

Potential effects of maternal factors on spawning stock–recruitment relationships under varying fishing pressure

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Abstract: The use of spawning stock biomass as a direct measure of reproductive potential may not be valid because of age- or size-specific differences in fecundity and the effect of maternal size and condition on offspring viability. In this study, we examine the potential significance of these effects using modelled Atlantic cod (*Gadus morhua*) populations. We quantify how changes in the age composition of the spawning stock, due to a range of fishing pressures and under different stock–recruitment relationships, could influence the reproductive output. Quantitative comparisons were made between a “standard” population where all age-classes only suffer natural instantaneous mortality ($M = 0.2$) and populations that suffer increasing levels of fishing pressure ($F = 0.0$ – 1.0). The results of the modelling exercise suggests that if the effects of the loss of more fecund older/larger individuals in the population are not considered, the number of potential recruits produced by populations under higher levels of fishing mortality could be overestimated by as much as 60%. When age/size-related maternal effects on egg viability are also considered, the amount of potential recruits can be overestimated by a further 10% in the heavily exploited populations.

Résumé : L'utilisation de la biomasse du stock de géniteurs comme mesure directe du potentiel reproducteur pourrait ne pas être valable en raison des différences de fécondité liées à l'âge ou à la taille et de l'effet de la taille et de l'état des génitrices sur la viabilité de la progéniture. Dans la présente étude, nous examinons l'importance de ces effets dans des populations de morues modélisées. Nous établissons quantitativement comment les changements dans la composition par âge du stock de géniteurs, liés à des pressions de pêche diverses et sous différentes relations stock–recrutement, peuvent influencer la reproduction. Nous avons effectué des comparaisons quantitatives entre une population « standard », dans laquelle toutes les classes d'âge ne subissent qu'une mortalité instantanée naturelle ($M = 0,2$), et des populations exposées à divers niveaux de pression de pêche ($F = 0,0$ à $1,0$). Les résultats de la modélisation indiquent que si les effets de la perte des sujets plus âgés, plus gros et plus féconds dans la population ne sont pas considérés, le nombre de recrues potentiellement produites dans les populations sous les niveaux plus élevés de mortalité par pêche pourrait être surestimé d'un pourcentage pouvant atteindre 60%. Si, en outre, on tient compte des effets de l'âge et de la taille des génitrices sur la viabilité des oeufs, le nombre de recrues potentielles peut être surestimé de 10% de plus dans les populations fortement exploitées.

[Traduit par la Rédaction]

Introduction

The true nature of stock–recruitment relationships may be obscured by the use of spawning stock biomass as a direct measure of reproductive potential. This is because population fecundity (the total egg production for a given stock biomass) can vary due to changes in reproductive parameters such as age at first maturity (Stearns and Crandall 1984;

Jorgensen 1990) and age- or size-specific fecundity (Hodder 1965; Hislop 1988; Kjesbu et al. 1991; Mackenzie et al. 1998; Marshall et al. 1998). In addition, there is now accumulating evidence that maternal size and condition may influence offspring viability, as it has been shown for Atlantic cod (*Gadus morhua*) that the size, age, and condition of females influence the size of eggs and larvae (Kjesbu 1989; Chambers and Waiwood 1996; Chambers 1997; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Trippel 1998). The influence of female spawning experience on hatching success is demonstrated by lower hatching success among first-time spawners compared with second- or third-time spawners (Solemdal et al. 1995; Trippel 1998). Positive correlations have been detected between female condition and larval feeding success and larval specific growth rates (Marteinsdottir and Steinarsson 1998). Additionally, larvae from large eggs, which are initially larger at hatching, have been shown to start feeding earlier, exhibit greater feeding success, have a greater tendency to develop functional swim bladders successfully, and exhibit higher rates of swimming activity and growth (Knutson and Tilseth 1985; Solemdal et al. 1992; Marteinsdottir and Steinarsson 1998). All of these

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factors suggest that maternal factors influence viability such that older age-classes may have a disproportionate contribution to the number of successful recruits.

The level of fishing exploitation influences the age and size structures of spawning populations and can result in a severe depletion of spawners from the older age-classes (Trippel et al. 1997 and references therein). Excessive removal of the older and larger individuals from fish stocks may be more important to recruitment than changes in absolute spawning stock biomass. For example, recruitment in Icelandic cod was found to be influenced more by the age structure than by the size of the spawning population such that the stock–recruitment relationship was improved extensively by including information on age diversity of spawners (Marteinsdottir and Thorarinsson 1998). On the whole, maternal effects on viability have largely been overlooked by fisheries management, but they may account for significant uncertainty found in most stock–recruitment relationships (Mackenzie et al. 1998; Marshall et al. 1998).

Using life history parameters for Icelandic cod as our modelled multiple spawner, this study quantifies the relative potential impact of maternal factors on the production of recruits. Traditionally, the calculation of potential recruits from the recruitment versus spawning stock biomass relationships (Ricker 1954; Beverton and Holt 1957) is based on the assumptions that (i) there is a mean number of eggs produced per unit biomass and (ii) all offspring have equal survival probabilities. We investigated the effects of these two assumptions independently as well as in combination and over a wide range of realistic fishing pressures.

Materials and methods

To investigate the effects that differences in the mean number of eggs produced per unit biomass could have on potential reproductive output, we created two idealised scenarios that encompass two extremes of stock–recruitment relationships. In the first scenario, hereafter referred to as “constant biomass,” all modelled populations maintain a constant spawning stock biomass with increasing fishing pressure by allowing the numbers of recruits to increase proportionally with decreases in the biomass of older age-classes. This scenario allows us to quantify the number of potential recruits produced, per unit biomass, due only to changes in the age structure of the populations. In the second scenario, hereafter referred to as “decreasing biomass,” the spawning stock biomass decreases with increasing fishing pressure by allowing only a constant number of recruits. This scenario allows us to quantify the simultaneous effects of age structure change and changes in spawning stock biomass.

To investigate the effects that unequal egg survival can have on potential reproductive output, we calculated the number of potential recruits per populations by summing age-specific fecundities. We first assumed that all offspring have equal survival probabilities (hereafter referred to as the “fecundity method”). Second, we quantified potential recruitment with the survival of eggs being dependent on maternal factors such as size and age (hereafter referred to as the “viability method”). To investigate the effects of differing fishing pressure, under each of the stock–recruitment scenarios and for both recruitment production methods, we created sets of six different populations whose age-class structures are defined by the level of fishing pressure that the populations receive (Fig. 1).

Model species

To parameterise our model of a multiple spawner, we used life history traits from female Icelandic cod, as there have been recent investigations indicating that differences in the viability of eggs are related to female age, size, and condition (Marteinsdottir and Steinarsson 1998). Specifically, larval viability measured by the occurrence of swim bladders within the first 15 days from hatch has been related to egg and larval size as well as to larval growth rates and feeding efficiency (Marteinsdottir and Steinarsson 1998). Larger eggs are produced by older, larger females (Kjesbu 1989; Chambers and Waiwood 1996; Marteinsdottir and Steinarsson 1988). Therefore, we used mean length at age (centimetres) to calculate the corresponding mean egg diameter (millimetres) for that length at age (eqs. 1 and 2). We then calculated viability as a function of the frequency of swim bladder occurrence (Y) in Icelandic cod larvae and egg diameter (eqs. 3 and 4). For Icelandic cod, the mean weight, length, and fecundity at age were derived from spawning females on the main spawning ground south of Iceland in 1996 ($n = 2917$, G. Marteinsdottir et al., unpublished data; Marteinsdottir and Steinarsson 1998):

- (1) $\text{Length}_{(\text{age})} = 43.4 + 6.52 \times \text{age}; r^2 = 0.43$
- (2) $\text{Egg diameter}_{(\text{age})} = 1.23 + 0.002 \times \text{length}_{(\text{age})}; r^2 = 0.31$
- (3) $\log(Y_{(\text{age})}/(1 - Y_{(\text{age})})) = -18.278 + 12.899 \times \text{egg diameter}_{(\text{age})}; \chi^2 = 19.23, \text{df} = 43$
- (4) $\text{Viability}_{(\text{age})} = e^{Y_{(\text{age})}}/(1 + e^{Y_{(\text{age})}})$

To produce estimates of fecundity at age for all methods and scenarios, we calculated the numbers of eggs produced for each age-class based on the average weight at age (eqs. 5 and 6). To calculate population fecundity, the cumulative sum of the fecundities at age is produced by multiplying the number in each age-class by the age-specific fecundity:

- (5) $\text{Weight}_{(\text{age})} = (198.3 \times (\text{age}^{1.837}))/1000; r^2 = 0.34$
- (6) $\text{Fecundity}_{(\text{age})} = -1\,396\,801 + 1\,044\,446 \times \text{weight}_{(\text{age})}; r^2 = 0.93$

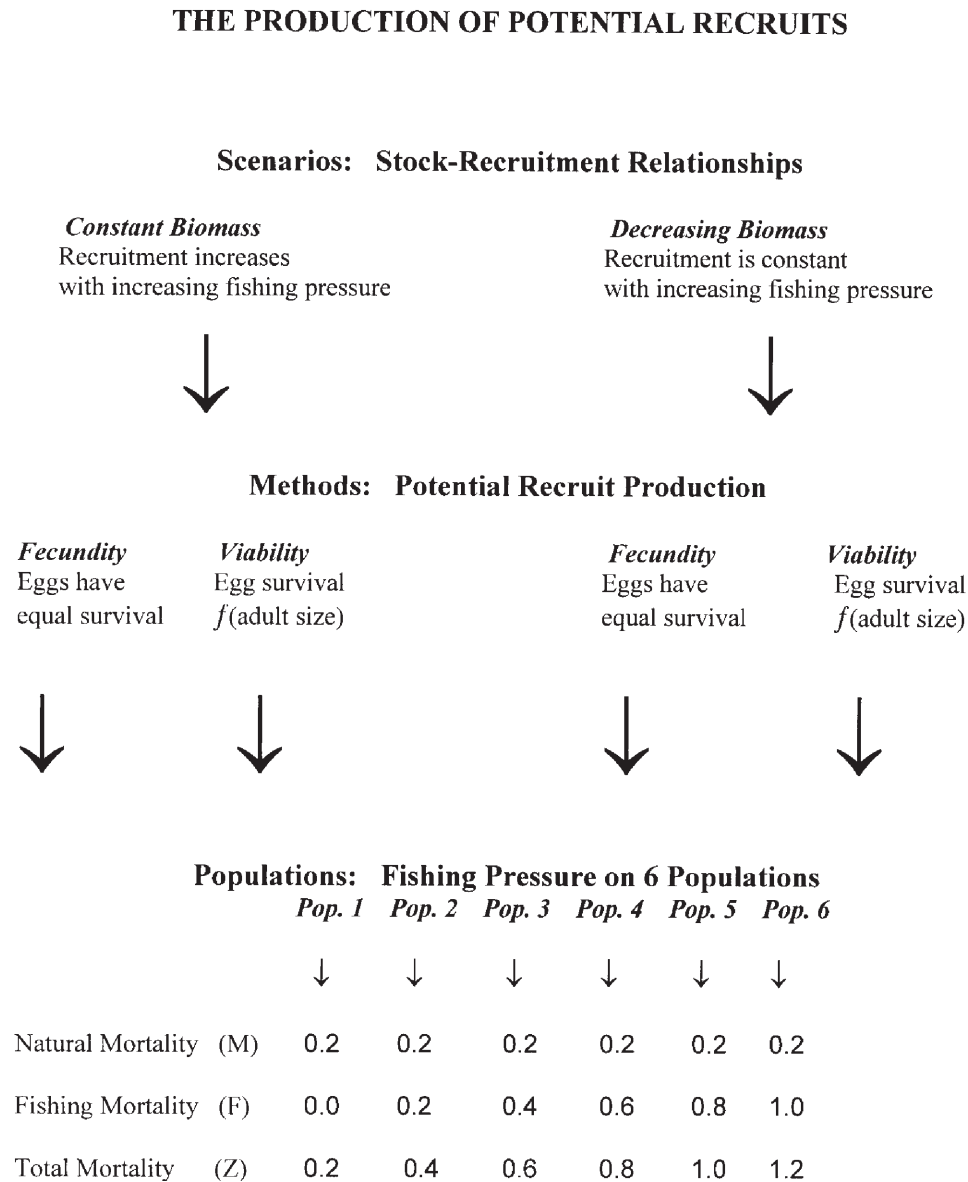
Female Icelandic cod do not begin to mature until 4 years of age, with only 10–40% of the population reaching maturity in their fourth year. Not until cod reach 7–9 years of age are 100% of the individuals sexually mature (G. Marteinsdottir, unpublished data). In this study, we have defined each population as having 25% of 4-year-olds, 50% of 5-year-olds, and 75% of 6-year-olds spawning. For all other age-classes, 100% of the individuals are assumed to have spawned. We have not considered aspects of male life history traits in this study, as male cod do not seem to show any change in sperm quality with size (Trippel and Neilson 1992). As well, male cod may tend to mature slightly earlier than females, but the trend in more recent years has been to mature at an age similar to that of females (Jørgensen 1990; Trippel 1995).

Constant and decreasing biomass stock–recruitment scenarios

To create each set of six populations, we first calculate the numbers for each age-class, starting at the age of maturity:

- (7) $\text{Number}_{(\text{age}+1, \text{population})} = \text{number}_{(\text{age}, \text{population})} \times e^{-Z_{(\text{population})}}$

Fig. 1. Flow diagram demonstrating the pathways in which the production of potential recruits is calculated under the two main stock–recruitment scenarios, two types of recruit production, and the sets of six populations representing the six different levels of fishing pressure.



The total instantaneous annual mortality (Z) for each of the six populations is made up of natural mortality ($M = 0.2$) and fishing mortality (F) (Fig. 1). Therefore, the six populations have different age-class structures (the numbers of individuals in each age-class) that result solely from the differences in total annual mortality. Within the six populations, each reproductive age-class (4–14) suffers the same constant annual mortality. Population 1 is the standard against which all quantitative comparisons are made, as it is considered to represent the “equilibrium” or “traditional” population, which experiences only natural mortality ($M = 0.2$). By design, in each set of populations, population 1 has the same number of individuals in each age-class and the same total spawning stock biomass.

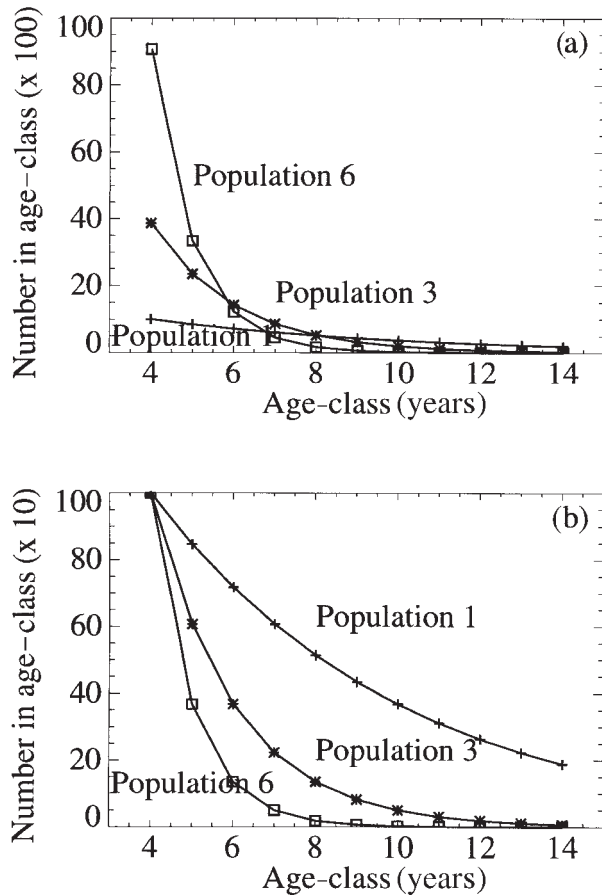
For the decreasing biomass stock–recruitment scenario, the numbers of recruits (at the age of sexual maturity) for each of the six populations is a constant (1000). This scenario represents one extreme of potential stock–recruitment relationships. When recruitment is held constant, then the effects of increasing fishing pressure continuously reduce the spawning stock biomass. Therefore,

the subsequent numbers at each successively older age-class within each population are solely functions of the total annual instantaneous mortality (eq. 7). The spawning stock biomass (SSB) for each population is the sum of the numbers times mean weights at age of all the age-classes (eq. 8; Fig. 2). The proportions, by biomass, that each age-class represents are calculated using eq. 9. Under this stock–recruitment scenario, the populations with higher mortality rates (populations 4–6) have similar numbers of younger individuals but have greatly reduced biomass and are composed of far fewer older/larger fish:

$$(8) \quad SSB_{(\text{population})} = \sum (\text{number}_{(\text{age, population})} \times \text{weight}_{(\text{age})})$$

$$(9) \quad \text{Proportion}_{(\text{age, population})} = (\text{number}_{(\text{age, population})} \times \text{weight}_{(\text{age})}) / SSB_{(\text{population})}$$

Fig. 2. Numbers in each age-class for populations 1, 3, and 6 under the (a) constant and (b) decreasing biomass stock–recruitment scenarios.



For the constant biomass scenario, the numbers at each age-class for each of the six populations were calculated using the same proportions (by biomass), per age-class, as were derived for the decreasing biomass scenario. The number of individuals within each age-class is calculated using eq. 10. Therefore, under this scenario, the populations with higher mortality rates (populations 4–6) have the same biomass as populations with less intensive fishing pressure (populations 1–3) but have much higher numbers of younger individuals and are composed of far fewer older/larger fish (Fig. 2). This scenario represents the other extreme of potential stock–recruitment relationships, that the effects of fishing mortality are completely compensated for and recruitment replaces all lost biomass:

$$(10) \quad \text{Number}_{(\text{age}, \text{population})} = (\text{proportion}_{(\text{age}, \text{population})} \times \text{SSB}_{(\text{constant})}) / \text{weight}_{(\text{age})}.$$

The two stock–recruitment scenarios therefore allow us to quantify (i) the number of potential recruits produced due only to the effects of age structure change and (ii) the number of potential recruits produced due to the simultaneous effects of age structure change and changes in spawning stock biomass.

Fecundity and viability recruit production

In order to compare the numbers of potential recruits produced by each of the production methods (fecundity method: survival of all eggs is equal; viability method: survival of eggs depends on maternal factors), we must first calculate a “standard” survival rate for

both methods. To calculate a standard survival rate, we assumed that population 1, with an annual instantaneous natural mortality of $Z = 0.20$, represents a stable state. Therefore, the standard fecundity survival rate of the eggs could be back-calculated by assuming that the total spawning stock fecundity of population 1, multiplied by a constant survival rate, must reproduce the total number of incoming recruits (1000). This standard fecundity survival rate ($\text{SFS} = 2.51 \times 10^{-8}$) was then used in eq. 11 to calculate the number of potential recruits for the fecundity method for both sets of six populations under each stock–recruitment scenario:

$$(11) \quad \text{Potential recruits}_{(\text{fecundity})} = \sum (\text{number}_{(\text{age})} \times \text{fecundity}_{(\text{age})} \times \text{SFS}).$$

The viability method introduces a change in survival rates due to maternal age and size. Therefore, the standard viability survival rate must take on a slightly different value than the one that was calculated for the fecundity method for population 1 to also produce 1000 recruits. This standard viability survival rate ($\text{SVS} = 4.36 \times 10^{-8}$) was then used in eq. 12 to calculate the total number of potential recruits for each population under the viability method for the two sets of six populations under both stock–recruitment scenarios:

$$(12) \quad \text{Potential recruits}_{(\text{viability})} = \sum (\text{number}_{(\text{age})} \times \text{fecundity}_{(\text{age})} \times \text{SVS} \times \text{viability}_{(\text{age})}).$$

Quantifying potential recruitment

We quantified differences in potential reproductive output between scenarios, production methods, and fishing pressures in two ways. First, we compared the number of potential recruits produced and, second, we compared the number per unit biomass of potential recruits produced with the expected number or expected number per unit biomass that the traditional method would predict. The expected number of potential recruits produced for each population (ENR) is calculated by multiplying the spawning stock biomass of each population by the standard number of potential recruits per unit biomass (eq. 13). The standard number of potential recruits per unit biomass (SRUB) is defined as the number of recruits produced by the standard population, population 1, divided by its biomass:

$$(13) \quad \text{ENR}_{(1-6)} = \text{SRUB} \times \text{SSB}_{(1-6)}.$$

The number of potential recruits per unit biomass (NRUB) for each population was calculated by dividing the number of recruits per population by its respective biomass:

$$(14) \quad \text{NRUB}_{(1-6)} = \text{recruits}_{(1-6)} / \text{SSB}_{(1-6)}.$$

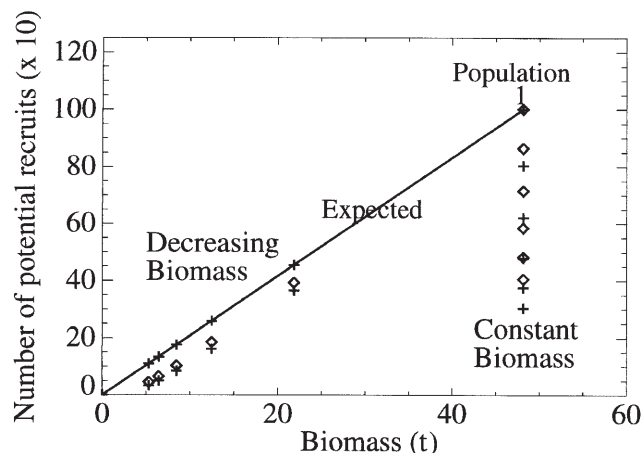
One minus the NRUB/SRUB ratio produces what we have termed the percent overestimate of recruitment production. We call it an overestimate, as it represents the difference, per unit of spawning stock biomass, between the number of recruits that a traditional population (one with a full complement of age-classes) would be predicted to produce and the number of recruits that populations with increasing fishing pressure (i.e., truncated age-class structure) actually produce. The added effect of viability (over and above the effects of fecundity) is calculated by subtracting the percent overestimate produced by the fecundity method from the percent overestimate produced by the viability method.

Table 1. Constant biomass scenario.

Population	Biomass (kg)	Expected number of recruits	Fecundity method number of recruits	Difference between expected and fecundity method	Viability method number of recruits	Difference between expected and viability method
1	48 140	1000	1000	0	1000	0
2	48 140	1000	864	136	805	195
3	48 140	1000	715	285	621	379
4	48 140	1000	584	416	478	522
5	48 140	1000	482	518	375	625
6	48 140	1000	405	595	305	696

Note: The numbers of expected potential recruits are compared with the actual number of recruits produced under the fecundity and viability methods of production. The difference between the expected number of recruits and those produced by the two methods of production is presented.

Fig. 3. Number of potential recruits produced versus the spawning stock biomass under the constant and decreasing biomass stock–recruitment scenarios. Population 1 is indicated on the figure, as it the standard reference point and has the same number of potential recruits under all scenarios and production methods. Numbers produced via the fecundity method are represented by diamonds; numbers produced via the viability method are represented by plus signs.



Results

Age-class structure under varying fishing pressure

The numbers at age for each of the sets of six populations of cod under the constant and decreasing biomass scenarios are presented in Fig. 2. The constant biomass scenario produces six populations that experience increasing levels of fishing pressure but retain a constant biomass due to the number of recruits being allowed to increase relative to decreases in spawning stock biomass. Under this scenario, the populations that experience heavier fishing pressure have greater numbers of cod. The increase is entirely due to the increase of numbers in the younger age-classes where the recruiting age-class (4) increases by a factor of 9 and age-class 5 increases by a factor of 4 between population 1 and population 6. The older age-classes, however, decrease in numbers, with age 10 showing a 94% reduction between population 1 and population 6. The decreasing biomass scenario produces six populations that experience increasing levels of fishing pressure but have constant recruitment. The subsequent populations have drastic declines in their spawning stock biomass and corresponding decreases in the num-

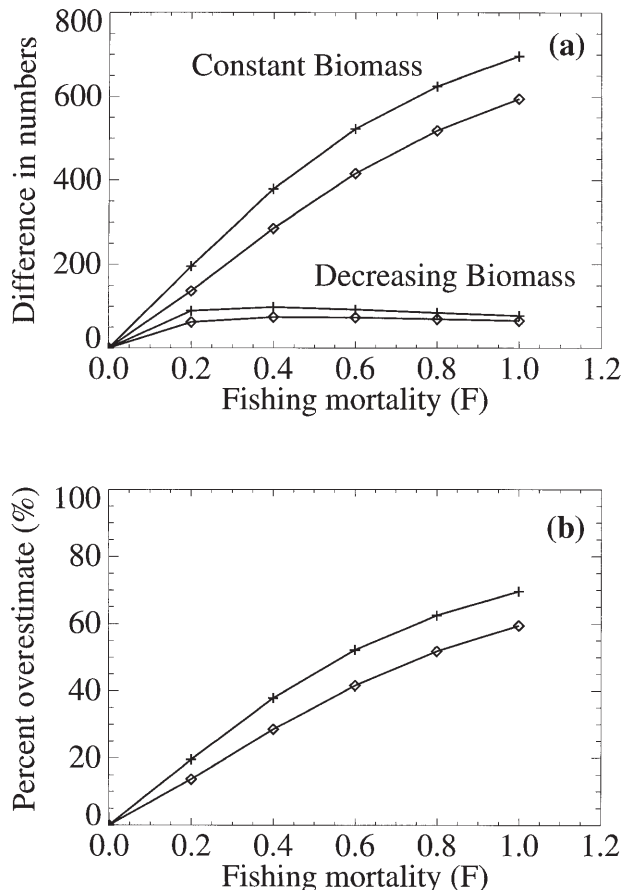
bers of fish in all age-classes. Under this scenario, cod numbers drop by 57% in age-class 5 and by 99% in age-class 10 between population 1 and population 6.

By design, the proportion by biomass of fish per age-class is the same under both the constant and the decreasing biomass stock–recruitment scenarios. Therefore, under both scenarios, within the populations that receive little or no fishing mortality (populations 1–3), the first three mature age-classes (ages 4–6) represent between 20 and 50% of the population spawning stock biomass. For the populations under moderate to high exploitation (populations 4–6), the first three mature age-classes represent the vast majority (70–85%) of the population spawning stock biomass. Spawning stock biomass is, of course, constant across all six populations under the constant biomass stock–recruitment scenario, but under the decreasing biomass scenario, relatively low levels of fishing pressure produce large differences in the spawning stock biomass of the different populations. In population 3, where $F = 0.4$, there a decrease of 75% in the spawning stock biomass compared with population 1. The spawning stock biomass of population 6, where $F = 1.0$, is 90% less than that of population 1.

Potential recruit production: numbers

Across stock–recruitment scenarios and recruit production methods, the populations that experience greater fishing pressure produce substantially fewer numbers of recruits. Under the constant biomass scenario, the expected number of recruits is always 1000. However, within those populations that experience greater fishing pressure, the age structure is severely truncated and the loss of those older/larger, more fecund individuals increases the difference between the expected number of recruits produced with the traditional assumptions and the actual number produced. Under the fecundity method of production (all eggs have equal survival), the number of potential recruits produced decreases from 1000 to 405 (Table 1; Fig. 3), which is a difference of 40.5% (Fig. 4a). The number of potential recruits produced via the viability method (eggs from larger/older females have increasing survival rates) shows an even greater decrease, with the extreme of only 30.5% of the expected 1000 recruits being produced in population 6 (Table 1; Figs. 3 and 4). Increasingly removing the more fecund, older/larger individuals causes a range of predicted numbers of potential recruits at a constant spawning stock biomass. This result suggests that age structure differences could be one of the main factors responsible for most stock–recruitment rela-

Fig. 4. (a) Difference between the expected and the produced absolute number of recruits for the constant and decreasing biomass stock–recruitment scenarios for each of the six populations at increasing levels of fishing pressure and (b) percent overestimate of the difference between the expected and the produced number of recruits per unit of spawning stock biomass at increasing levels of fishing pressure. Numbers produced via the fecundity method are represented by diamonds; numbers produced via the viability method are represented by plus signs.



tionships having such large residual deviations at a given stock biomass (Fig. 3).

Under the decreasing biomass scenario, the age structure is truncated in a pattern similar to that under the constant biomass scenario. However, in this scenario, there is also a loss of spawning stock biomass within the populations that experience higher levels of fishing pressure. This loss of biomass decreases the number of expected potential recruits (Table 2). Therefore, even though the number of potential recruits produced via both the fecundity and viability methods showed dramatic decreases (as high as a 97% reduction in total recruit production; Fig. 3), the difference between the expected number and the actual number produced stays essentially constant, with an average difference of 69 for the fecundity method and 88 for the viability method, which equates to an error of 7–9% (Fig. 4a).

Potential recruit production: numbers per unit biomass

By design, when viewing the results in terms of per unit biomass, the constant and decreasing biomass scenarios col-

lapse into the same output, as they contain the same proportion of biomass per age-class. The expected number of potential recruits per unit biomass is a constant (2.08×10^{-2}) for all populations and equals the number of recruits per unit biomass calculated for population 1. The produced number of potential recruits per unit biomass decreases across the populations with increasing fishing pressure (Table 3). Under the fecundity method, at the lowest levels of fishing pressure in population 2, where $F = 0.2$, the percent overestimation of potential recruits is 13.7%. As fishing pressure increases to 1.0 (populations 3–6), the overestimation of potential recruits, per population, continuously rises. However, the rate of increase of overestimation with increasing fishing pressure starts to decline between F values of 0.6 and 0.8, with a total overestimate of potential recruits of 59.5% within the most heavily fished population (Fig. 4b). Under the viability method of production, these percent overestimates increase from 19.5 to 69.6% as F increases from 0.2 to 1.0. Therefore, the added effect of differences in egg survival ranges from a 5.8 to a 10.7% overestimation (Table 3; Fig. 4b).

These results indicate that, when viewed on a per unit biomass basis, a decline in spawning stock biomass does not conceal the proportional changes in potential recruit production, as is the case when only the absolute number of recruits is analysed. This difference in results is due to the loss of older/larger individuals that are much more fecund, per unit of weight, than the younger fish left in the heavily fished populations. The number of eggs per gram of weight for a 4-year-old first-time spawner is 493 eggs/g, whereas an 8-year-old has 890 eggs/g. These results also suggest that for species whose first-time spawners have relatively low fecundities compared with older age-classes, the effects of even low levels of fishing pressure lead to large overestimates of potential recruits relative to the standard stock–recruitment relationships. However, as populations are more heavily fished and contain fewer and fewer older/larger individuals, the overestimate of potential recruits will reach a maximum.

Discussion

The use of spawning stock biomass as a measure of population fecundity has been criticised because it fails to account for changes in relative fecundity (number of eggs per weight of female) and egg survival that may result from differences in age, size, or condition (Hislop 1988; Kjesbu et al. 1991; Trippel 1998). This study, using a simple strategic model, quantifies how changes in the age composition of the spawning stock due to (i) increasing fishing pressures, (ii) different stock–recruitment relationships, and (iii) different potential recruit production methods could influence the reproductive output in terms of potential recruitment. The quantitative comparisons are made between a standard population where all age-classes experience only $M = 0.2$ and populations that suffer increasing levels of fishing pressure (F increases from 0.0 to 1.0). The results are viewed in terms of absolute numbers and numbers per unit biomass of potential recruits.

Table 2. Decreasing biomass scenario.

Population	Biomass (kg)	Expected number of recruits	Fecundity method number of recruits	Difference between expected and fecundity method	Viability method number of recruits	Difference between expected and viability method
1	48 140	1000	1000	0	1000	0
2	21 825	454	392	62	365	89
3	12 448	259	185	74	161	98
4	8 452	176	103	73	84	92
5	6 448	134	65	69	50	84
6	5 303	110	45	65	33	77

Note: The numbers of expected potential recruits are compared with the actual number of recruits produced under the fecundity and viability methods of production. The difference between the expected number of recruits and those produced by the two methods of production is presented.

Table 3. Potential recruits per unit biomass.

Population	Expected number of recruits	Fecundity method number of recruits	Fecundity method % overestimate	Viability method number of recruits	Viability method % overestimate	Additional effect of viability method
1	2.08×10^{-2}	2.08×10^{-2}	00.0	2.08×10^{-2}	00.0	00.0
2	2.08×10^{-2}	1.79×10^{-2}	13.7	1.67×10^{-2}	19.5	5.8
3	2.08×10^{-2}	1.49×10^{-2}	28.5	1.29×10^{-2}	37.5	9.4
4	2.08×10^{-2}	1.21×10^{-2}	41.6	0.99×10^{-2}	52.2	10.6
5	2.08×10^{-2}	1.00×10^{-2}	51.8	0.78×10^{-2}	62.5	10.7
6	2.08×10^{-2}	0.84×10^{-2}	59.5	0.63×10^{-2}	69.6	10.1

Note: The numbers of expected potential recruits produced per unit biomass (using the traditional assumption that the number of eggs per unit biomass is a constant) are compared with the actual number of potential recruits produced per unit biomass under the fecundity and viability methods of production. The percent overestimate of potential recruits that the traditional method would produce when compared with the two other methods of production is presented. The additional effect of the viability method (after the effect of the fecundity method is taken into account) is presented separately.

Age-class structure

The age-class structure of fish populations is largely determined by a combination of fishing pressure and stock–recruitment relationships. We found that even low to moderate levels of fishing pressure dramatically truncated the age-class structure of a population. An instantaneous fishing mortality value of 0.4 led to 53% of the population being made up of only the first three mature age-classes. An increase in F to 0.6 increased that proportion to 70%, with the first-time spawners (age-class 4) accounting for 30%. In Icelandic cod populations, as with most multiple-spawning species, the proportion of individuals within the first three maturing age-classes that actually spawn can be well below 100%, with the initial recruiting age-class having the lowest proportion of spawners. This suggests that even fish populations that receive low to moderate levels of fishing pressure have first-time spawners representing the vast majority of their spawning individuals. Percentages of first-time spawners caught in the commercial catch have been as high as 95% for Northeast Atlantic cod (Jørgensen 1990), and percentages of immature George's Bank cod, which are within the size range of being first-time spawners, have been as high as 42% of the commercial catch (Hunt 1996).

High levels of exploitation can also lead to lowering the age and size at which maturity is reached (Trippel 1995). This change in age at maturity can have a compensatory effect on egg production. Using a hypothetical stock of Atlantic cod, Trippel et al. (1997) demonstrated that lowering the age of maturity by 1 year led to a 16% increase in the number of eggs produced compared with what would have been

produced given no decrease in the age of maturity. This clearly demonstrates that changes in life history characteristics need to be taken into account when calculating potential recruit production. We have not included these sorts of changes in our current strategic model, as the actual mechanism for changes in age and size at maturation is not the fishing pressure per se but may be due to the subsequent changes in population density (Trippel 1995). Also, environmental influences may be much more important in determining age and size at maturation (Kjesbu et al. 1991; Marshall et al. 1998), and including environmental variation is beyond the scope of this study.

Stock–recruitment relationships

Stock–recruitment relationships can take many different shapes due mainly to density-dependent and environmental factors. In this study, we consider two idealised extremes of stock–recruitment relationships: the constant and the decreasing biomass scenarios. The constant biomass scenario assumes that there is an increase in recruitment proportional to the loss of biomass such that all six populations maintain a constant spawning stock biomass. This scenario allows us to look at the effects on reproductive output due only to changes in age-class structure. The decreasing biomass scenario dictates a constant number of recruits for each population such that increased fishing pressure inevitably leads to a decrease in the population spawning stock biomass as well as changes in the structure of the age-classes. Reality, of course, is somewhere in between these two extremes, but by exploring the extremes, we hoped to show the largest possi-

ble quantitative range of effects and be able to identify the mechanisms responsible for the changes in reproductive output.

Potential recruit production: numbers

We found that even at a constant spawning stock biomass, our model predicts a wide range of potential numbers of recruits, decreasing with increasing fishing pressure (Fig. 3). The difference between the expected number of recruits predicted by the assumption within the traditional stock–recruitment relationship and the actual number produced can be as high as 60% in the heavily fished population. Once the potential maternal effects on egg survival are included in the model, the difference can be as high as 70% (Fig. 4a). This difference in the number of recruits, at the same spawning stock biomass, is driven by the decrease in the number of older/larger, more fecund individuals and not by changes in the stock biomass, as each population contains the equivalent number of younger individuals to maintain the biomass. This result suggests that age structure differences could be one of the main factors responsible for the large amount of residual deviance around most stock–recruitment relationships. And indeed, in the few studies so far where age structure has been taken into account, the stock–recruitment relationship was improved (Marshall et al. 1998; Martensdottir and Thorarinnsson 1998).

Under the decreasing biomass scenario, where age structure changes are simultaneous with changes in spawning stock biomass, we found that, relative to a traditional population, a heavily fished population suffers a loss of 95–97% of the number of potential recruits that it could produce (depending on whether the fecundity or viability method was used; Fig. 3). However, under this scenario, we did not find large differences between the expected and predicted number of potential recruits. In fact, we found only a small, almost constant error of 7–9% (Fig. 4a). This implies that when viewed in terms of expected numbers of recruits from a stock–recruitment relationship, the simultaneous decline in spawning stock biomass conceals the effect of the decrease in the number of older/larger individuals in the more heavily fished populations. The reason for the relatively small difference in expected and produced absolute numbers of recruits is that the declines in spawning stock biomass are so drastic. Even the lowest level of fishing pressure, where $F = 0.2$, leads to a 55% reduction in stock biomass relative to the traditional population. Therefore, the concealing of the effects of age structure changes by the simultaneous changes in spawning stock biomass is the most likely reason why the critical assumption in the traditional stock–recruitment relationship (that there is a constant mean number of eggs produced per unit biomass) has not been severely challenged.

Potential recruit production: numbers per unit biomass

However, if the results are viewed in terms of the number of potential recruits per unit of spawning stock biomass, then both stock–recruitment scenarios provide the same result. The percent overestimate of the expected number of recruits per unit biomass increases dramatically as fishing pressure increasingly removes the older/larger individuals, which are more fecund and more successful (higher egg via-

bility) per unit of weight. Our model suggests that the percent overestimate of potential recruits very quickly rises from 14 to 60% as F increases from 0.2 to 1.0. When age- and size-related maternal effects on egg viability are considered, the overestimate of potential recruits can be another 5–10% higher. The relative quantity of this “error” suggests that this assumption needs to be addressed and that we cannot continue to produce stock–recruitment relationships that do not take into account potential changes in the number of eggs being produced per unit biomass due to changes in age structure.

Conclusions

This study provides further support for the developing paradigm that age and size structure of the spawning stock should be considered in fisheries management (Trippel et al. 1997; Mackenzie et al. 1998; Marshall et al. 1998; Martensdottir and Thorarinnsson 1998; Trippel 1998). Our results imply that spawning stock biomass alone is a flawed index of recruitment due to the invalid assumption that egg number and quality stay constant per unit biomass. This view contrasts with the emphasis of current management advice on defining a threshold level of spawning stock biomass below which historic data suggest that the probability of poor recruitment increases. This view also sheds doubt on some of the developing ideas of fisheries management, such as the suggestion that total allowable catches and effort should only be adjusted enough to allow all fish to spawn at least once (Myers and Mertz 1998). This quantitative study suggests that allowing the management of the fishery to continue, as it is at present, such that the majority of spawning fish are first-time spawners, is a very inefficient use of the resource and a potentially risky option.

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