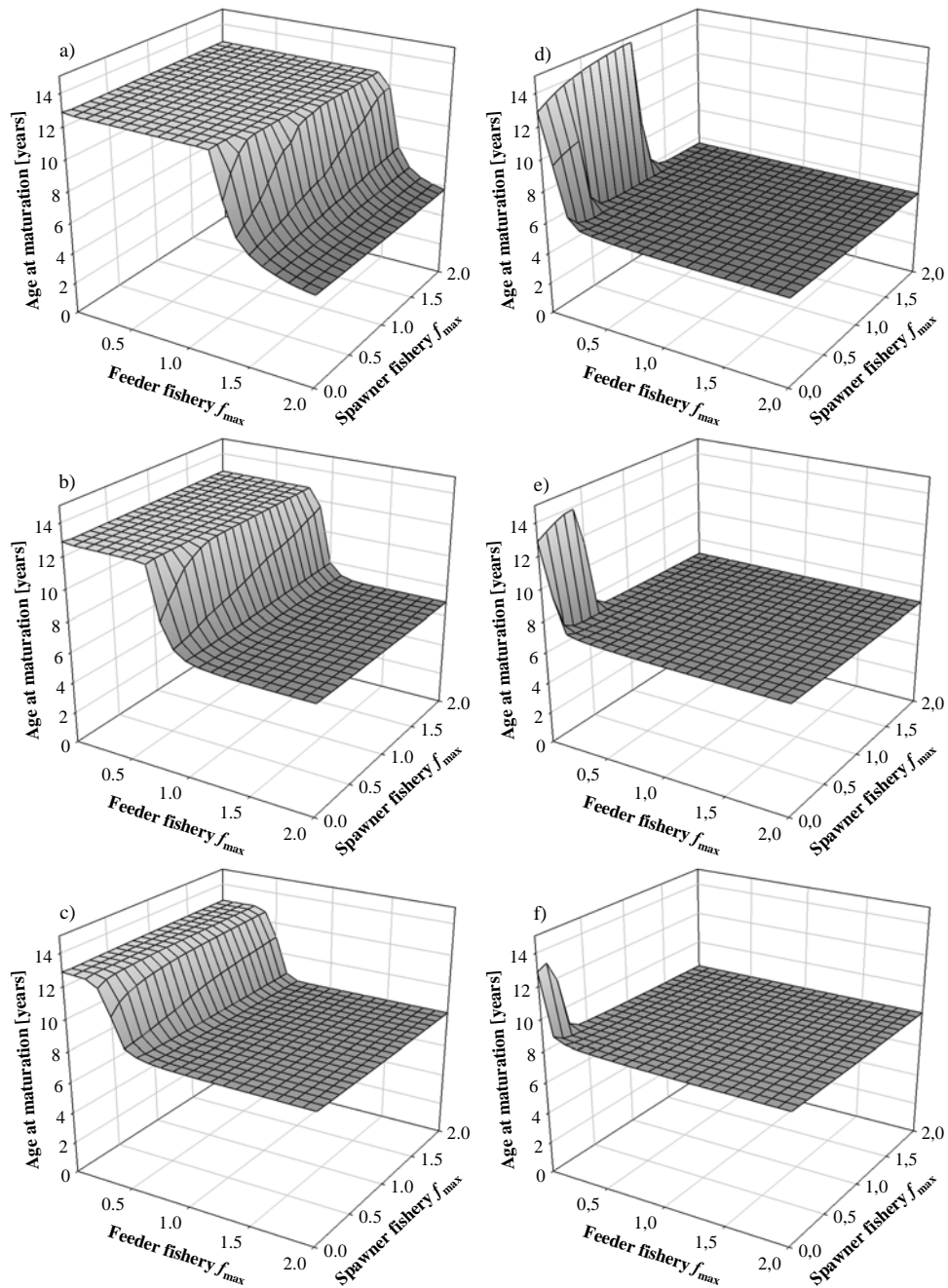
Figure 4. Optimal age at maturation in the Northeast Arctic cod, shown for increasing fishing mortality rates f_{max} [year^{-1}] in the feeder and spawning fishery. a-c) with bell-shaped size-selectivity curves as is typical for gillnets, and d-f) with sigmoid size-selectivity curves for example with trawls. Maximum selectivity L_{max} is at: a,d) 70 cm; b,e) 90 cm; and c,f) 110 cm. See legend to figure 3 for further explanation of axes.

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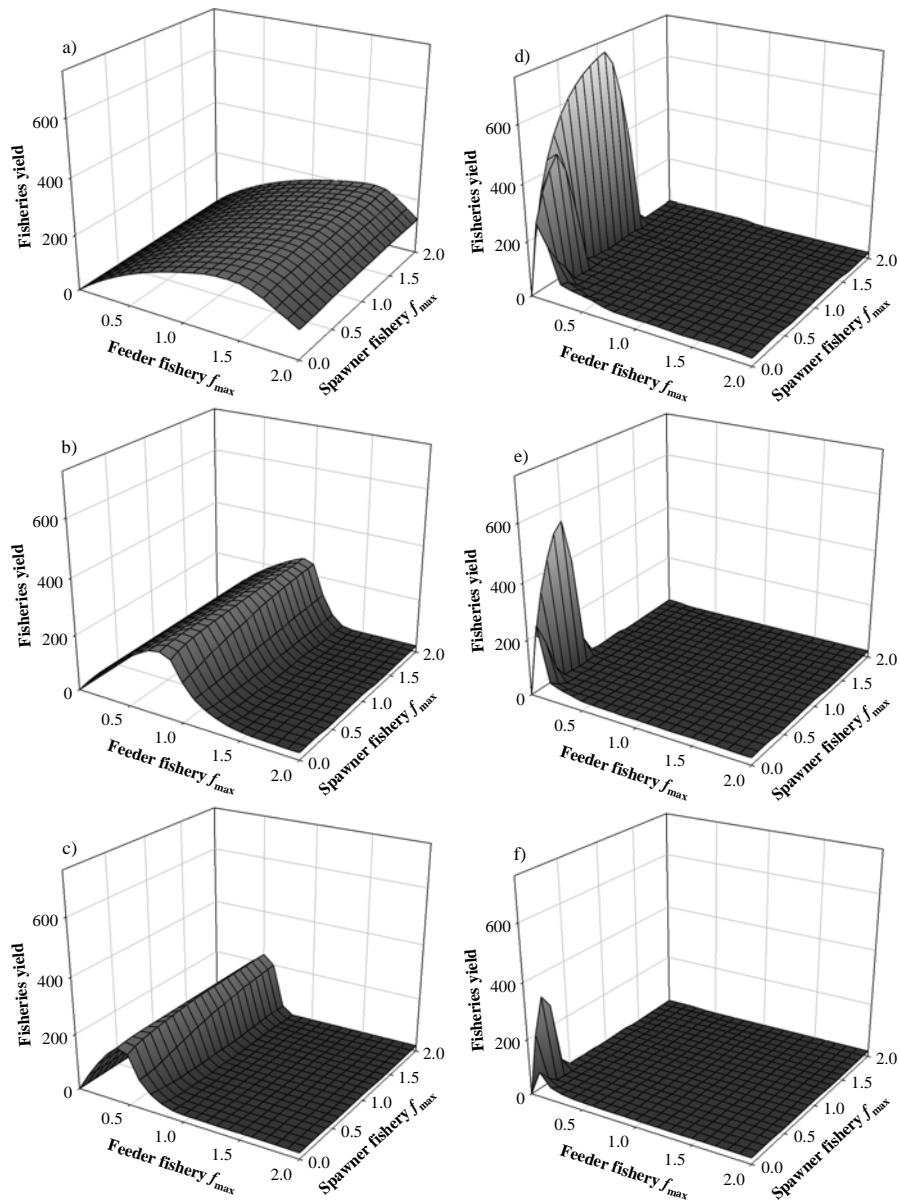
Figure 5. Long-term equilibrium yield as in Figure 6, but with the assumption that the Beverton-Holt total egg production-recruitment curve is rescaled so that the equilibrium population always produces the same number of recruits. The recruitment curve has thus increased in steepness as harvest becomes stronger, as in Fig. A1b). Bell-shaped size-selectivity: a) L_{max} = 70 cm; b) L_{max} = 90 cm; c) L_{max} = 110 cm. Sigmoid size-selectivity: d) L_{max} = 70 cm; e) L_{max} = 90 cm; f) L_{max} = 110 cm. Further legend is given in Figure 3.

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Size-selective fishing gear and life history evolution in the Northeast Arctic cod

*Christian Jørgensen, Bruno Ernande, and Øyvind Fiksen*

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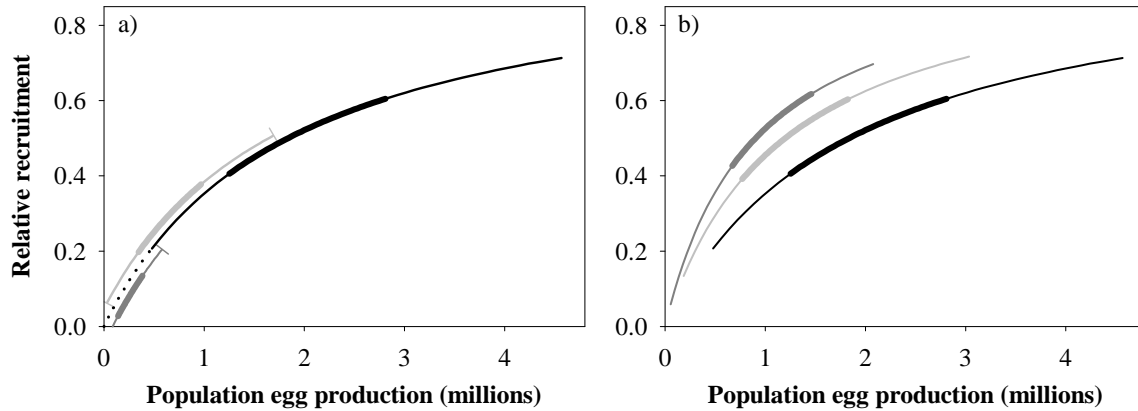
Figure A1. Beverton-Holt stock recruitment curves used in two scenarios to calculate long-term fisheries yield at evolutionary equilibrium when cod life histories evolve in response to size-selective fishing gear. a) In the first scenario we assume that the stock recruitment curve remains constant. The black curve shows the range of total egg production and corresponding recruitment for the stock prior to harvest, with the thin line representing the 90% range and the thick line the 50% range. The dotted line is the continuation of this curve to the origin. After harvesting and resulting life history evolution, the stock produces fewer eggs annually and recruitment is correspondingly lower (the lines are displaced slightly to improve readability; light grey lines harvest rate 0.1 year^{-1} in both the feeder and spawner fishery; dark grey lines harvest rate 0.3 year^{-1}; all fish were harvested with equal probability regardless of size as in Fig. 3a of the main manuscript). b) In the second scenario we rescaled the steepness of the Beverton-Holt curves so that a population with lower egg production produces the same number of recruits on average also after life histories have evolve (shading corresponds to harvest rates as in panel a).

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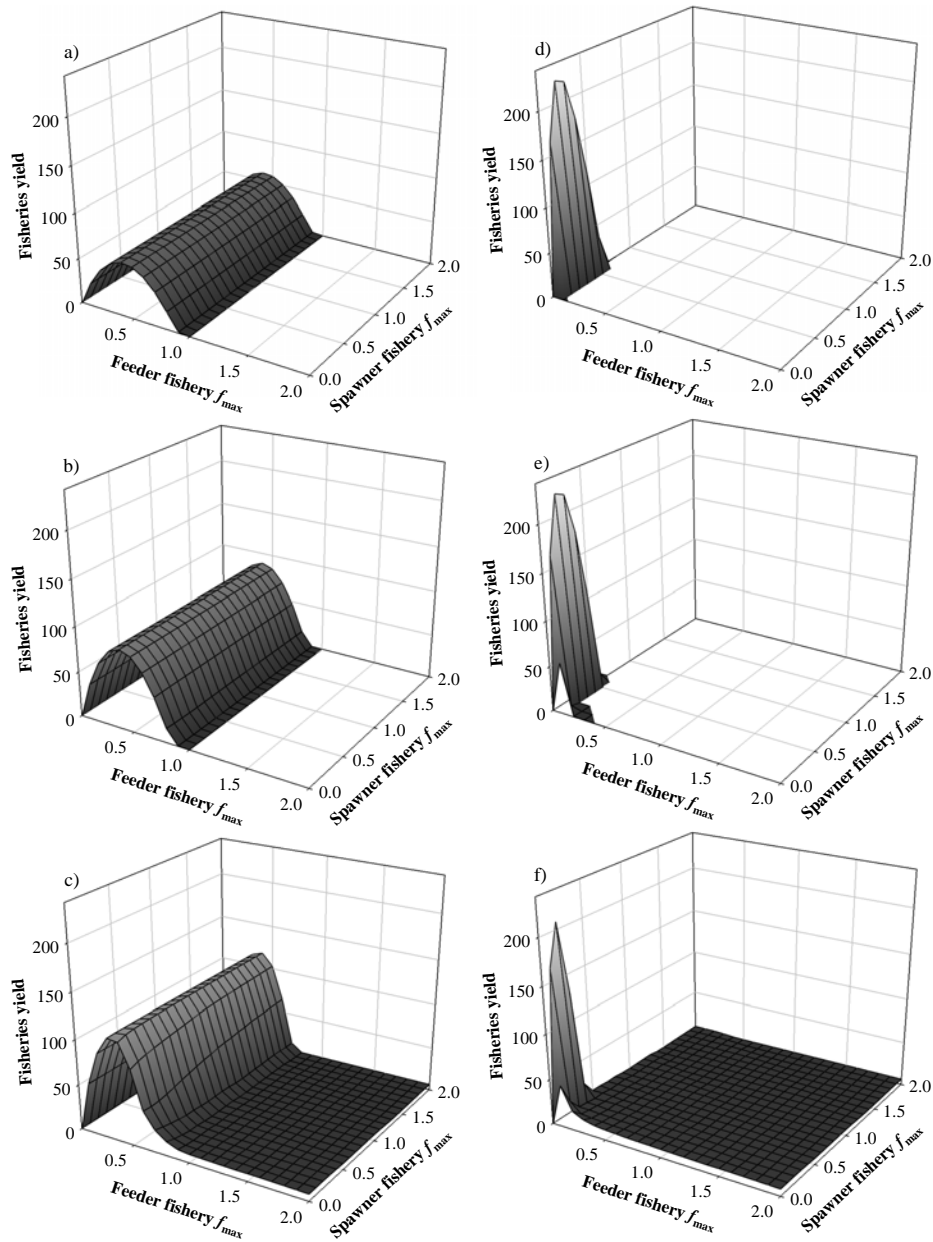
Figure A2. Long-term equilibrium yield for the optimal life history strategies under different harvest levels when the Beverton-Holt total egg production-recruitment curve is assumed to remain constant with the parameters as in the pre-harvest situation. Bell-shaped size-selectivity: a) L_{max} = 70 cm; b) L_{max} = 90 cm; c) L_{max} = 110 cm. Sigmoid size-selectivity: d) L_{max} = 70 cm; e) L_{max} = 90 cm; f) L_{max} = 110 cm. For further explanation of axes see Fig. 3 in the main article.

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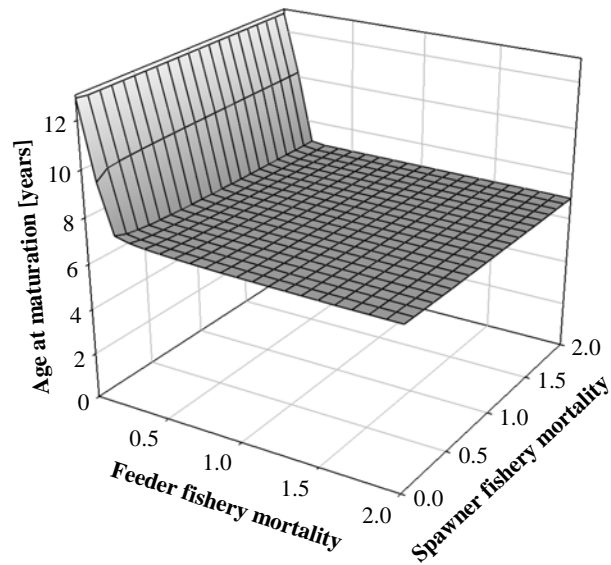
Figure A3. Optimal age at maturation in when gear selectivity reflects the gear types used in the fishery for Northeast Arctic cod, that is trawling with sigmoid size-selectivity at the feeding grounds and gillnets and longline with bell-shaped selectivity curves at the spawning grounds. For both gear types we used L_{max} = 90 cm. The axes are further explained in the legend to Fig. 3 of the main article.