

Sex-specific life history strategies in capelin (*Mallotus villosus*)?

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Abstract: The life history of capelin (*Mallotus villosus*) is presently suggested to be sex specific: while males follow a semelparous batch-spawning strategy, females are iteroparous. This hypothesis is based on predictions from a life history simulation model of Barents Sea capelin that shows that iteroparity is more profitable than semelparity for females, but for males, semelparity with several matings with females may be as profitable as iteroparity. These predictions are supported by (i) reports of males mating with several females during a spawning season, (ii) males having a lower gonadosomatic index than females and instead spending their energy on mating and somatic growth, and (iii) an observed higher mortality for males after spawning. The Darwinian fitness of female capelin is limited by the amount of eggs they can carry, and offspring production may only be increased by undertaking several spawning seasons with yearly intervals. Added together, these indices suggest that male and female capelin follow different life history strategies.

Résumé : À l'heure actuelle, il semble que le cycle biologique du capelan (*Mallotus villosus*) soit différent selon le sexe : les mâles sont semelpares avec reproduction en lots, tandis que les femelles seraient itéropares. Cette hypothèse repose sur les prévisions d'un modèle de simulation du cycle biologique du capelan de la mer de Barents qui montre que l'itéroparité est plus avantageuse que la semelparité chez les femelles; mais, chez les mâles, la semelparité associée à plusieurs accouplements avec des femelles peut être aussi avantageuse que l'itéroparité. Ces prévisions sont appuyées par (i) des mentions d'accouplements de mâles avec plusieurs femelles pendant une saison de ponte, (ii) l'existence chez les mâles d'un indice gonadosomatique plus faible que celui des femelles et l'utilisation, chez les mâles, de l'énergie pour l'accouplement et la croissance somatique et (iii) une mortalité observée plus élevée chez les mâles après la reproduction. La valeur adaptative darwinienne des femelles est limitée par le nombre d'oeufs qu'elles peuvent porter, et plusieurs saisons de ponte à intervalles annuels sont nécessaires pour augmenter le nombre de descendants. Tous ces indices combinés portent à croire que les capelans mâle et femelle ont un cycle biologique différent.

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Introduction

The capelin (*Mallotus villosus*) is a small pelagic planktivorous fish with circumpolar Arctic distribution. Historically the largest stocks in the North Atlantic have been found around Newfoundland, Iceland, and in the Barents Sea (Templeman 1948; Jangaard 1974; Stergiou 1989) where, due to its high abundance, it is an important commercial resource (for review, see Jangaard 1974). Capelin mature at 2–4 years of age (Olsen 1968) and are often considered to be semelparous (Jangaard 1974; Gjøsæter 1995). At Iceland and Newfoundland, however, female capelin may undertake several spawning seasons with yearly intervals (Templeman 1948; Shackell et al. 1994; Vilhjálmsson 1994). The capelin at Newfoundland are, with a few exceptions, beach spawners (Templeman 1948) whereas at Iceland and in the Barents Sea, spawning takes place at depths between 10 and 100 m (Sætre and Gjøsæter 1975; Vilhjálmsson 1994).

Life history strategies have been defined as “programs of decision rules where an individual chooses between available developmental or behavioural alternatives at critical control points” (Cohen 1993). Differences in juvenile and adult survival have important implications for the life history strategy

of an organism (Cole 1954; Murphy 1968; Orzack and Tuljapurkar 1989; Armstrong and Shelton 1990; Roff 1992). While variable or high juvenile mortality generally favours iteroparity (Murphy 1968; Orzack and Tuljapurkar 1989), high adult mortality may force the optimal life history strategy towards semelparity. In the Barents Sea, juvenile mortality (defined here as mortality until spawning) of capelin is usually excessive for year-classes produced when immature Atlantic herring (*Clupea harengus*) are abundant, due to herring predation on the larvae (Hamre 1988; Fossum 1992; Huse and Tøresen 1995). Such recruitment failure occurs at irregular intervals. Juvenile mortality is variable for the capelin stocks at Iceland and Newfoundland as well, but the main cause for this mortality seems to be larval starvation rather than predation (Frank and Carscadden 1989; Vilhjálmsson 1994). Predation by Atlantic cod (*Gadus morhua*) (Mehl 1989; Methven and Piatt 1989; Lilly 1991; Shackell et al. 1994; Vilhjálmsson 1994) and marine mammals (Piatt et al. 1989; Haug et al. 1996) causes high mortality on the older juvenile (2 years and older) and adult capelin (adult mortality defined as mortality between spawning seasons), especially during the spawning migration. Hence, capelin life history is constrained both by variable juvenile mortality and by high adult mortality. Female capelin shed their eggs in one batch (Jeffers 1931; Friðgeirsson 1976). After spawning the females leave the spawning ground while the males stay and may mate with several females (Templeman 1948; Møller and Olsen 1962; Friðgeirsson 1976). To increase her Darwinian fitness, a female must rebuild the gonads and return to spawn the following year. However, a male

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Table 1. Description of the different strategies and fitness equations applied in the model.

Strategy	Strategy applies to:	Fitness equation
00010 ($M = 1$)	Males	$\ln(S_{0-4} \cdot F \cdot M)/4$
00020 ($M = 2$)	Males	$\ln(S_{0-4} \cdot F \cdot M)/4$
00030 ($M = 3$)	Males	$\ln(S_{0-4} \cdot F \cdot M)/4$
00002 ($M = 2$)	Males	$\ln(S_{0-4} \cdot S_{4-5} \cdot F \cdot M)/5$
00004 ($M = 4$)	Males	$\ln(S_{0-4} \cdot S_{4-5} \cdot F \cdot M)/5$
00011 ($M = 1+1$)	Males	$S_{0-4} \cdot F \cdot M \cdot e^{-r \cdot 4} + S_{0-4} \cdot S_{4-5} \cdot F \cdot M \cdot e^{-r \cdot 5}$
00010 ($M = 1$)	Females	$\ln(S_{0-4} \cdot F_4 \cdot M)/4$
00001 ($M = 1$)	Females	$\ln(S_{0-4} \cdot S_{4-5} \cdot F_5 \cdot M)/5$
00011 ($M = 1 + 1$)	Females	$S_{0-4} \cdot F_4 \cdot M \cdot e^{-r \cdot 4} + S_{0-4} \cdot S_{4-5} \cdot F_5 \cdot M \cdot e^{-r \cdot 5}$

Note: Seven of the strategies are calculated by the relationship $r = \ln(R_0)/G$ where r is the intrinsic rate of increase, R_0 is the net reproductive rate, and G is generation time (e.g., Roff 1992). The 00011 strategies are solved using the Euler–Lotka equation (e.g., Roff 1992) by iteration. S_{0-4} is survival from egg stage until age 4 (see text), S_{4-5} is survival from age 4 to age 5, M is number of matings, and F is fecundity. It is assumed that males have an equal probability of mating with a 4- or 5-year-old (drawn using Monte-Carlo simulations). The F_4 and F_5 values refer to age-specific fecundities of capelin, and the S_{0-4} , F_4 , and F_5 values are drawn randomly from Table 2 using Monte-Carlo simulations.

may achieve this by concentrating his reproductive effort within one spawning season in which he may fertilise the entire egg production of several females. Which strategy is the most profitable will be a trade-off between interannual variability in juvenile mortality and the level of the adult mortality.

My hypothesis in the present study is therefore that male and female capelin have different life history strategies. A model is developed that simulates the profitability of various life history strategies for males and females. The predictions from this model will be discussed with reference to a field investigation of gonad investment and a literature review of sex-specific features of capelin in mortality rates, size, spawning behaviour, and energy allocation pattern. An underlying assumption is that over evolutionary time, organisms have become adapted to their environment through the process of evolution by natural selection (Darwin 1859).

Materials and methods

Field investigation

The material was collected on cruises with RV *G.O. Sars* and RV *Johan Hjort* in February 1996. Capelin (120 males and 70 females) caught at four different stations in the southern Barents Sea were included in the study. The capelin were captured in areas close to shore using a demersal trawl and were frozen immediately following capture. In the laboratory, capelin were thawed, measured to the nearest millimetre, and weighed (0.1-g resolution). Otoliths were removed, embedded in Histokitt® on trays, and read according to standard methods (Gjøsæter 1985). The abdomen was then opened and the gonads were removed, dried (110°C for 24 h, Kjesbu et al. 1991), and weighed (0.01-mg accuracy). The gonadosomatic index (GSI) was estimated as dry gonad weight divided by the total wet weight of the fish.

Life history model

A model was developed to test the profitability of different capelin life history strategies. Three basic strategies are compared: early semelparity, delayed semelparity, and iteroparity. Different outcomes

Table 2. The S_{0-4} values give the probability of an egg laid to survive until spawning at age 4 for a year-class produced in the given year, and the F_4 and F_5 values give the average fecundity of the 4- and 5-year-olds of the spawning stock that produced the year-class.

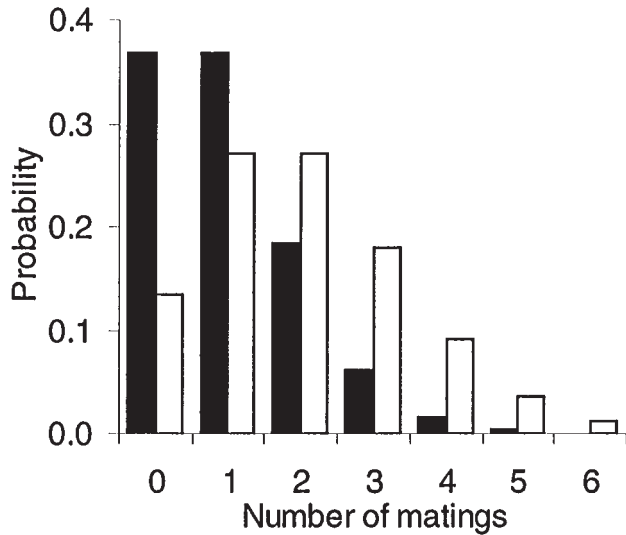
Year	F_4	F_5	S_{0-4}
1973	12 569	14 468	3.08×10^{-4}
1974	9 269	15 527	2.15×10^{-4}
1975	10 056	13 078	7.53×10^{-5}
1976	11 194	13 276	8.10×10^{-5}
1977	13 473	15 392	1.44×10^{-4}
1978	13 325	15 302	5.99×10^{-5}
1979	11 790	15 482	1.10×10^{-4}
1980	14 147	17 044	2.60×10^{-5}
1981	13 570	16 448	7.95×10^{-5}
1982	15 392	17 128	4.11×10^{-5}
1983	14 476	14 709	5.69×10^{-6}
1984	14 147	18 036	2.28×10^{-7}
1985	11 522	12 877	2.02×10^{-6}
1986	12 212	13 078	5.78×10^{-5}
1987	12 212	15 509	1.94×10^{-3}
1988	13 619	15 509	4.11×10^{-4}
1989	16 231	15 509	2.01×10^{-3}
1990	18 036	14 985	1.98×10^{-5}
1991	14 662	19 228	5.36×10^{-6}

of these strategies are tested, and the fitness equations of the strategies and their outcomes are shown in Table 1. The model considers a 5-year life span where spawning occurs at age(s) 4 and (or) 5, which is consistent with capelin life history (Olsen 1968). The strategies are named by their age-specific number of matings: 00011 means that there are no spawnings in the first 3 years, one in the fourth year, and one in the fifth year. It is assumed that females spawn all their eggs in one batch (Jeffers 1931; Friðgeirsson 1976). Hence, some of the outcomes are only available to males (such as 00030) whereas others (such as 00010 and 00011) are available to both males and females. The outcomes 00010 and 00020 are potential outcomes of the same semelparous strategy. The fecundity values in Table 2 are calculated using a fecundity–weight relationship taken from Huse and Gjøsæter (1997):

$$F_i = 2410 \cdot W_i^{0.61}$$

where F_i and W_i are the average fecundity and the average weight, respectively, of age group i (4 or 5) in a given year. Average weights and number of capelin are taken from life tables (Anonymous 1996; H. Gjøsæter, IMR, N-5024 Bergen, Norway, unpublished data). Population fecundity (Serebryakov 1990) was calculated by multiplying the age-resolved average fecundity F_i by the number of mature females at each age (Anonymous 1996) and adding this together for each year. Fish greater than 14 cm were assumed to be mature (Forberg and Tjelmeland 1985). In addition to the 4- and 5-year-olds, eggs produced by 3- and 6-year-olds were included in the population fecundity in years when these were present in the spawning stock. The S_{0-4} values (Table 2) are calculated by dividing the number of 4-year-olds by the estimated population fecundity of the spawning stock that produced them (Anonymous 1996). Hence, S_{0-4} is the probability of a spawned egg to survive until spawning at age 4. It is assumed that all eggs produced are spawned. The cruises from which the figures for the 4-year-olds are taken are carried out in September–October (Dommasnes and Røttingen 1985) when the capelin are 3.5 years old. The S_{0-4} values are therefore slightly overestimated. To include the mortality from September–October until March–April when the

Fig. 1. Arbitrary probability distribution of number of matings per male assuming that this can be described by a Poisson distribution with parameters 1 (solid bars) or 2 (open bars).



spawning occurs, a fixed survival of 0.76 (24% mortality) is set for the 6-month period (Hamre and Tjelmeland 1982).

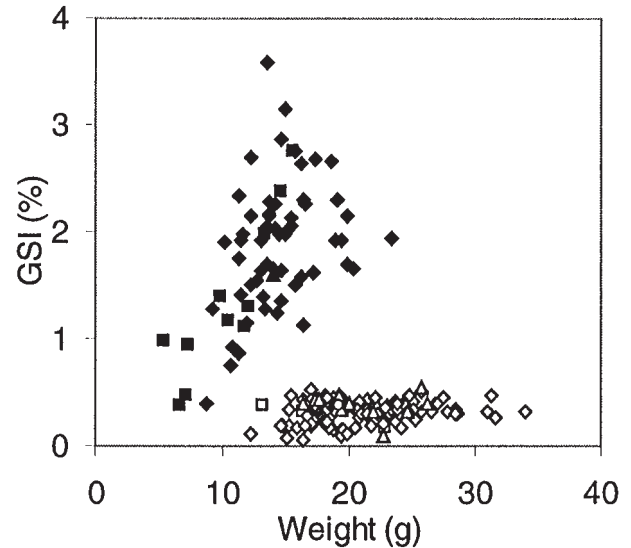
A considerable body of literature exists regarding what is the appropriate Darwinian fitness measure to use, and the topic is still a matter for debate (for reviews, see Roff 1992; Yoshimura and Clark 1993). I used the intrinsic rate of increase r to calculate the fitness of the different outcomes (Table 1). Since λ is a nonnegative fitness measure, as opposed to the intrinsic rate of increase r , it can be used to calculate geometric mean fitness over a number of generations. When fitness varies between generations, geometric is preferred to arithmetic mean fitness (Roff 1992). The r values are therefore transformed to the finite rate of increase λ using the relationship $\lambda = e^r$ (e.g., Roff 1992). The geometric mean λ_i ($G\lambda_i$) of 100 000 Monte-Carlo simulations of each strategy is calculated as

$$G\lambda_i = \prod_{j=1}^n \lambda_{ij}^{1/n}$$

where n is the number of simulations of strategy i and λ_{ij} is the fitness of strategy i in simulation (generation) j . The geometric mean λ is analogous to the stochastic growth rate a (Orzack and Tuljapourkar 1989), since $\ln \lambda = a$. This means that the exponent of the average stochastic growth rate of each strategy is calculated. For each simulation, a year with corresponding S_{0-4} , F_4 , and F_5 values is drawn randomly from Table 2, and each year has an equal probability of being selected in each simulation. The fitness of the strategies is then calculated using the parameter values for the chosen year, and this process is repeated over and over. The model is run over a range of different S_{4-5} values. The population fecundity estimates in Table 2 are somewhat lower than estimates carried out by Serebryakov (1990) for a 14-year period. However, the correlation in population fecundity between the studies was quite good (correlation coefficient 0.73).

The model is extended to include variability in the number of matings actually achieved, since this affects the fitness of the different male strategies. Poisson-distributed mating probabilities are used to give the number of matings achieved in a year. This is carried out by drawing the number of matings achieved in a year using Monte-Carlo simulations in the same way as with the fecundity and survival data. The mating data are drawn randomly from the distributions in Fig. 1. When using the Poisson distribution, it is assumed that the number of matings achieved is a random process (e.g., Bhattacharyya and Johnson 1977). The model is run with Poisson parameters of 1 and 2

Fig. 2. GSI (dry weight of gonads over wet body weight) of different ages of male (open symbols) and female (solid symbols) capelin versus wet body weight. Squares indicate 2-year olds, diamonds indicate 3-year olds, triangles indicate 4-year olds, and circles indicate 5-year olds.



(one and two matings expected, respectively). Since geometric means are applied to calculate the fitness, a finite growth rate equal to 0 in one simulation will bring the long-term fitness to 0. To avoid this, the number of matings is set to 0.1 when the number of matings drawn is 0, so that the fitness still can be calculated using geometric means.

Results

Field study

There were great differences in GSI between male (average 0.32%) and female (average 1.8%) capelin ($P < 0.001$, Kruskal–Wallis). The GSI was highly size dependent for females ($P < 0.01$, regression analysis), but was size independent for males ($P > 0.05$, regression analysis) (Fig. 2). For the females, the 2-year-olds had significantly lower GSI than the older ones ($P < 0.05$, Kruskal–Wallis), but there were no such differences among the males ($P > 0.05$, Kruskal–Wallis).

Model results

Male strategies

The profitability of the iteroparous strategy decreases as the adult mortality ($1 - S_{4-5}$) increases (Fig. 3). When adult mortality is below 0.52 the profitability of iteroparity (00011) is higher than for the other outcomes calculated (Fig. 3). The 00002 outcome is poorer than the 00020 outcome for all levels of adult mortality (Fig. 3). The 00010 strategy is the poorest of all and it intercepts with the 00011 strategy for an adult mortality of 1. The profitability of the delayed semelparous strategy falls steeply with increasing adult mortality risk, but the fitness of the early semelparous strategy (00010) is obviously unaffected by adult mortality.

Female strategies

The fitness of the iteroparous strategy is much higher than that of the semelparous strategies except when the adult mortality

Fig. 3. Fitness (geometric mean finite rate of increase, λ) of 100 000 Monte-Carlo simulations of different male (solid lines) and female (broken lines) life history strategies given observed fecundity and survival probabilities of the Barents Sea capelin. Basic run. Parameter values are given in Tables 1 and 2. The strategies that only reproduce at age 5 (00001, 00002, 00004) have a zero fitness when adult mortality ($1 - S_{4-5}$) is 1. The scale on the y-axis is shortened to enhance the readability of the figure.

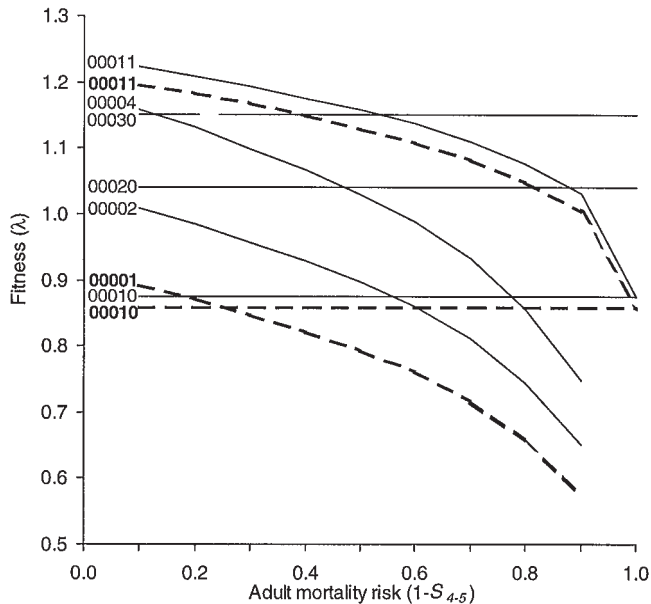
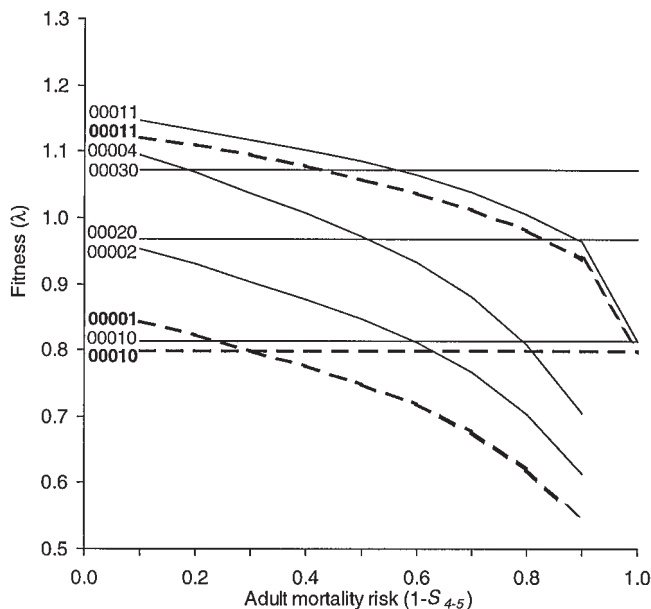
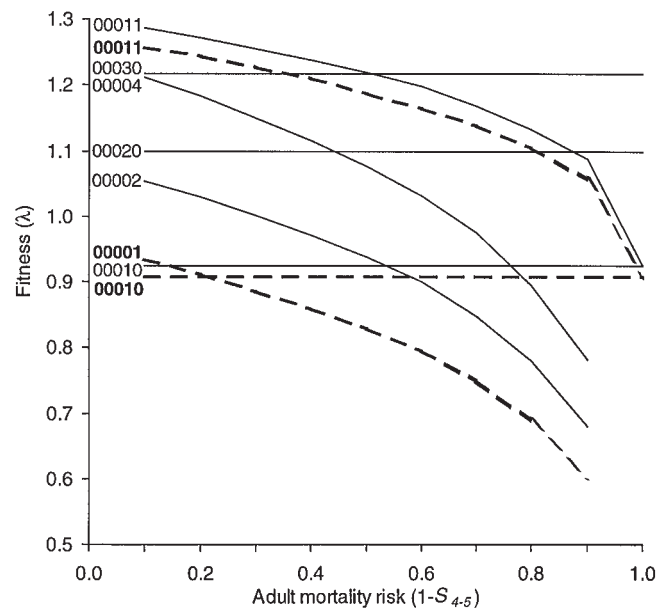


Fig. 4. Fitness (geometric mean finite rate of increase, λ) of 100 000 Monte-Carlo simulations of different male (solid lines) and female (broken lines) life history strategies given observed fecundity and survival probabilities of the Barents Sea capelin (see Fig. 3). Sensitivity run with fecundity decreased by 25%.



is 1 (Fig. 3). When adult mortality is below 0.24, delayed semelparity (00001) is more profitable than early semelparity (00010). The female 00011 and 00010 strategies are slightly

Fig. 5. Fitness (geometric mean finite rate of increase, λ) of 100 000 Monte-Carlo simulations of different male (solid lines) and female (broken lines) life history strategies given observed fecundity and survival probabilities of the Barents Sea capelin (see Fig. 3). Sensitivity run with fecundity increased by 25%.



less profitable than the corresponding male strategies, since males are given an equal probability of mating with a 4- and 5-year-old (with higher fecundity than the 4-year-olds) female.

Sensitivity analysis

A sensitivity analysis was carried out to assess the impact of differences in the parameters on the profitability of the different strategies. Fecundity (F_i) and juvenile survival (S_{0-4}) were hence decreased and increased by 25%. The model is affected equally by changes in these parameters, and only the results with changes in fecundity are shown here. Decreased fecundity reduces the fitness of the early semelparous strategy relative to the delayed semelparous and iteroparous strategies (Fig. 4). Increased fecundity, on the other hand, improves the profitability of the early semelparous strategy compared with the delayed semelparous and iteroparous strategies (Fig. 5). The relative profitability of delayed reproduction depends on whether λ is smaller or greater than 1. In growing populations ($\lambda > 1$), early semelparity (shorter generation time) is favoured whereas delayed semelparity (longer generation time) has a relatively higher fitness in decreasing populations ($\lambda < 1$) (e.g., Roff 1992). This result is intuitive and can be obtained from the formulas in Table 1.

Poisson-distributed matings

In the computer runs above, it is assumed that the number of matings achieved for a male is deterministic. When this assumption is relaxed and the number of matings is drawn randomly from a Poisson distribution, the profitability of the different male strategies changes. For a Poisson parameter of 1 (one mating on average) the fitness of the semelparous strategy is reduced (Fig. 6) compared with one mating per male (Fig. 3). With a Poisson parameter value of 2 the profitability

of the semelparous strategies increases and approaches that of the iteroparous strategy. Since the λ of most of the semelparous strategies is below 1, delayed semelparity is relatively more profitable than early semelparity.

Discussion

Life history theory

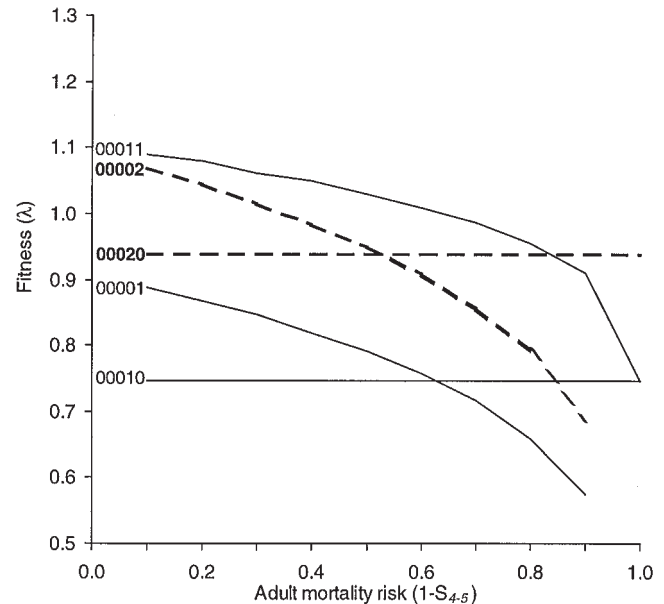
In general, high or variable juvenile mortality selects for iteroparous life history strategies, while high adult mortality selects for semelparous strategies (Cole 1954; Murphy 1968; Orzack and Tuljapourkar 1989; Roff 1992). The present model compares the profitability of essentially three different life history strategies given the observed recruitment pattern and population fecundity of the Barents Sea capelin. It is assumed here that the observed juvenile survival and population fecundity figures are representative for those governing the life history evolution of the Barents Sea capelin. The model results can therefore be used to discuss the relative profitability of semelparity and iteroparity.

The advantage of a semelparous strategy is to escape from high adult mortality at the cost of all offspring being produced within one spawning season. At high interannual variation in recruitment success, the "fitness risk" associated with a semelparous strategy is high. The difference in fitness between the semelparous and iteroparous female strategies is great, which means that a female capelin will have a lot to gain by moving from either semelparous strategy to an iteroparous strategy. The "fitness costs" of such a move seem very low for females, as they only have to maintain enough energy reserves (which is traded off against egg production) to be able to take up feeding and prepare for the northward migration. Female capelin should hence be expected to follow an iteroparous strategy where the survival until the second spawning is conditional, determined by the predation pressure from cod (Mehl 1989) among other factors. The fitness difference between the iteroparous and semelparous (00010) strategies of male capelin is similar to that of the female. However, a male may increase his fitness without having to face the harsh adult mortality embedded in the iteroparous strategy if he can mate with two (00020) or three (00030) females within the same spawning season. I therefore predict that male capelin should follow a batch-spawning semelparous strategy, since the male can fertilise the egg production of several females. For males the potential of several matings within one season may therefore remedy the lack of spreading the offspring production over several years.

The computer runs with variability in the number of matings show that λ decreases compared with the initial deterministic runs. Since it seems likely to assume that mating success of males varies, these computer runs are probably more realistic than the deterministic runs. If one spawning event seriously limits the possibility of undertaking another, then the distribution would be closer to one female per male compared with the Poisson distribution. It is difficult to conclude either way, but it seems reasonable to assume that multiple matings by males are common, as observed by Friðgeirsson (1976).

The fitness of the 00010 strategies were found to be below 1, which indicates that one spawning per female was not enough to ensure population growth in the capelin stock over

Fig. 6. Fitness (geometric mean finite rate of increase, λ) of 100 000 Monte-Carlo simulations of different male reproductive strategies given observed fecundity and survival probabilities of the Barents Sea capelin (see Fig. 3). The number of matings is drawn from a Poisson distribution (Fig. 1) with parameter 1 (solid lines) and 2 (broken lines). Basic run parameter values are applied.



the period 1973–1991. During this period the Barents Sea capelin stock went through some tremendous changes in numbers (Gjøsæter 1995), with extremely low abundance at times. This may explain the low fitness of what appears to be the most common reproductive output of female capelin (00010). The fitness of the various strategies will be affected by errors in the abundance measurements and population fecundity estimates. Potential effects of errors were seen in the sensitivity analysis. Although the fitness level varied between the sensitivity runs, only small changes in the relative profitability of the different strategies were found. A review of how the model predictions conform to observations on capelin is given below.

Spawning behaviour

The capelin generally spawn during March–April at Iceland and in the Barents Sea (Sætre and Gjøsæter 1975; Vilhjálmsson 1994) and during June–July at Newfoundland (Templeman 1948). Prior to spawning, the sexes separate, as observed both in field studies (Templeman 1948; Bakke and Bjørke 1973; Sætre and Gjøsæter 1975) and in an aquarium study (Friðgeirsson 1976). The males stay just above the bottom at the spawning location and the females enter the area in large groups to mate (Templeman 1948; Sætre and Gjøsæter 1975). According to Friðgeirsson (1976), at least one male would quickly approach a female and mate with her when she entered the part of the aquarium occupied by the males. During spawning the male and female are joined together and roe and milt are released simultaneously while the male is rapidly digging his abdomen into the gravel to bury the eggs in the substrate (Jeffers 1931; Friðgeirsson 1976). This digging behaviour is probably the cause of the extensive injuries on the anal and caudal fins of capelin males observed after spawning

(Templeman 1948; Sætre and Gjøsæter 1975; Friðgeirsson 1976). There will probably be a surplus of males for each group of females, which means that there will be competition between the males for mating opportunities and the possibility of female choice. Sometimes, female capelin will be engaged by one male on each side trying to copulate simultaneously (Templeman 1948; Friðgeirsson 1976; Vilhjálmsson 1994), which underlines the competition between males for access to females. According to Friðgeirsson (1976), the spawning act takes about 2 s, after which the female is spent. At Newfoundland, beach spawning is timed to take up to 5 s (Jeffers 1931), which should give the female time to release all her eggs in one batch. Males stay for a prolonged period of time at the spawning ground and try to mate with several females (Templeman 1948; Møller and Olsen 1962; Friðgeirsson 1976).

Mortality

The model predicts that sex-specific life history strategies could evolve in Barents Sea capelin if three matings or more are achieved, given that the mortality risk between spawning seasons is greater than about 0.52. If the average number of matings for a male is to be higher than one, females must be iteroparous (assuming a 1:1 sex ratio prior to age-at-maturity). This means that a semelparous batch-spawning male strategy is more likely to evolve when females are iteroparous. At Newfoundland the capelin sex ratio is skewed towards female dominance for mature age groups (Shackell et al. 1994). The proportion of females spawning in more than one year at Iceland and Newfoundland may be up to 47% (Vilhjálmsson 1994) and 50% (Shackell et al. 1994), respectively, as determined from the skewed sex ratios. In the Barents Sea, however, the number of females spawning repeatedly seems to be low (Gjøsæter 1995). Since female capelin, at least at Newfoundland and Iceland, seem to be iteroparous, the average number of matings per male can be higher than one and semelparity may hence evolve. For example, semelparity may evolve with two matings on average (deterministic) if the mortality risk is above 0.88. The natural mortality risk of 4- to 5-year-olds has been estimated to be as high as 0.93 for some years (Dommasnes and Røttingen 1985). Although this figure includes male postspawning mortality, it is above the level needed for semelparity with two matings to evolve. The mortality risk of immature capelin (3- to 4-year-olds) is estimated to around 0.48 (Hamre and Tjelmeland 1982), which is much lower than for the 4- to 5-year-olds. At this mortality risk, two matings at age 5, for example, is more profitable than one at age 4.

Male spawning survival is close to 0 for the Icelandic and Barents Sea stocks (Sætre and Gjøsæter 1975; Friðgeirsson 1976; Vilhjálmsson 1994), but at Newfoundland, a small proportion of males (up to 13% are registered) may survive (Shackell et al. 1994). Samples of dead capelin from demersal trawling on spawning grounds in the Barents Sea consist entirely of spent males (Bakke and Bjørke 1973). The proportion of males at the spawning ground has been observed to decline during the spawning season from above 0.6 in February to 0.2 in April (Møller and Olsen 1962). Furthermore, there have been observations in August of recovering spent females maturing for the second time (Prokhorov 1960; Møller and Olsen 1962). Even as early as April, spent females have been observed with food in their stomachs (H. Gjøsæter, IMR, N-5024

Bergen, Norway, personal communication). This indicates that females have a higher postspawning survival than males in the Barents Sea as well. One reason for the lack of repeated female spawning in the Barents Sea may be that capelin have to migrate through areas of high abundance of cod to spawn at the Norwegian coast (Mehl 1989). Thus, although females survive spawning, the probability of making it back to the feeding area is low due to predation by cod. The adult mortality due to predation varies between years (Dommasnes and Røttingen 1985), even though it is less variable than the juvenile mortality. It hence follows that the profitability of the various strategies will vary accordingly. Such variability will counteract variation in juvenile mortality and increase the selection pressure for semelparity. The female is still likely to be iteroparous, since the cost of iteroparity is low.

Allocation pattern

The differences in GSI emphasise contrasting priorities: while female capelin spend their lipid reserves on egg production, male lipid catabolism is associated with physical activity (Henderson et al. 1984). The study by Henderson et al. (1984) was carried out on a local fjord population of capelin that does not undertake an extensive spawning migration, and therefore shows that males spend a lot of energy on physical activities related to spawning besides migration costs. As noted by Sager et al. (1989), capelin (males especially), in contrast with other species of fish, accelerate their growth in the year of sexual maturation. The spawning migration of the Barents Sea capelin from central areas of the sea to the Norwegian coast is a long journey that demands high energy reserves, as it takes place during winter when the feeding conditions are poor. The energetic costs of undertaking this migration can be estimated to be around 123 kJ at optimum speed (assuming a capelin of 15 cm and 18 g and a migration distance of 250 km), as calculated using equations provided by Viedeler (1994, p. 194). The fat reserves of a 15-cm capelin contain about 125 kJ of energy (assuming a maximum fat percentage in autumn of 19% of wet weight, K. Lie, SSF, Kjerreidviken 16, N-5033 Fyllingsdalen, Norway, personal communication), which only just covers the migration costs estimated above. In addition, male capelin need energy for an exhausting spawning period with a high level of physical activity, which probably means that he totally empties his energy reserves. Larger males can hold greater reserves, which is likely to be beneficial, since males need energy for spawning activities after migration. Since mating can be achieved using a small amount of milt due to the effective pairwise mating (Friðgeirsson 1976), males can allocate more energy to growth and mate seeking. Females only need to approach the males, spawn, and leave the spawning ground (Templeman 1948; Friðgeirsson 1976), and instead allocate energy to gonad production. This may explain the size dimorphism seen for capelin, and may sometimes favour delaying reproduction for males.

Conclusions

Added together, I think that the predictions from the simulation model supported by the field observations and the literature review suggest that male and female capelin have different optimal and actual life history strategies. The basis for this difference is mainly sex-specific abilities that are general for most animals: the ability of males to fertilise several females

and hence have a potential number of offspring that is much higher than for females (e.g., Davies 1991). In the case of capelin, the male strategy may be seen as an adaptation to a high adult mortality level and possibly female iteroparity. Such sex-specific strategies may be a general feature in animals experiencing high adult mortality. The evolution of sex-specific life history strategies is suggested to be species specific for capelin rather than stock specific, since the stocks have similar ecological roles in their respective ecosystems.

One testable prediction emerging from the present hypothesis is that spent male capelin should have a lower fat (energy reserve) content than spent females because females should maintain some energy reserves for a postspawning life. Another prediction is that the fraction of repeat-spawning females will be inversely proportional to the abundance of cod or other predators. Predictions like these should be tested to fully recognise sex-specific life history strategies in capelin.

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