# Exploring the BOFFFF Hypothesis Using a Model of Southern African Deepwater Hake (*Merluccius paradoxus*)

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The Big Old Fat Fecund Female Fish (BOFFFF) hypothesis is explored quantitatively using an age-structured stock production model in which the usual stock:recruit relationship is replaced by a three-stage recruitment process based on maternal age. The recruitment process is decomposed into three age-dependent stages: 1) number of eggs spawned per batch per female, 2) number of batches spawned per year (related to the length of the spawning season), 3) increased survival of young stages with maternal age. The first two stages together give the stock recruitment potential and can be well justified by experimental observation in many fish species. The third stage is affected by both maternal age and also environmental conditions. The results indicate that the number of batches spawned per year is the most important component. They also indicate that a few old fish potentially contribute many times more recruits to the population than many younger fish. It is argued that the concept of spawner stock biomass (which is heavily weighted by the large numbers of young first time spawners, especially in heavily exploited populations) should be replaced by the concept of stock recruitment potential, which takes the age-structure of the population in to account. The conclusion is that for many long-lived fish populations such as hake and cod, management should aim to maintain the age-structure of the population, rather than encouraging, or even targeting, exploitation of large, old fish.

**KEYWORDS**   spawner biomass; stock recruitment potential; effects of maternal age; age-structured population model

## 1. Introduction

Marteinsdottir and Steinarsson (1998), Scott *et al*. (1999), Longhurst (2002), Berkeley *et al*. (2004a, b), Palumbi (2004), and Scott *et al*. (2006) have hypothesized that Big Old Fat Fecund Female Fish (BOFFFF) are essential for the successful maintenance of many long-lived fish populations. The essence of the argument is that fish longevity has evolved to cope with the variability in recruitment of young fish into populations whose young stages need to survive variable mid-latitude pelagic environments (Longhurst 2002). In these stocks it seems that successful recruitment occurs very seldom, say one year in 20, so some individual fish need to live for at least that period of time in order to reproduce successfully so that the population can be maintained.

It has long been known that large females produce many more eggs than smaller, younger females (e.g. Morita *et al*. 1999; Osborne *et al*. 1999). In spite of this knowledge, most traditional management models are based on stock–recruit curves that assume that all female fish contribute equally (per unit biomass) to future recruitment. Many management strategies, moreover, are based on the assumption that after fish have spawned once they can be fished, thus targeting older, larger fish and reducing the age-structure of the population to younger age classes under the age of an arbitrary (often 50%) age of sexual maturity. Recent findings, however, indicate that not only do large older females spawn exponentially more eggs than smaller females, but that often these eggs are larger and contain more oil (Morita *et al*. 1999), and that this in turn leads to 60–80% better survival rates than the offspring of younger, smaller females (Ojanguren *et al*. 1996; Berkeley *et al*. 2004a). The size and number of eggs spawned are functions of the individual mother's biomass, which increases with age, and therefore maternal age is referred to hereafter, rather than maternal size.

The truncation of the distribution of age-structure associated with targeting older fish may result in a number of negative impacts on fish spawning. These negative impacts include: a shortening and change in timing of the spawning season (Wieland *et al*. 2000; Berkeley *et al*. 2004b; Scott *et al*. 2006), a decrease in the production of eggs and larvae (Berkeley *et al*. 2004a, b; Cardinale and Svedäng 2004; Birkeland and Dayton 2005; Macchi *et al*. 2005), a reduction in the probability that favourable conditions will be encountered by at least some larvae, a decrease in the average survival potential of larvae (Conover and Munch 2002; Berkeley *et al*. 2004b), and a reduction in genetic heterogeneity (Law 2000). These factors affect the chances of recovery of populations that have been overexploited (Law 2000; Birkeland and Dayton 2005) and together suggest that the effects of sustained heavy exploitation may not be reversible.

This paper sets out to explore quantitatively the implications of the BOFFFF hypothesis for recruitment, using Southern African deepwater hake as an example of a fairly long-lived fish (about 25 years maximum age-span; R. Leslie, MCM, pers. comm.) that inhabits a mid-latitude environment on the west coast of Namibia and South Africa from about 16–36°S.

## 2. The Fishery

Cape hakes have been the target of major trawl fisheries since the start of the South African trawl fishery in about 1900, with *Merluccius capensis* being fished in shallower water (*ca*. 50–350 m) and *M. paradoxus* (also known as deep-water hake) in deeper water (from 250–600 m). *M. paradoxus* inhabits the outer continental shelf from the Agulhas Bank in the south (*ca*. 36°S) to northern Namibia in the north (16°S). Both species have been managed as a single stock
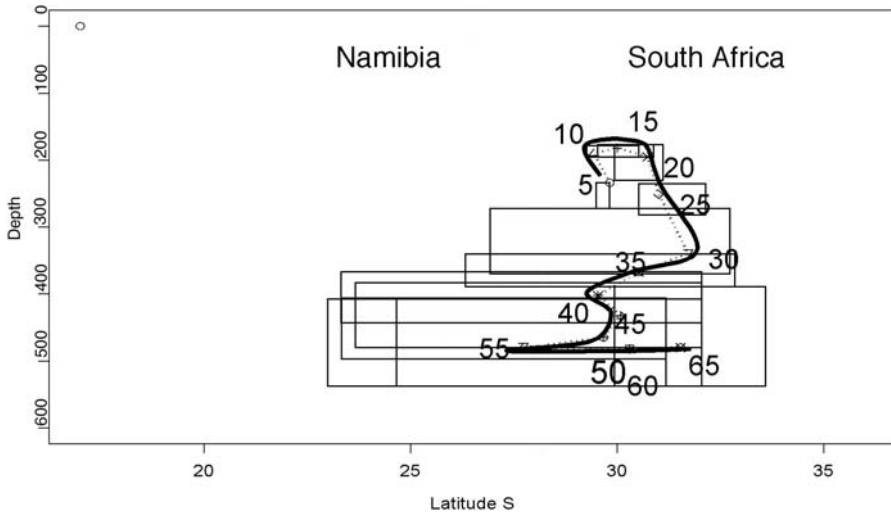
**Fig. 1.** Diagram depicting the changing centres of distribution of different size-classes of *Merluccius paradoxus* in 2006 off the coasts of South Africa and Namibia. Latitude is given on the *x*-axis and depth on the *y*-axis. Size classes are numbered according to their upper limits (cm), with 50 percentile distribution boxes for each size class (From Stroemme *et al.* in prep.).

until very recently, largely because of the difficulty in distinguishing the two species commercially, although the Namibian fishery has been managed separately from the South African one. The hake fisheries have been relatively stable except during the period of 1960–1976 when international fleets heavily exploited both species in international waters beyond the 12 n. mile limit. South Africa declared a 200 n. mile exclusive economic zone in 1976 and introduced strict controls on the local fleet in order to rebuild the stocks, but in Namibian waters hakes continued to be heavily exploited by international fleets until Namibia's independence in 1990, when stricter controls were introduced there too. Since the 1990s the heavy demand for large fresh hake in top condition in Europe, encouraged the development of long line fisheries in both countries. This has the effect of targeting larger fish and exploiting fish on rocky ground that bottom trawlers traditionally avoided. At the same time it encouraged trawlermen to explore deeper waters for large hake, waters that had previously been less economic to fish than shallower water. This had the double effect of exploiting previous refugia for larger, older fish of both species on rocky ground and in deep water (deeper than about 600 m depth) for *M. paradoxus*.

The life history of Cape hakes has been described by Botha (1986) and Payne (1989) who noted that juveniles are found inshore of the adults and that the size of hake increases with depth. Juveniles feed largely on euphausiids and other crustacea, and the diet becomes more piscivorous as the fish grow. Large *M. paradoxus* feed on smaller *M. capensis* (pseudo-cannibalism) where their distributions overlap, and there is also a strong element of cannibalism in both species. Until very recently, little work had been done on the early life history of the hakes. Stroemme *et al.* (in prep.) have shown that *M. paradoxus* tends to spawn in the south (*ca.* 34°S), recruit inshore on the west coast of South Africa and then migrates north and offshore as they grow larger (Fig. 1).
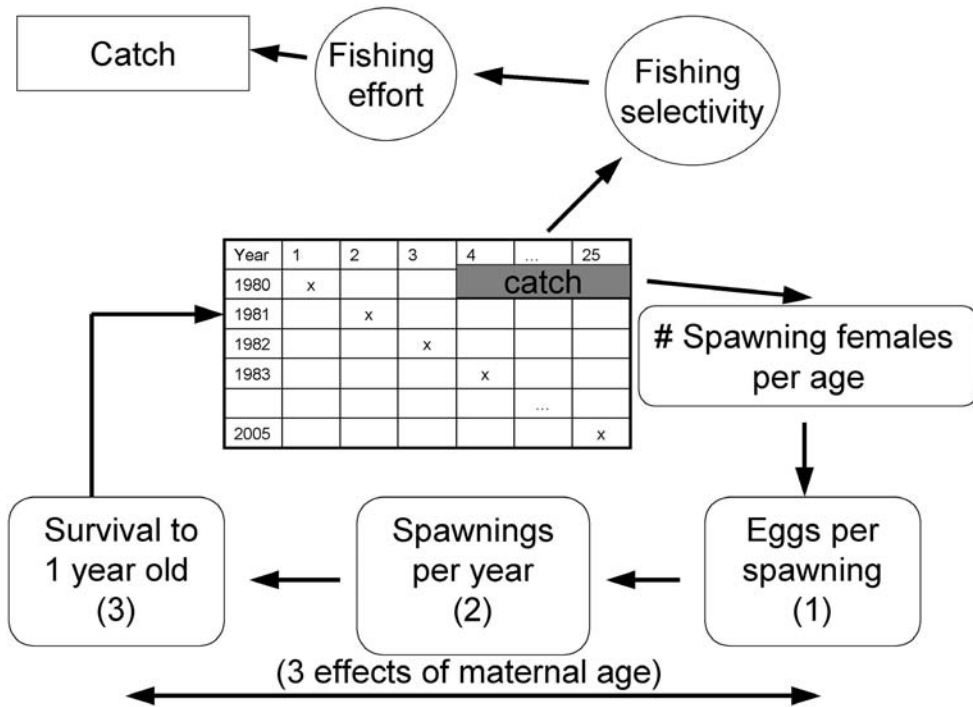
**Fig. 2.** Diagram depicting the age-structured population model for *M. paradoxus*. Recruitment is depicted as the product of three processes dependent upon maternal age ("3 maternal effects").

### 3. The Model

We use an age-structured production model (ASPM) on a simple spreadsheet (Fig. 2). In a conventional ASPM, recruitment is modelled using a stock–recruit curve. We substitute three "maternal effects of age" for the stock–recruit curve. The first maternal effect is the increasing batch fecundity with age (and size). Our assumption is based on the work of Osborne *et al.* (1999) on *M. paradoxus*, but extrapolated beyond the size and age range of that work, since the size range of the fished population had already been somewhat truncated by then, with very few large, old females in the research survey catches.

The number of females is assumed to be half the numbers in each age class (Botha 1986), and (Eggs_per_female)$_a$ is the number of eggs spawned in a batch per female at age $a$, which depends on fish size (Osborne *et al.* 1999):

$$(\text{Eggs\_per\_female})_a = 8.02 L_a^{2.67} \qquad (1)$$

where $L_a$ is the length at age $a$.

The second maternal effect is the number of batches spawned per season. There have been no studies of the spawning frequency of Cape hakes, but spawning frequency is positively related to the maternal age or size of most fish species, including Argentine hake *Merluccius hubbsi* (Murua *et al.* 1998) and European hake *Merluccius merluccius* (Macchi *et al.* 2004). Based on the above hake studies we assume that the spawning frequency increases linearly from once per year at age 2 to 14 times per year at age 15, and remains constant at 14 batch spawnings per year thereafter (Fig. 2).

The third maternal effect is increased survival rate with maternal age. Here we make the assumption that survival rate ranges linearly from 30% below the mean survival rate to 30% above the mean over the range of maternal ages (4–25 years). This is based on studies of two unrelated groups of fish, black rockfish *Sebastes melanops* (Berkeley *et al*. 2004a) who found an increase of 60% in survival rate with age, and brown trout *Salmo trutta* (Ojanguren *et al*. 1996) who found an 80% increase in fry fork length and survival rate with maternal size. The mean survival rate was estimated by running the model of the unfished population to steady state.

Recruitment was calculated by multiplying the number of females per age class by batch fecundity, by the number of batches spawned per year (eggs_per_female), by the survival rate for eggs spawned by each age; these were then summed over all the ages:

$$\text{Recruits} = \sum_{a=2}^{25} \left\{ (\#\text{ females})_a \times (\text{eggs\_per\_female})_a \right.$$
$$\left. \times (\text{batches})_a \times (\text{survival})_a \right\} \quad (2)$$

where *a* is maternal age, batches is the number of spawnings per year, and survival rate ranges from 0–1. The subscript *a* denotes age-dependence.

The standard average von Bertallanffy growth model was used to calculate the size of fish as they grow into the next age class, based on the parameters for South African hake of Punt and Leslie (1991). Similarly, fish populations decrease exponentially in numbers according to the sum of natural and fishing mortality. The stock was assumed to have been lightly fished until 1950, so this year was used as the base for starting the model, using population parameters given by Rademeyer (2003). Density dependence was implicitly modelled by capping recruitment at a maximum value of 300 million recruits per year. This does not take account of can-

nibalism after recruitment at age 0, which is included as a density-independent value for natural mortality used to tune the model. The maximum number of recruits was estimated by running the model of the unfished population to steady state. The model was run for 50 years and tuned by varying fishing and natural mortality to give realistic population age distributions and yields at steady state.

## 4. Results and Discussion

Figure 1 gives 50% percentiles of the distribution of of *M. paradoxus* from research surveys in 2006. It is interesting to note that these limits are much narrower for the early stages in the life cycle than the older stages, indicating fairly restricted survival of eggs and larvae coupled with tight schooling behaviour of these early stage survivors to specific nursery localities. This lends support for the hypothesis that only a few of the batches spawned find windows of opportunity in an environment favourable for survival. It also lends credence to the idea that some predatory young fish survive best by adopting tight schooling behaviour in which the fastest growing juveniles may become cannibalistic on their slower growing cohorts, further enhancing the growth and survival of some in the school at the expense of the slow growing ones. This appears to be a reproductive strategy favouring fecundity in numbers of eggs at the expense of producing fewer larger eggs (Nishimura and Hoshino 1999). As the fish grow older they disperse more widely, presumably reducing the incidence of cannibalism and extending their diet to crustacea such as copepods and euphausiids, before becoming more piscivorous at a size of about 20 cm (Pillar and Wilkinson 1995). The older fish migrate to deeper water, with centres of distribution that also tend to move northwards into Namibian waters, before returning south to spawn again.

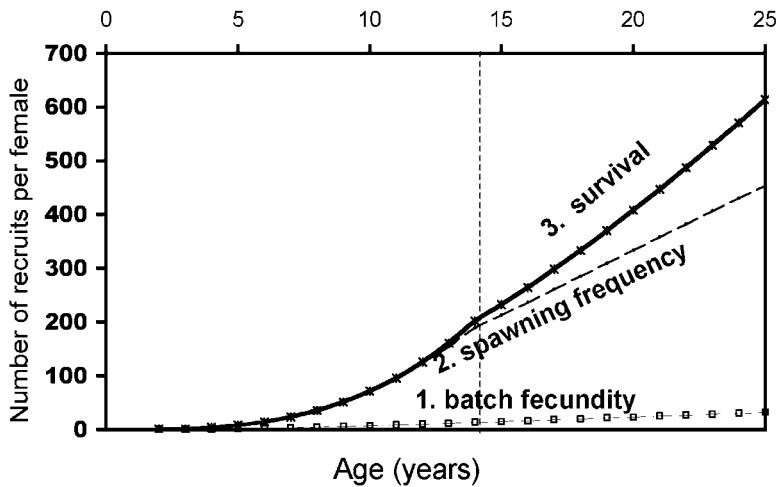Figure 3 shows the cumulative results of each of the 3 maternal effects of age on

**Fig. 3.**    Cumulative contributions of the 3 maternal effects to recruitment: 1. Effect of increasing batch fecundity with age; 2. Increasing spawning frequency with age; 3. Increasing survival to recruitment with age of mother. *Y*-axis gives potential number of recruits per female, *x*-axis the age of female (years). Note that the major effect is given by the increased number of spawnings per year.

potential recruitment. The first effect of maternal age (increasing batch fecundity) has a relatively small effect on potential recruitment, the second effect (increased spawning frequency) is largest, and the third effect (survival) adds to the overall contribution. It is notable that increased spawning frequency is not only important quantitatively, but also translates into increased duration (and often timing, Wieland *et al*. 2003) of the spawning season. This is particularly important in a variable pelagic environment, as it opens more windows of opportunity provided by favourable conditions, such as the timing of plankton blooms in spring or after upwelling events. The first two maternal effects are well founded on data in the literature for hakes, the third effect is not as firmly founded and there are no published data for hake on egg size or oil content relative to maternal size or age. Nevertheless, the first two effects alone are sufficient to cause us to rethink management strategies based on stock–recruit curves that assume equal contributions of all females per unit biomass, to

recruitment. The point of inflection of the cumulative potential recruitment curves at 14 years reflects the assumption that spawning frequency increases linearly from 2–14 years of age and then remains constant.

An interesting outcome of the study suggests that each really old female produces up to 300–600 potential recruits. Initially this may seem high, but these values need to be considered in the light of the high mortality rates of young fish as they grow through the age classes to an age when they are likely to make a real contribution to the future population. It is also likely that there are strongly density-dependent effects caused by cannibalism of younger fish, in addition to other predation. These have not been explicitly modelled in our initial model, which introduces density dependence by putting a maximum value to recruitment.

Figure 4 shows the steady state age structure of the model hake population when unfished compared to the recent levels of fishing ($F = 0.3$) and selectivity from age 2 caused by minimum mesh size regulations
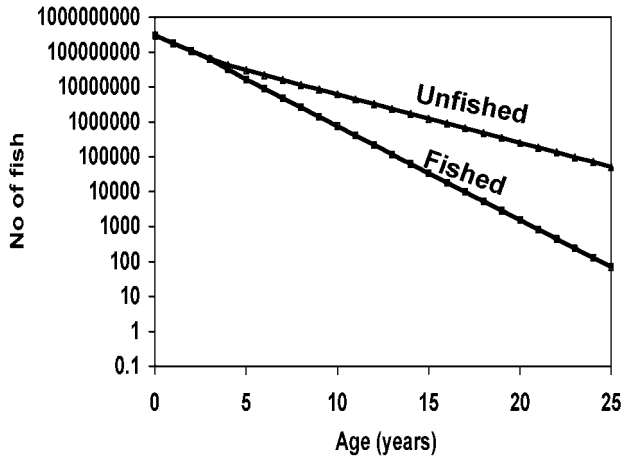
**Fig. 4.**   Age structure of model unfished population of *M. paradoxus* compared to the population fished according to present trawl harvesting strategy and fishing mortality (*F* = 0.3), with increasing selectivity of fish aged 2+ and full selectivity from 4+. Note the logarithmic *y*-axis.

for the commercial trawl cod end. It can be seen that there is exponential decline in the age structures of both fished and unfished populations, but the decline is much steeper in fished populations, even without modelling the increased targeting of older fish that is believed to occur now. The model result shown is based on trawl fishing only with constant selectivity from age 4 years. This is very conservative.

## 5.  Conclusion

This study replaces the commonly used stock:recruit curves with three model assumptions based on known biological relationships that vary with maternal age, the "three effects of maternal age": 1) number of eggs per batch spawned, 2) number of batches spawned per year and 3) increased survivorship of eggs and larvae of older fish. It is shown that number of eggs per batch alone has a moderate effect on recruitment with increasing maternal age. Increasing survival of larvae with maternal age also has a moderate effect, but the number of batches spawned per year has a major effect on re-

cruitment. This is probably particularly significant because the increase is number of batches spawned per year with age is manifest mainly by an increase in the duration of the spawning season. This is likely to result in exposure of more batches of eggs spawned to "windows of opportunity" created by environmental conditions favourable for recruitment in the variable pelagic environment created by a pulsed upwelling system in the southern Benguela region where the hake spawn. Furthermore, new results suggest that there is tight schooling of young hake into specific nursery grounds inshore on the west coast of South Africa, and this may lead to cannibalism of slow growing individuals by their faster growing cohorts, enhancing the growth and survival of fast growing young. As they get older the distribution range of deep water hake widens and they migrate to deeper water, with centres of distribution that tend to move northwards into Namibian waters (See Fig. 1).

The concept of spawner biomass used in stock:recruit relationships is heavily weighted in favour of young fish in stocks that have truncated size distributions, simply

because of the large numbers of small, young fish. This is commonly the case in heavily fished stocks. We suggest that it would be much more accurate to adopt the concept of Stock Recruitment Potential (SRP) (Solemdal 1997; Scott et al. 1999; Scott et al. 2000; Jarre-Teichmann et al. 2000), which takes into account the number of eggs spawned by different size- or age-classes. Thus in this paper the SRP is based on the first two effects of maternal age: eggs per batch and batches per year. These are both strongly age- and size-dependent. The third maternal effect is the survival rate. This is also likely to be dependent upon maternal age (Ojanguren et al. 1996; Berkeley et al. 2004a), and depends very heavily upon environmental conditions, but no more so than the variability found in stock:recruit relationships. By basing the first two stages on sound biological observations, we are moving a step closer to understanding the complex relationships between environment and recruitment, that will ultimately allow improved management of fisheries.

It has long been known that small young fish have much higher natural mortality rates than larger older fish, because as fish grow larger, they have fewer fish bigger than themselves to prey on. Natural selection favours fast growing fish that quickly grow out of the predator pit into larger size classes. There is some genetic evidence for this in cod, indicating that moderate selective effects act mainly through size-specific mortality and fecundity (Case et al. 2006). If we catch more young small fish, we add to the high natural mortality of such ages. By targeting large fish, humans tend to reverse natural selection by targeting fast-growing fish, possibly altering the gene pool permanently, and certainly reducing the recruitment potential of the stock, as shown by the results of this model. If we target large old fish, we act against nature. Of course there is a caveat, in catching young fish we must leave enough fish in the water to survive and grow into large, old ones.

The final conclusion is that, for many long-lived fish species, fisheries management measures need to take into account the exponentially greater importance to recruitment of Big, Old, Fat, Fecund Female Fish (BOFFFF). Perhaps the best management strategy for such fairly long-lived fish as cod and hake is to manage these fish stocks in such a way as to maintain the age-structure of the population (Longhurst 2002; Berkeley et al. 2004b; Birkeland and Dayton 2005). This may be achieved through discouraging the targeting of big fish. This is not easy, but is probably best achieved through marine protected areas that prohibit fishing in habitats frequented by the large old fish, if they are not highly migratory.

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