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Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*)

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Abstract

In this study, we model daily reproductive output over an entire spawning season for a range of simulated age/size-structured populations of Atlantic cod (*Gadus morhua*), which are created under contrasting stock–recruitment and fishing pressure scenarios. An individual-based modelling approach is used to link empirical relationships with flexible reproductive parameters to quantify and qualify the effects that individual female condition and egg quality can have on stock reproductive potential (SRP) and the temporal distribution of reproductive output. The results of this study indicate that, even with a set of steady state populations that have equal spawning stock biomass (SSB), the differences in population structure brought about by a difference of fishing mortality (F) from 0 to 1.0 will substantially reduce the SRP. Compared to a non-fished population the decline in SRP will range from 48 to 74%, depending upon respective assumptions of egg size on viability. The truncation of population age/size structure due to fishing mortality will also lead to a 4 weeks shorter spawning season and a 2 weeks shift in the date of peak spawning. The effect of low condition of individuals can lead to almost total reproductive failure for the population and the effect of increased condition is dependent upon the population structure in question. Results as such support the view that predictions of recruitment can no longer be based solely as a function of SSB. More careful analysis of the population structure as well as annual dynamics of condition factors and exploration of functional relationships between female characteristics and egg quality are needed to assess and accurately predict survival and the probability of recruitment levels.

Keywords: *Gadus morhua*; Cod; Egg quality; Fish condition; Individual-based modelling; Population structure; Stock reproductive potential

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1. Introduction

The importance of spawning time has long been recognised as a critical factor in the recruitment process of marine fish stocks due to its affect on the initial synchrony between larvae and favourable environmental conditions (Hjort, 1914; Cushing, 1975; Cury and Roy, 1989; Mertz and Myers, 1994). However, the spawning season of many fish species is not a short event but extends over several weeks to months. Indeed, as many commercially exploited species are serial spawners this fact deserves closer inspection. The protracted spawning season of Atlantic cod (*Gadus morhua*) is achieved both by individuals spawning repeatedly (where spawning can last between 2 and 8 weeks for an individual fish) and by individuals beginning to spawn at different times such that a population can spawn from 4 to 15 weeks (Kjesbu, 1989; Kjesbu et al., 1991; Marteinsdottir and Björnsson, 1999). Many species are known to exhibit size or age-related change in the onset and duration of spawning where large individuals spawn over a longer time period and start spawning either earlier or later than the smaller individuals (DeMartini and Fountain, 1981; Parrish et al., 1986; Lambert, 1990; Hutchings and Myers, 1994; Marteinsdottir and Björnsson, 1999; Secor, 2000). For such species, removal of the larger and older individuals from a population may result in a shorter spawning season and significant changes in the peak time of egg production. In the highly variable temporal and spatial environments of marine systems, a reduction in the length of possible time overlap with favourable conditions can lead to a large reduction in the probability of successful reproduction.

In addition to the timing and length of the spawning season, it is important to explore the indications that the quantity and quality of the eggs spawned also changes during the spawning season. The temporal differences in the quantity and quality of egg production over a spawning season are functions of the size, age and condition of individual fish. Older, larger and better conditioned fish produce more batches of eggs and more eggs per batch, which are comprised of larger and more viable eggs than those produced by smaller, lower conditioned fish (Knutsen and Tilseth, 1985; Hislop, 1988; Kjesbu, 1989; Kjesbu et al., 1991; Chambers and Trippel, 1997; Trippel et al., 1997; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Marteinsdottir and Begg, 2002). There is also evidence that there are large differences in the viability of eggs that a first-time (recruit) spawner produces relative to a repeat spawner, even if the fish are similar in size and condition (Solemdal et al., 1992; Trippel, 1998; but see Clemmensen et al., 2003). Furthermore, for the same individual, the size and quality of eggs changes over the spawning period, with larger and more viable eggs being produced earlier during the individual's spawning period rather than later (Kjesbu, 1989; Chambers and Waiwood, 1996; Marteinsdottir and Steinarsson, 1998; Vallin, 1999; Marteinsdottir and Begg, 2002). It has been shown that such size/age-related changes in reproductive output correlates with influence the variability in recruitment (Trippel et al., 1997; Marshall et al., 1998; Marteinsdottir and Thorarinsson, 1998).

It is clear that the effect of moderate to heavy, fishing pressure will decrease the proportion of older/larger individuals within a population. The more heavily fished a population, the more likely it is made up of only younger, smaller size/age classes (Law and Grey, 1989; Trippel et al., 1997; Jennings et al., 1998, 1999). In an earlier study, we provided modelled evidence that differences in stock structure alone could account for up to a 2.5-fold differences in stock reproductive potential even if the stocks contained the same spawning stock biomass (SSB) (Scott et al., 1999). If egg viability was also considered, we demonstrated that there could be up to a 3.3-fold difference in stock reproductive potential due only to differences in the age/size structure of the population. This study indicated that the traditional assumption that SSB is a useful predictor of recruitment needed to be re-visited. In fact, Trippel (1999) and Marteinsdottir and Begg (2002) make a clear case for abandoning the use of SSB and moving towards a more accurate representation of a stock's ability to produce viable eggs and larvae which Trippel has referred to as the stock reproductive potential (hereafter referred to as SRP).

In this present modelling investigation, we take the concept of SRP further, into a temporal dimension, and ask the questions: (1) 'What are the effects of the temporal dynamics of flexible reproductive traits on the seasonal distribution of daily reproductive output and on SRP over a range of age/size structured pop-