Effects of cannibalism, maternal age and varying fishing selectivity in age structured models of deep water hake populations

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I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own

Contents

ABSTRACT

An Age Structured Model (ASM) was develop in which dynamic and density-dependent cannibalism was included as a top-down control on a modeled population of *M. paradoxus* which used spawner biomass and maternal based recruitment. The ASM was used to evaluate the effects cannibalism had on age structure, recruitment and spawner biomass of the modeled population. The development of the model was described and evaluated with special emphasis on incorporating cannibalism and maternal based recruitment. The model was further used to evaluate the hypothesis made by Lleonart (1985), which stated that a cannibalistic population such as Cape hake would experience enhanced fishery recruitment from a management strategy which removed the more cannibalistic portion of the population. This was modeled using a longline fishing selectivity function which caught the larger individuals within the population. The idea behind this management strategy is confounded by the Big Old Fat Fecund Female Fish (BOFFFF) hypothesis, which states that BOFFFF are essential for the successful recruitment of long lived fish species such as Cape hake, and a more evenly distributed catch selectivity (such as trawling) has been suggested to maintain BOFFFF numbers in a population. The effect on recruitment, potential uncapped BOFFFF recruitment and age structures were compared between the two fishing selectivities on a cannibalistic population. It was found that with trawling, potential recruitment increased as the value of   increased, and decreased with longlining, showing an inverse relationship to what Lleonart's hypothesized. Effects of different fishing selectivities on the modeled fish population were compared, and results suggest that longlining selectivity is more suited at maintaining higher levels of spawner biomass in the fishery, resulting in a greater MSY and more than double the spawner biomass when compared to trawling.

General introduction: Cape hake

Cape hakes (*Merluccius spp.*) have supported a major trawl fishery around southern Africa since the early 1900s. The shallow-water hake (*M. capensis*) is caught at water depths of 50 to 350 m and the deep-water hake (*M. paradoxus*), which is morphologically very similar to the shallow-water species, is found in waters from 250 to 1000 m (Botha 1985, Boyer and Hampton 2001). Stocks of both species are shared between Namibia and South Africa, with each country managing their fisheries independently. In both South Africa and Namibia the hake fisheries have only recently been managed as single-species fisheries. According to Field et al. (2008), this was mainly because of the difficulty the fishing industry had in differentiating the two species. The populations of both species off South Africa and Namibia have remained relatively stable since a period of heavy exploitation by international fishing fleets in the 1960 - 70s, when as much as 1.1 million tons of hake were caught in 1972 in the South Eastern Atlantic (Botha 1985). In 1976, a management strategy was introduced through the guidance and recommendations of the International Commission for the Southeast Atlantic Fisheries (ICSEAF), in an effort to rebuild the South African stocks. This was done by defining the 200 nm exclusive economic zone (EEZ) for South Africa and, in 1979, by a decrease in overall total allowable catch (TAC) and individual quotas and increased mesh sizes. Since the bulk of the catch was taken by foreign vessels prior to the introduction of the EEZ, the exclusion of foreign effort resulted in a large reduction in catches and the increased mesh size also afforded some measure of protection to juvenile hake (Botha 1985). Annual hake catches in Namibia averaged about 500 000 tons from 1973 until Namibia's independence in 1990. Currently,

annual landings range from 60 000 to 200 000 tons for Namibia and a fairly consistent 150 000 tons for South Africa (Figure 1) (Butterworth and Rademeyer 2005, Shannon et al. 2006).

South Africa's current management strategy to rebuild the hake stocks is supported by the fishing industry. An economic incentive is that improvements in management procedures can help support the Marine Stewardship Council's (MSC) accreditation for exportation of hake to the European Union. Under careful management of the fishery, there has been a healthy increase in the *M. capensis* population and by the end of 2007 the biomass was estimated to be about 68% more than the biomass that would be needed to produce maximum sustainable yield (MSY). The deep-water hake experienced smaller than expected recruitment, with spawner biomass at 40% of that required to achieve MSY (Tingley et al. 2007, Tingley et al. 2008).
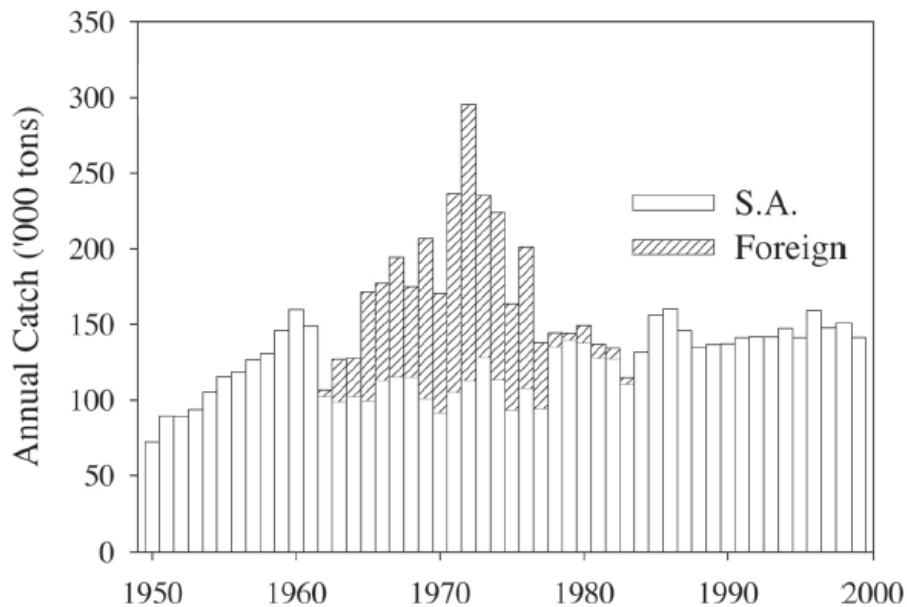

Figure 1. Combined catch time series for South African hake species (taken from Butterworth and Rademeyer 2005).

Trawling dominates demersal fishing around the world, and mainly targets species on soft-bottom ground. Longlining, which can target fish residing on and around rocky ground, has recently been used to catch hake in those rocky areas that were natural refugia from demersal trawl nets. Longlining has been considered friendlier to the environment when compared with trawling, because it causes no damage to the substratum and tends to be size- and species-selective (Japp and Wissema 1999). Longlining can however have a large by-catch of various seabirds (Barnes 1994). The first experimental longline permits in South Africa were issued in 1983 for kingklip (*Genypterus capensis)* (Japp 1988) and an experimental hake-directed longline fishery was initiated in 1994. Longlines generally catch larger hake than trawls, and also catch a greater portion of females (Japp 1995). In various studies it has been shown that longline fishing is superior to trawling on a spawner-biomass per recruit basis, because it targets larger fish (Cochrane et al. 1997, Jayiya 2001). However, there are some concerns about the biological impacts of longline fishing. Longliners target large (female) fish within a population, thereby removing the breeding stock (Field et al. 2008). In many areas the average catch sizes of longliners (and other fisheries) are decreasing and the declines may indicate high levels of fishing removing the old females in the population, which in turn results in reduced recruitment (Berkeley et al. 2004a).

Most hake are exported to markets desiring large-sized hake fillets, such as in Europe, the USA and Australia. In the early 1990s, there was an expansion and change in behaviour of the hake fisheries, with a shift towards trawling in deeper waters and the introduction of the longline fishery. The demand for large fillets, the decreasing availability of large, shallow-water hake and recent advances in fishing technologies have resulted in the industry targeting deep-water hake stocks off southern Africa. Currently the average demersal trawl reaches to about 600 m depth and is mainly

limited by depth-related technological constraints. Previously untouched, deep areas served as a refuge for the "Big Old Fat Fecund Female Fish" (BOFFFF), which are likely to be disproportionately large contributors to the production of recruits compared with other age classes of the spawner population (Scott et al. 2006, Field et al. 2008). BOFFFF are believed to be essential for the successful maintenance of many long-lived fish populations, such as hake and cod (Marteinsdottir and Steinarsson 1998, Berkeley et al. 2004a, b, Field et al. 2008). With the introduction of longline fishing and deeper water trawling, an increased number of large individuals are being caught. The longline fishing sector targets only large preferred hakes and is able to fish in rocky areas avoided by the trawling sector. These rocky areas probably served as naturally occurring marine protected areas for hake, at least with regard to demersal bottom trawling. Since the BOFFFF hypothesis suggests that old fish are responsible for maintaining the integrity of the stock in long-lived fish, it is important to understand the implications of BOFFFF for potential recruitment and management of the hake population.

A contrasting hypothesis to the impact BOFFFF have on a population's recruitment is that of cannibalism within a population, which acts as a recruitment-controlling mechanism. As the proportion of large individuals in a cannibalistic population increases, there is also an increase in the average mortality rate within the population until a stable state is reached. As both species of Cape hake grow, they become increasingly piscivorous and cannibalistic (Payne et al. 1987, Traut 1996). This cannibalistic dynamic can potentially act as a population-capping mechanism by continually depleting young cohorts, regulating population age structure to favour old fish. This increasing rate of cannibalism as the hake grow and age suggests that fishing focused on large individuals should

lower the extent of cannibalism and natural mortality rates in the hake population (Lleonart et al. 1985), and thereby increase potential fisheries yield.

Biology

Spawning

Both species of hake are believed to spawn in midwater, although the actual depth of spawning is as yet unknown (Punt and Leslie 1991, Grote et al. 2007). Both species of hake spawn throughout the year, with peak concentrations of eggs and larvae being found off Cape Point, between the 200 m and 500 m isobaths from June to October (Grote et al. 2007). The peak spawning season for hake on South Africa's west coast is bimodal, with a major peak in November/ December and a less intensive period in February/ March (Punt and Leslie 1991). It is believed that only *M. capensis* spawn in Namibian waters, with eggs found there throughout the year and with peak abundance occurring inshore of the 200 m isobath from September to December, especially around the Walvis Bay area (Gordoa et al. 1995). There is currently no conclusive evidence of *M. paradoxus* spawning in Namibia. The current view is that *M. paradoxus* in Namibia come from the South African spawning and nursery areas (Boyer and Hampton 2001). As the fish grow they are believed to move northwards and deeper offshore, with juvenile *M. paradoxus* being found mainly off South Africa and in the extreme southern Namibian waters between the 200 m and 300 m isobaths (Boyer and Hampton 2001).
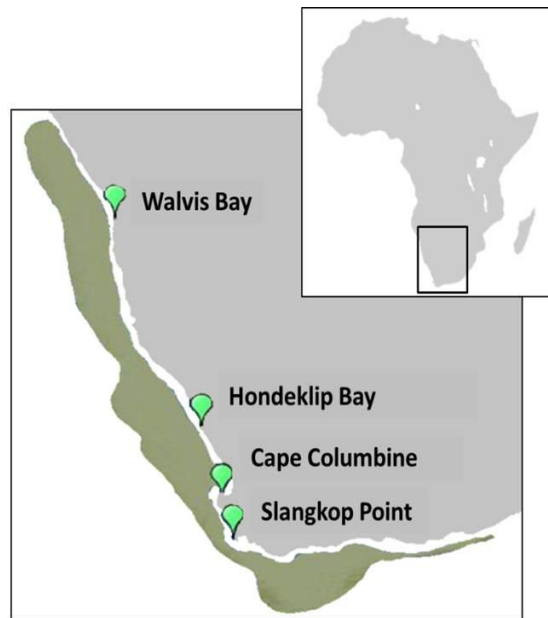
Figure 2. Distribution of both *M. capensis* and *M. paradoxus* along the southern Africa coast (modified from Payne 1989).

Effects of maternal age on recruitment

Stock recruitment has usually been explained as a density-dependent function, with a positive relationship between spawner biomass and recruitment when stocks are reduced. This density dependent relationship has been recently refined to not only consider total spawner biomass but to relate potential recruitment to the maternal age structure of the population (Scott et al. 2006, Field et al. 2008). It is typical for the fecundity of fish in each age class to differ, with old females being more fecund than young females and producing larger eggs with more yolk (Morita et al. 1999). According to Berkeley et al. (2004a), this may lead to 60 – 80 % better survival rates than for the progeny of younger, smaller females. Not only are the eggs larger as the females increase in size and age, but large females are able to spawn more often each season than are small, recently-matured females. According to a modeling study by Field et al. (2008), the number of eggs spawned in each batch per female, the number of batches spawned per year and the increased survival rate of larvae produced from older females all significantly impact recruitment. Their model results

indicate that the number of batches spawned per year is potentially the most important component for increased survival and recruitment of the species. Field et al. (2008) and Gibberd (2009) found that the mode of the distribution of the model hake age classes responsible for recruitment was about 10 years of age when there was no fishing. The old portion of the model population was responsible for most of the recruitment, even though the numbers of young fish in the models far exceeded the old fish. As fishing truncated the age structure of populations, there was an increasing reliance on the younger age classes to contribute to recruitment.

Feeding

It is believed that hake are opportunistic feeders, with diet varying with age (Payne et al. 1987, Roel and Macpherson 1988, Traut 1996). Young *M. capensis* and *M. paradoxus* feed predominantly on planktonic crustaceans (mainly euphausiids) and lanternfish, and become increasingly piscivorous with age (Payne et al. 1987). Piscivorous adult hake (> 4 years) feed close to the bottom and in midwater, and tend to leave the bottom at night (Payne et al. 1987, Huse et al. 1998). Squid, epipelagic fish and mesopelagic fish constitute a significant proportion of the diet of adult *M. capensis* but the greatest portion and preferred food items for large (> 50 – 60 cm) *M. capensis* are small *M. paradoxus* and small *M. capensis* (Payne et al. 1987, Macpherson and Gordoa 1994). Diet composition varies mainly with the size of the predator, but variation is also evident between areas in the southern Benguela and with depth (Payne et al. 1987). Cannibalism is more important in the north, especially for predators larger than 50 cm (Payne et al. 1987, Macpherson and Gordoa 1994, Traut 1996).

The shared distribution depths of the two species of hake and overlapping depth ranges of different size classes allows for considerable cannibalism and inter-specific predation, particularly on fish of ages 0 to 2 years (Punt and Leslie 1995). Diet studies of both species of hake off southern Africa show that cannibalism is a common occurrence, especially in large adults, and increases with fish size (Payne et al. 1987, Roel and Macpherson 1988, Gordoa 1994). Punt et al. (1992) have estimated that hake in South African waters could consume as much as 6 million tons of food annually, of which high proportions are conspecifics. According to Payne et al. (1987) and Macpherson and Gordoa (1994), more than 70 % of the prey items eaten by large *M. capensis* (> 60 cm) consist of conspecifics, eating on average about 71 small conspecifics each year per individual. The high occurrence of cannibalism in both species of Cape hake makes cannibalism the main cause of their own natural mortality (Lleonart et al. 1985), especially in *M. capensis*.

The two major driving forces on the rate of cannibalism in Cape hake are the number of large, cannibalistic individuals (> 60 cm) and the degree of overlap in distribution of the size classes. In South African waters, juvenile *M. paradoxus* share a degree of overlap with both adult *M. capensis* and *M. paradoxus,* and are the preferred food type for both *M. capensis* and *M. paradoxus* adults (Payne et al. 1987). The degree of overlap between juvenile *M. paradoxus*, adult *M. paradoxus* and adult *M. capensis* is important for predicting natural mortality rates (and recruitment) of *M. paradoxus.* The overlap in distribution changes annually and can be influenced by numerous environmental effects, such as deep, low-oxygen waters shifting inshore or offshore (Macpherson and Gordoa 1994). In studies by Payne et al. (1987) and Shannon et al. (2003), *M. paradoxus* was estimated to account for as much as 20 % of its own natural mortality by cannibalism in the 1980s and 1990s, and *M. capensis* as much as 30 – 50 %. In a study by Traut (1996), the main outstanding

features noted in the diet of *M. paradoxus* compared to that of *M. capensis* are the importance of small prey types such as crustaceans and small, deep-water fish species and the relatively low proportions of hake as a prey.

Since the Cape hake species are strongly affected by cannibalism, it is important to explore potential effects that cannibalism can have on the population dynamics and recruitment of Cape hake. This study focused on *M. paradoxus* because it built on a previous model of the deep-water hake population (Field et al. 2008).

Cannibalism

Cannibalism and pseudo-cannibalism (predation between closely related species of the same genus) are a management concern because they influence fisheries productivity. Cannibalism can also be an important evolutionary survival mechanism to allow for the continued existence of a species during extended seasons of poor recruitment or very low food availability, as found in open ocean environments (Folkvord 1997). It is possible that in many fish species cannibalism could be responsible for a high mortality of young age classes (< 3years old), resulting in recruitment failure for the population until the cannibals within the population are sufficiently reduced.

The analysis by Traut (1996) found that there is a large degree of dietary variability in Cape hake, for various sizes, areas and at various depths, similar to descriptions given by Payne et al. (1987). It was found that *M. capensis* are much more cannibalistic than *M. paradoxus*, especially as one moves

southwards. Even in the 20 – 29 cm predator group, hake made up as much as 40 % of prey found in the stomachs of the young *M. capensis*. In the northern waters of the Benguela, off Namibia, gobies (*Sufflogobius bibarbatus*) were found to be the preferred prey type for large hake, but as one moves towards the central and southern areas of the Benguela, there seems to be an increasing dependence upon conspecifics for both Cape hakes.

In the study conducted by Payne et al. (1987), dietary preferences among Cape hake from four sites were compared in the Benguela. Near Port Nolloth, no cannibalism was found for *M. paradoxus* whereas *M. capensis* > 40 cm showed a high degree of dependency on other hake. From Hondeklip Bay towards Cape Columbine *M. paradoxus* showed a high degree of cannibalism, especially in individuals > 70 cm, where as much as 90 % of their diet consisted of conspecifics, and substantial cannibalism (10 – 15 % of diet) was evident from about 50 cm. The cannibalism by *M. capensis* in the same area was substantial by individuals as small as 30 cm. From Cape Columbine southwards, cannibalism in both Cape hake species continued to increase, with *M. paradoxus* starting to cannibalize substantially from > 30 cm. The results of the study by Traut (1996) on *M. capensis* are similar to those of Payne et al. (1987), but showed considerably lower cannibalism rates for *M. paradoxus* over the entire Benguela.

Traut (1996) found that there were no significant seasonal changes in feeding intensity for either species during the study period. It was also found that the size of cannibalized hake ranged from 7 cm to more than 50 cm, and there was an increase in the size of measurable hake prey as the cannibal size increased. In cannibals smaller than 60 cm, the largest prey found in the stomachs

were about 25 cm (Traut 1996), whereas in a similar study conducted by Macpherson and Gordoa (1993), hake < 60 cm consumed conspecifics to a maximum size of about 40 cm. Velasco and Olaso (1998) describe how European hake, *Merluccius merluccius,* were found eating prey up to 85 % the length of the predator. According to the studies by Macpherson and Gordoa (1994) and Traut (1996), the highest numbers of measurable hake that were cannibalized were smaller than 25 cm.

Using a mass balance trophic model (*Ecopath,* with *Ecosim,* Christensen and Pauly 1992) of the southern Benguela, Shannon et al. (2003) were able to estimate the percentage by weight that *M. paradoxus* cannibalism might have on its own total mortality. According to the balanced diet composition matrix (Shannon et al. 2003), in the southern Benguela for the 1980s and 1990s, *M. paradoxus* adult diets consisted of 15 % of young (< 3 years) *M. paradoxus* and approximately 2 % of adult (> 3 years) *M. paradoxus.*

Intracohort cannibalism

A relatively low rate of cannibalism is expected in the early larval stages of a cohort. This is because of low initial size variability observed among conspecifics just after hatching. Feeding (and cannibalism) is limited by the larval gape size, as has been found for Atlantic cod (*Gadus morhua L.*) larvae (Folkvord et al. 1994). Potential intracohort cannibalism by larvae is only expected to occur following metamorphosis when variability in growth rates between individuals within a cohort starts to increase (Folkvord et al. 1994). In the very early larval life stages, after the yolk sac has been depleted, small food particles are relatively freely available. As the larvae increase in size and require larger and more specific food particles, low food abundance and increased competition can

cause density-dependent intracohort cannibalism. The larger the differences in sizes between individuals in a group, the greater the likelihood of cannibalism becoming a significant factor in the mortality of the larvae (Folkvord 1997). In many species of broadcast-spawning fish it is expected that cannibalism could be a major source of the naturally high mortality rates experienced by larvae.

Intracohort cannibalism occurs among silver hake (*Merluccius bilinearis*) as small as 22 – 25 mm, accounting for over 25 % of the stomach content by weight in juveniles larger than 46 mm (Koeller et al. 1989). In the South African Cape hake stocks, spawning lasts throughout the year, with spawning peaks within certain months according to the location of the sub-populations along the coast (Punt and Leslie 1991). Such an extensive spawning period should produce co-occurring juveniles of a sufficiently large size disparity for cannibalism to occur (Folkvord 1997). Intracohort cannibalism and competition can be reduced by spatial segregation of the offspring as a result of advection (Economou 1991) and the shoaling behaviour of young hake can also reduce intracohort cannibalism because fish prefer to shoal with conspecifics of a similar size (Pitcher and Parrish 1993). In a study conducted by Sumida and Moser (1980), it was found that the diet of Pacific hake (*Merluccius productus*) larvae consisted primarily of copepod eggs, nauplii and copepod adults. Only a single case of cannibalism was found in their study, in which two yolk-sac larvae were preyed upon by a 5.5 mm hake larva. They concluded that intracohort cannibalism by larvae in Pacific hake (*Merluccius productus*) rarely occurred.

Intercohort cannibalism

According to J. P. Roux (National Marine Information and Research Center, Lüderitz, Namibia, pers. comm.), some of the variation in annual Cape hake recruitment off Namibia can be explained by intercohort cannibalism within the first two juvenile cohorts. Juvenile Cape hake younger than 2.5 years (6 – 24 cm) are pelagic. As the fish age they become more demersal and there is spatial separation between different sizes. Large *M. paradoxus* and *M. capensis* move into deeper waters as they grow and there are therefore fairly weak interactions between size classes compared with the pelagic phase (J. P. Roux, National Marine Information and Research Center, Lüderitz, Namibia, pers. comm.).

Adult Cape hake preferentially feed on small hake, irrespective of their density or the occurrence of alternative prey (Macpherson and Gordoa 1994). According to the study by Payne et al. (1987), both *M. paradoxus* and *M. capensis* only showed significant cannibalism rates at a size greater than 40 cm (> 4 years). An increase in the proportion of large fish in a population can lead to an increased rate of cannibalism, lowering the rate of recruitment in a negative feedback loop. According to Lleonart et al. (1985), up to 48 % of the natural mortality experienced by hake around South Africa can be attributed to intercohort cannibalism.

Fisheries management

The demersal hake fishery of South Africa is currently managed by an operational management procedure (OMP), which is used in setting the annual TAC. The OMP is species-specific and uses both fisheries data and independent government survey information in its TAC calculation (Butterworth and Rademeyer 2005). The current TAC uses a standard stock-recruitment relationship, which does not account for changes in stock recruitment potential with changes in age structure of the population (Butterworth and Rademeyer 2005). Field et al. (2008) suggested that spawner stocks of fish populations are heavily weighted by the large number of first-time spawners. Therefore they advocated the use of a stock reproduction potential index, which could account for changes in the age-structure of a fish population under fishing instead of a standard density dependent stock-recruitment relationship (Scott et al. 2006, Field et al. 2008).

Most international management goals follow the idea of focusing fishing on the larger individuals in a population, whereas the BOFFFF hypothesis suggests that the old and large females are essential for healthy recruitment for a fish population (Morita et al. 1999, Scott et al. 2006, Field et al. 2008). The complexity of the management is further confounded in the context of hake, because of the high cannibalism rate within the population. The high degree of cannibalism within the population motivated Lleonart et al. (1985) to suggest that an effective management strategy could be to remove the large cannibalistic section of the population because of a possible enhancement effect it could have on survival of early year classes.

This study aims to examine the effects these two conflicting management strategies would have on a modeled *M. paradoxus* population. The methods for introducing BOFFFF recruitment and cannibalism into an Age Structured Model (ASM) are described. This study then compares the resulting population age structure, stock reproductive potential and fishery yield between the two strategies.

CHAPTER 2

Combining BOFFFF and cannibalism in modeling hake recruitment

Introduction:

The shallow-water hake (*M. capensis*) and the deep-water hake (*M. paradoxus*) are currently the basis of Namibia and South Africa's most valuable fisheries (Butterworth and Rademeyer 2005). Until recently Cape hake have been managed as a single stock (Butterworth and Rademeyer 2005). This combined stock management strategy was the result of poor differentiation between the species in commercial catches, mainly as a result of morphological similarities between them (Field et al. 2008). Prior to 1976, both Cape hake species were heavily fished by local and international fishing fleets. This heavy exploitation led to steadily decreasing catches between 1973 and 1976. Successful stock rebuilding management measures were applied to the fishery in 1976. This was accomplished through a decrease in the overall TAC, increased mesh sizes and exclusion of foreign fleets from South African waters, with the introduction of the South African EEZ (Botha 1985).

In South Africa, hake have traditionally been caught with the use of trawl nets, but following a longline experimental fishery in the 1990s, both longlining and handlining for Cape hake are allocated a share of the annual TAC. Demersal trawling targets fish species mainly on soft-bottom fishing grounds, whereas longlining is able to target areas that were previously protected from trawling, such as natural refuge areas around rocky grounds. Longlining is believed to be a more environmentally friendly and economically superior way of fishing, because it targets large fish and is

more species-specific. Longlining also results in good quality fish, producing high-priced fillets, and doesn't cause damage to the substratum (Japp and Wissema 1999).

In long-lived fish species such as hake and cod, a fishing strategy should be selected in which recruitment is optimized (Marteinsdottir and Steinarsson 1998, Morita et al. 1999, Osborne et al. 1999, Berkeley et al. 2004a and Field et al. 2008). Big Old Fat Fecund Female Fish (BOFFFF) of long-lived species are believed to be important for successful recruitment and maintenance of long-lived fish populations. These individuals are likely to be disproportionately large contributors to the annual production of recruits when compared with other age classes of the spawner population (Scott et al. 2006, Field et al. 2008). It is suggested that an appropriate management strategy for such populations would be to protect BOFFFF and harvest evenly throughout the population to maximize recruitment potential.

A common management strategy for long-lived species involves harvesting the larger and older portion of the fish population and allowing the younger individuals an opportunity to spawn before they recruit into the fishery (Scott et al. 2006). According to Lleonart et al. (1985), Waldron (1992) and Lance and Link (2000), this is the preferred management strategy for species such as the Cape hakes, due to the large degree of cannibalism in their diet. Lleonart et al. (1985) hypothesized that harvesting the large cannibalistic portion of the population will allow for greater potential fishery yields due to a lowering of the natural mortality rate of small hake, giving the young fish a better chance to recruit into the fishery. Cannibalism has often been described as a recruitment-capping

mechanism in a population, preventing young age classes entering into a fishery (Waldron 1992, Folkvord 1997).

In a study done by Punt and Hillborn (1994), the importance of including cannibalism in Cape hake stock assessment and fishery recruitment models was explored with the use of an Age Structured Production Model (ASPM). They compared a traditional Schaefer-type model to an age-aggregated model that included cannibalism of older fish on younger fish. It was shown at the time of their study that there was not necessarily an improvement in the prediction potential of a single species model when incorporating cannibalism in assessment and management procedures (Punt and Hillborn 1994). At the time of the study by Punt and Hillborn (1994), the idea that BOFFFF played an important role in the successful recruitment of a population was not yet fully developed, and interactions between BOFFFF and cannibalism rates were not accounted for.

This chapter will explore the effect of incorporating cannibalism into an *M. paradoxus* ASM that bases recruitment either on maternal-age effects or only on total spawner biomass, using a density dependent Beverton - Holt recruitment function (Beverton and Holt 1957). This study will compare the effects of contrasting fishing strategies by adjusting fishing selectivities mimicking trawling and longlining. The trawl fishery will capture the younger ages (< 8 years) of the population, whereas longlining will focus mainly on the old, large and more cannibalistic portion of the population. The effects varying levels of cannibalism have on the age structure of the population will also be explored. Since the stock recruitment potential is dependent on the age structure of the population (Scott et al. 2006, Field et al. 2008), a comparison between the resulting age structures from a

trawled and a longlined fish population would reveal the preferred sustainable fishing strategy to optimize fishery yield, egg production and recruitment into the fishery.

Objectives

The objectives of this study are a) to develop a method of incorporating dynamic cannibalism functions into an age structured model, b) to investigate the effects of differing rates of age-dependent cannibalism on total mortality and age structure, and thereby select a parameter value for the cannibalism percentage to be used in the model, c) to test Lleonart's hypothesis that catching big fish enhances potential recruitment in a cannibalistic population, and d) to assess the different fishery yields and sustainable spawner biomass under different size selective fishing strategies (mimicking trawling and longlining) and to evaluate the effect of changing the fishing strategy in a heavily trawled fish population.

Methods

An ASM was constructed using MS Excel spreadsheets to simulate population dynamics of *M. paradoxus.* BOFFFF recruitment and age-based cannibalism were both included in the model. Each year class of the population was tracked over time as individuals within each cohort either died (from 'natural' causes, cannibalism or fishing) or survived into the following year's age group.

Model equations

Initially the model of *M. paradoxus* was constructed in the absence of fishing to simulate a 'natural' population at equilibrium.

Numbers at age:

The numbers at each age were calculated as follows:

$$ \text{(1a)} $$

$$ \text{(1b)} $$

$$ \text{(2)} $$

where   is the number of fish at age   (in years) at the start of the year   and   is the number of 0 - year olds (recruits) at the start of that year. The initial numbers in the model were based on estimates from the model of Rademeyer (2003). She estimated the equilibrium spawner biomass of *M. paradoxus* to be near 599 000 tons with a   value of 419.4405 million individuals. The initial age structure for   was estimated using   and Equation 1a.

The total spawner biomass for year   was calculated using the following equation:

$$\tag{3}$$

The spawner biomass is a summed product of the number of individuals per age class   , their mean mass   (g) and the proportion that are mature   .

Recruitment using BOFFFF:

Potential recruitment values were dependent on the reproductive output from the previous year's spawner biomass. The recruitment for a given year was calculated by summing the potential recruits per female (Figure 3) for all the females of the age classes (Field et al. 2008).

$$\tag{4}$$

The assumption was made that there is an equal sex ratio within the Cape hake populations   and   represents the proportion of fish in age class   that are sexually mature (Punt and Leslie 1991). Environmental constraints were assumed to limit the maximum potential recruitment to 419.4 million recruits (Rademeyer 2003). The number of eggs spawned in each batch per age were calculated using the equation (Osborne et al. 1999):

$$\tag{5}$$

where   is the length (cm) at age . The estimated length at age was calculated using the von Bertalanffy growth equation with parameter values given in Table 1:

$$(6)$$

where   is the growth coefficient   and   is the hypothetical age at which the length of a fish would be zero. From the lengths, one can calculate the individual mass (g) per age   .

$$(7)$$

where   and   are growth parameters obtained from Punt and Leslie (1991) (Table 1).

Field et al. (2008) describe a method to estimate egg survival rates that depend on the mother's age (*egg_survival$_{ma}$*). This was assumed to range from 30 % below the mean survival at two years of age to 30% above the mean survival at 25 years of age. The average egg survival for *M. paradoxus* was estimated to be 3.24 x 10^{-6} per year (C.L. Moloney, University of Cape Town, *pers comm.*) and the estimated egg survival from each maternal age   class is given by the straight line equation:

$$(8)$$

The final maternal effect for BOFFFF used in this model was the spawning frequency   of different age classes (Field et al. 2008). There have been no case studies on spawning frequency of Cape hakes, so data were used from Argentine hake *Merluccius hubbsi* (Macchi et al. 2004), with frequency (number of batches per year) increasing linearly from once per year at two years of age to 14 times per year at 15 years of age, and then remaining constant at 14 spawnings per year (Field et al 2008).
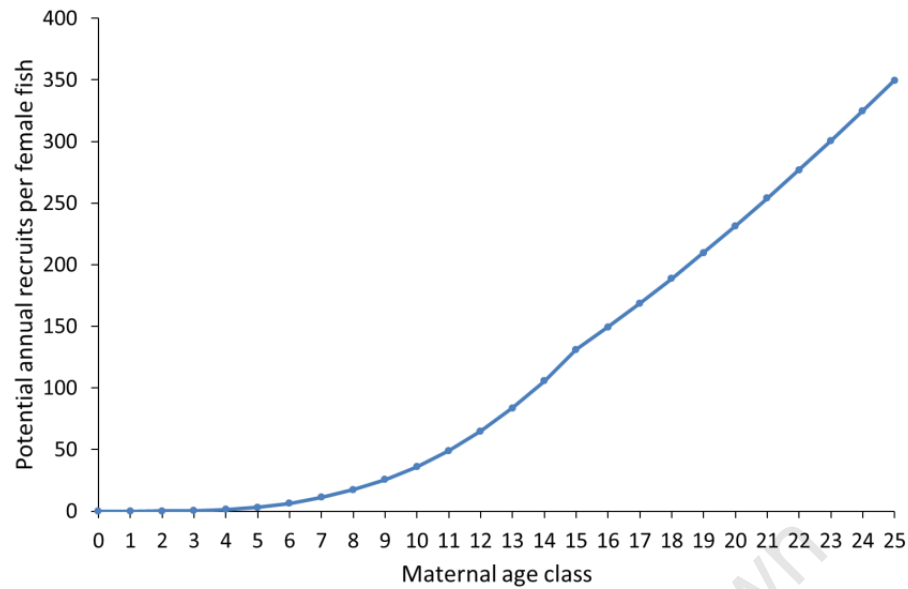
Figure 3. Line graph showing potential recruits per Big Old Fat Fecund Female Fish (BOFFFF), per maternal age class of
M. paradoxus (   ) after Field et al. (2008).

To compare stock recruitment potential between populations arising from the different fishing selectivities, indices were calculated using Equation 4, giving the estimated numbers of fish that could potentially recruit into the hake population due to maternal-based recruitment effects (before truncating them to 419.4 million).

<u>Recruitment using Beverton-Holt</u>

A traditional density-dependent stock-recruit relationship was included in certain experiments for comparison to the BOFFFF-based recruitment through the use of a Beverton-Holt function.

$$(9)$$

The values for α and β (Table 1) were estimated from values in Rademeyer (2003) where α = maximum number of recruits produced and β = spawning stock needed to produce a recruitment equal to $\alpha/2$.

Table 1. Parameters used in the Beverton - Holt recruitment function, the mass at length and the von Bertalanffy length at age calculations.

Parameter	Value	Units	Equation	Source
a	495	millions	B-H Recruitment	Rademeyer (2003)
ß	108390.48	tons	B-H Recruitment	Rademeyer (2003)
c	0.006	g.cm^{-d}	Mass at length	Punt and Leslie (1991)
d	3.046	-	Mass at length	Punt and Leslie (1991)
L_∞	219.4	cm	Length at age	Punt and Leslie (1991)
k	0	y^{-1}	Length at age	Punt and Leslie (1991)
a_0	-0.914	y	Length at age	Punt and Leslie (1991)

Figure 4 compares the recruitment curves at different levels of spawner biomass for Beverton-Holt and BOFFFF at F = 0 y^{-1}. The potential recruitment would change for the BOFFFF as the age structure of the spawner biomass changes. The maximum recruitment capping effect on the BOFFFF recruitment function made it unresponsive to low levels of fishing mortality, whereas the Beverton – Holt recruitment function becomes less responsive at higher levels of fishing mortality. The recruitment function which was most sensitive to the fishing mortality in each simulation was used to run the model simulation.
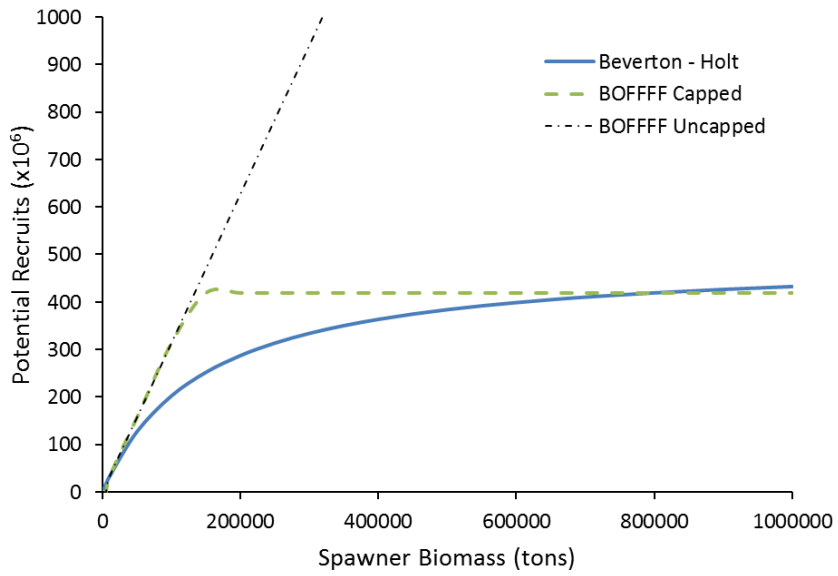
Figure 4. Comparison between Beverton – Holt and BOFFFF recruitment at different levels of spawner biomass. The curve for the BOFFFF recruitment is presented at $F = 0$ y^{-1} and would change as the population structure changes.

<u>Total mortality:</u>

The instantaneous total mortality rate   depends on two main factors: the instantaneous natural mortality rate   and the instantaneous fishing mortality rate   which varies with age as a result of age dependent gear selectivity   .

(10)

values vary according to the assumed fishing selectivity chosen (Figure 5).   values were modified from Butterworth and Rademeyer (2005) and   values were taken directly from Jayiya (2001). The parameters used in the model are presented in Table 2.
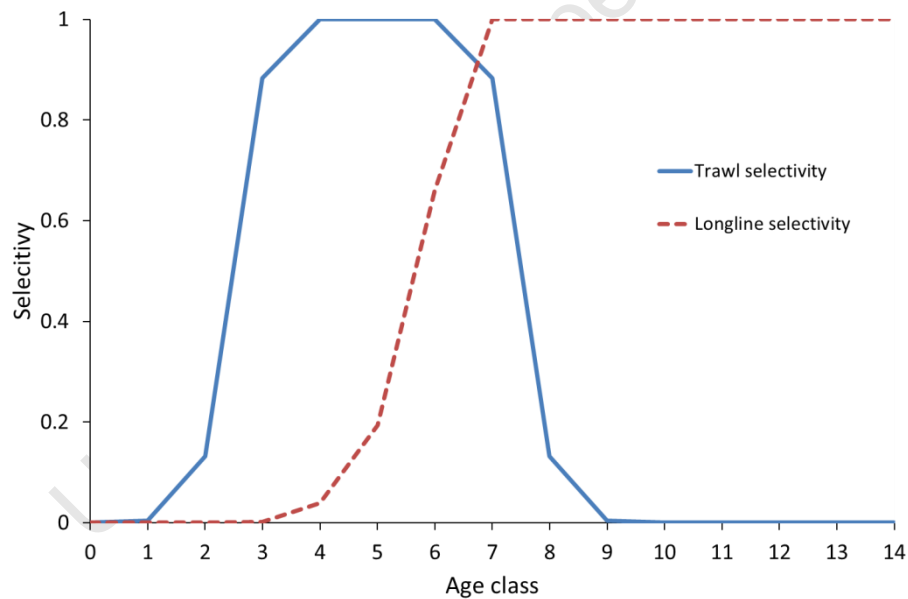

Figure 5. Line graphs showing the differences in the fishing selectivity rates between the trawling (modified from Butterworth and Rademeyer 2005) and longline (Jayiya 2001) hake fisheries.

Table 2. Parameters of the age classes used in the ASM. Instantaneous mortality rates , fishing selectivity for trawling (and longlining (, proportion sexual maturity (, spawning frequency , fecundity , egg survival rate , mean length and predators for each age class.

Age (years)	M_a	$S_{a\ (Trawl)}$	$S_{a\ (Longline)}$	a (Proportion sexually mature)	$batches_a$ (number per year)	fec_a (Number of eggs/ batch)	$EggS_a$ (number 10-6)	L_a (cm)	Predator age
0	0.511	0.0003	0	0	0	3372	1.45	9.61	2-3
1	0.511	0.004	0	0	0	22747	1.51	19.6	2-8
2	0.511	0.132	0	0.250	1	65537	1.57	29.2	4-14
3	0.415	0.883	0	0.50	2	135200	1.63	38.3	6-23
4	0.358	1	0.002	0.750	3	233038	1.68	47.0	7-25
5	0.319	1	0.004	0.850	4	358975	1.74	55.2	9-25
6	0.319	1	0.200	0.950	5	512029	1.80	63.0	11-25
7	0.319	0.883	0.660	1	6	690624	1.86	70.5	13-25
8	0.319	0.132	1	1	7	892802	1.92	77.6	15-25
9	0.319	0.004	1	1	8	1116383	1.98	84.4	17-25
10	0.319	0.0003	1	1	9	1359071	2.04	90.9	19-25
11	0.319	0	1	1	10	1618541	2.09	97.0	22-25
12	0.319	0	1	1	11	1892498	2.15	103	24-25
13	0.319	0	1	1	12	2178716	2.21	108	-
14	0.319	0	1	1	13	2475070	2.27	114	-
15	0.319	0	1	1	14	2779555	2.33	119	-
16	0.319	0	1	1	14	3090298	2.39	124	-
17	0.319	0	1	1	14	3405567	2.44	128	-
18	0.319	0	1	1	14	3723771	2.50	133	-
19	0.319	0	1	1	14	4043457	2.56	137	-
20	0.319	0	1	1	14	4363313	2.62	141	-
21	0.319	0	1	1	14	4682158	2.68	144	-
22	0.319	0	1	1	14	4998940	2.74	148	-
23	0.319	0	1	1	14	5312724	2.80	151	-
24	0.319	0	1	1	14	5622689	2.85	155	-
25	∞	0	1	1	14	5928119	2.91	158	-
	Du Buisson (2005)	Butterworth and Rademeyer (2005) Modified	Jayiya (2001)	Punt & Leslie (1991)	Du Buisson (2005)	Osborne et al. (1999)	Estimated	Estimated	Estimated

Table 3. Encounter index values for the *Stepped* and *Linear* functions and a size-based predator-prey encounter matrix constructed on the assumption that cannibals were likely to feed upon prey within a particular size range (between ¼ and ⅔ of the size of the cannibal).

EI values Stepped	Linear	Prey age class (years)	Predator age class (years) 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	1	0			x	x																						
1	0.92	1			x	x	x	x	x	x	x																	
1	0.85	2				x	x	x	x	x	x	x	x	x	x	x												
0.1	0.77	3						x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
0.1	0.70	4							x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
0.1	0.62	5								x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
0.1	0.54	6										x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
0.1	0.46	7												x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
0.1	0.38	8														x	x	x	x	x	x	x	x	x	x	x	x	x
0.1	0.31	9																x	x	x	x	x	x	x	x	x	x	x
0.1	0.23	10																		x	x	x	x	x	x	x	x	x
0.1	0.15	11																					x	x	x	x	x	x
0.1	0.08	12																							x	x		
0	0	13																										

Cannibalism and natural mortality

Time-varying cannibalism rates between fish at different ages are difficult to ascertain. Various values for cannibalism are estimated in the literature (Chapter 1) but the values given are normally aggregated in different ways and are therefore not in a form that can be used in the model. There is also little quantitative understanding of age-dependent selectivity for cannibalism. Consequently, probable encounter rates between potential prey and cannibalistic predators were used as a proxy for age-dependent cannibalism parameters in the model. A size-based predator-prey encounter matrix was constructed on the assumption that cannibals were likely to feed upon prey within a particular size range, between ¼ and ⅔ of the size of the cannibal (Table 3). The average sizes of prey per size class of predator were related to ages using the von Bertalanffy growth equation (Equation 6). It was assumed that cannibalism only begins in year two, as the hake leave the pelagic life stage and become demersal (Table 2 and 3). It was also assumed that once an individual survives to 13 years it will be too large to be cannibalized by older fish.

Potential encounter rates of prey with cannibalistic predators   were calculated by multiplying the numbers in each prey age class   by their relevant sum of predators (.

$$ \tag{11} $$

The encounter rate for each prey age class was standardized to an encounter index   which ranged from 0 - 1, by dividing all the encounter rates per year by the initial maximum   value. This tended to give much larger values for young fish, because they are most

numerous and it assumes equal selectivity across all sizes, whereas large prey might be expected to be preferred over small prey. These   values were thus square-root transformed. Two additional encounter index transformations, one stepped and one linear, were also explored and used for comparative analysis of the square-root function (Figure 6).

The final   values indicate a relative-abundance-based selectivity of cannibals for different aged prey, therefore showing a higher selectivity of the more abundant young fish than old fish.

$$\overline{}$$ (12)

$$\overline{}$$ (13)

(14)
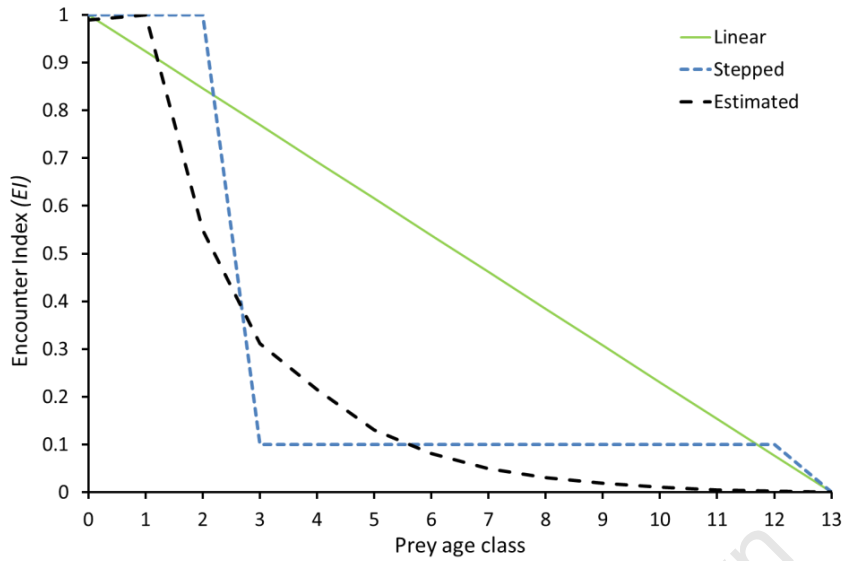
Figure 6. Three age-dependent encounter indices for the modelled population at steady state. The 'Estimated' function represents the square-root of expected encounter rates based on relative numbers. The 'Stepped' function represents very low cannibalism on ages > 3 years, with most of the cannibalism pressure on the younger age calsses. The 'Linear' function represents a linear decrease in encounter index with age.

When incorporating cannibalism into an ASM, an adjustment needs to be made to the parameter value of natural mortality at each age   . This is because a certain proportion of   is already allocated to cannibalism.   In the absence of fishing, the sum of the modified constant natural mortality   and the time-varying cannibalism *(CanM$_{y,a}$)* gives a new total mortality rate

     . To incorporate cannibalism without unduly affecting total mortality, a proportion   of natural mortality   from the model was apportioned to cannibalism mortality with the remaining natural mortality now termed   .

$$(15)$$

$$(16)$$

$$(17)$$

$$(18)$$

The reduced   value remains constant throughout the cannibalism simulations. The

rate varies as a function of the encounter index (Equation 18), which changes each year as the

numbers per age class change (Figure 7).   is a parameter that was tuned to ensure that the

total spawner biomass was at the same equilibrium when using the model with and without

cannibalism.

$$a)\ Z_{y,a} = M_a + S_a F_y \qquad b)\ Z_{y,a} = NatM_a + S_a F_y + StaticCanM_a \qquad c)\ Z_{y,a} = NatM_a + S_a F_y + CanM_{y,a}$$
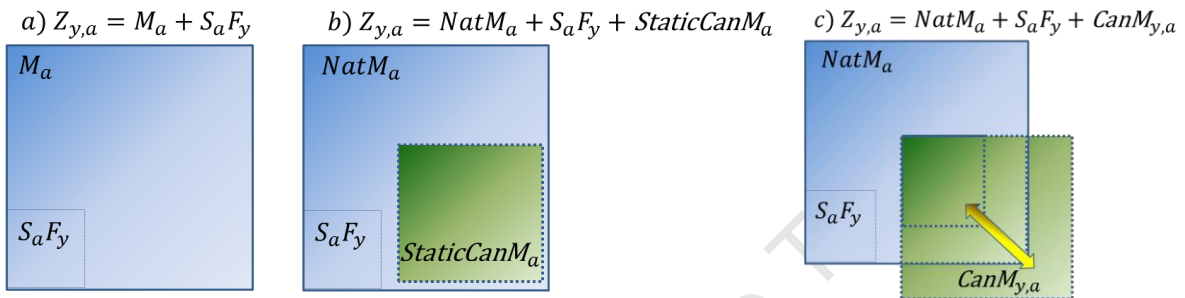
Figure 7. The shaded areas represent total mortality at a given age class (   ). The fishing mortality remains constant. (a) A fished population at equilibrium, no cannibalism, (b) A fished population at equilibrium, including a fixed proportion of cannibalism   and (c) a dynamic fished population responding to changes in cannibalism (   ).

Simulations

Simulations were carried out to address each of the four model objectives.

a) Sensitivity to   functions

The sensitivity of the model to the three different   functions was tested by comparing age structure and mortality at age at equilibrium. This was done using   = 0.2 and 0.5, with maximum capped recruitment (419.4 x10^6) and no fishing. The   value was changed each time to ensure a similar maximum spawner biomass. The square-root encounter index ("Estimated") was used for the remainder of the experiments.

b) Effects of different levels of cannibalism

To understand the effect of different levels of cannibalism on   and the population age-structures of unfished populations, simulations were done using values of   = 0.1, 0.3, 0.5, 0.7 and 0.9. A   value was selected that was representative of the *M. paradoxus* population according to estimated percentage deaths due to cannibalism given by Shannon et al. (2003). Shannon et al. (2003) used a mass-balanced model that gave estimates of cannibalism being responsible for 15 % (0 to 2 year old) and 2 % (> 3 year old) of *M. paradoxus* biomass dying in the southern Benguela during the 1980s and 1990s. Using trawl selectivity with a fishing mortality of F = 0.2 y^{-1} with the Beverton - Holt recruitment function, various   values were tested to identify which proportion of cannibalism would result in similar percentages of fish dying due to cannibalism. Comparisons between BOFFFF and Beverton – Holt recruitment were also undertaken to test each recruitment function's sensitivity to different fishing mortalities.

c) Testing Lleonart's hypothesis

To test Lleonart's hypothesis that catching big fish in a cannibalistic system benefits recruitment into the fishery (3, 4 and 5 year old fish), the resulting age structures using longline selectivity fishing mortalities of $F = 0.3$ y^{-1} and 0.6 y^{-1} were compared to an unfished population using Beverton-Holt (for $F = 0.3$ y^{-1}) and BOFFFF (for $F = 0.6$ y^{-1}) recruitment at $= 0$ and 0.2. To further test Lleonart's hypothesis, a simulation was carried out to test the relationship of different   values to potential BOFFFF-dependent recruitment for both longline and trawl selectivities.

d) Comparing size-selective fishing methods

Using the Beverton - Holt recruitment function in a cannibalistic population ($= 0.2$), the potential MSY, spawner biomass and age structure under different size-selective fishing strategies were compared. The population was initially fished at MSY ($F = 0.32$ y^{-1} at 20 300 tons/ year) for 30 years using a trawl selectivity, then two different fishing strategies were applied:

- Strategy one - Introduce longlining in addition to trawling and assign it 50% of the current fishery yield (combined $F = 0.06$ y^{-1}).

- Strategy two - Stop trawling the population and allow 100 % of the fishery yield to be caught using the longline selectivity ($F = 0.0.7$ y^{-1}).

Fishing mortality rates were adjusted in both of the fishing strategies to allow for consistent annual fishing yields as obtained in the previous 30 years at 20 300 tons/ year.

Results

a) Effects of *EI* selection on cannibalistic population

Figure 8 compares the effect the three different   functions have on the numbers of fish dying in the population at different ages and the resulting age structures at the two proportions of cannibalism.
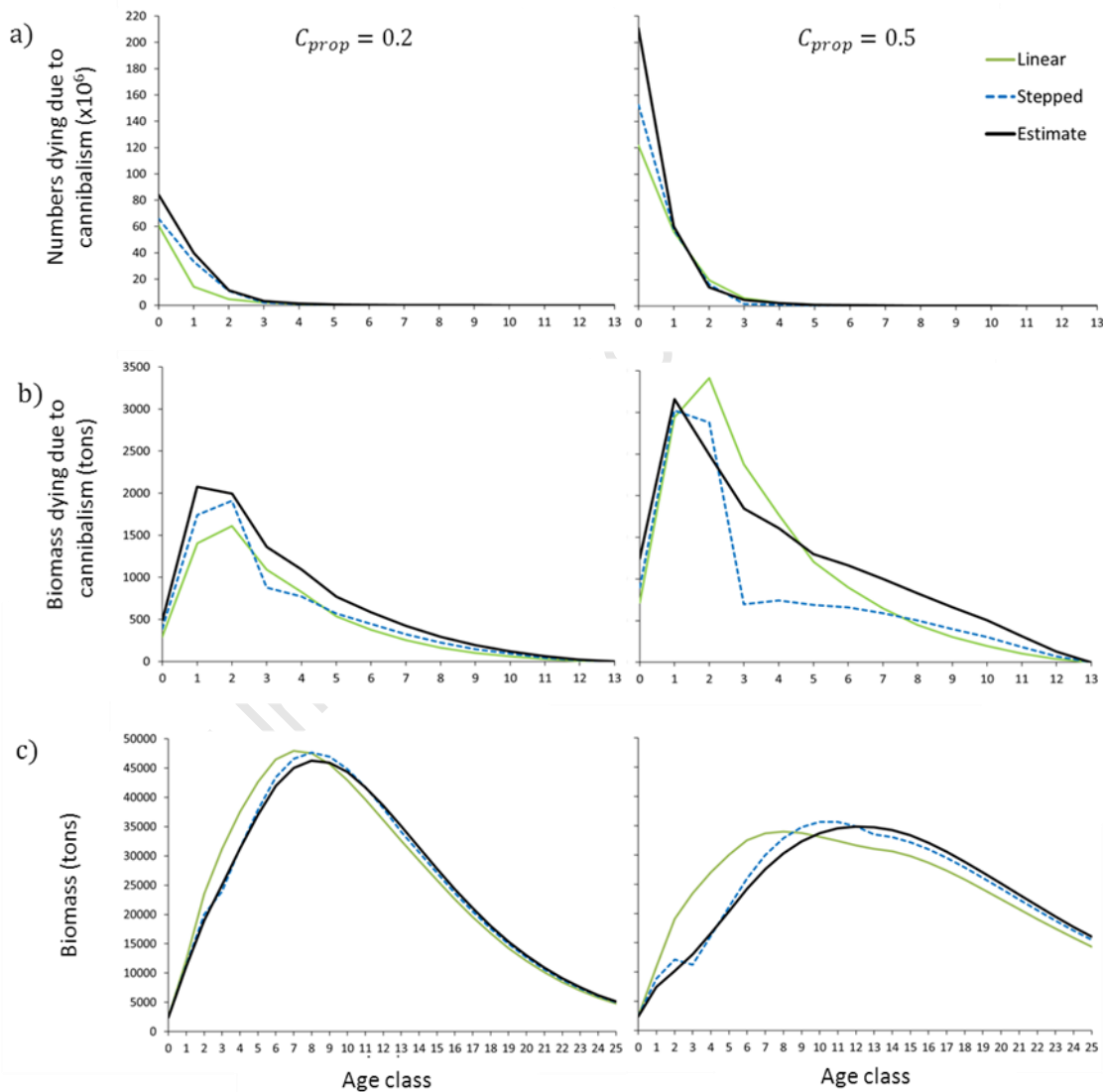

Figure 8. (a) Numbers (x10⁶) and (b) biomass (tons) of fish dying due to cannibalism at a   = 0.2 and 0.5, and (c) the resulting age structures using a fixed maximum recruitment (419.4 x 106) and no fishing mortatility, to compare the effects of using the three different   functions. The *Estimated* cannibalism function was used for the remainder of the simulations.

For each of the   functions, cannibalism results in the most deaths occurring in the first two age classes (0 and 1 year olds) (Figure 8a and b). As the   is increased to 0.5, all three functions behave in a similar fashion, with deaths caused by cannibalism increasing in all of the cannibalized age classes. The "Estimated" square-root function causes the highest number of deaths for the early age classes (< 2 year olds) and the > 5 year age classes when compared to the other functions and increases the number of deaths to the 0 year olds threefold when   = 0.5. The "Linear" function remains the most conservative for the early year classes but causes the highest number of deaths for the fish 2 to 5 years old (= 0.5).

The resulting age structure for each of the   functions with   = 0.2 show minor differences in distribution, with differences becoming more apparent as   is increased. The "Estimated" and "Stepped" functions result in a population structure having similar shapes and both result in the mode of the distribution lying between 10 and 13 years, whereas the "Linear" function results in a population with a greater biomass of young fish (< 7 year olds), with the mode of distribution at about 7 years.

b) Effects of differing levels of cannibalism on mortality rates in the population

Figure 9a shows the age-dependent values of natural mortality rates in unfished populations at increasing levels of cannibalism. As the proportion of mortality caused by cannibalism increases,   decreases over the whole range of ages (natural mortality rates between ages 13 to 25 year old age classes are identical) and $CanM_{y,a}$ increases, the latter increasing disproportionately in the young age classes compared with the older (5 to 13 years) age classes.

There is approximately a fourfold increase in the   rate for the 0 to 2 year olds at   = 0.9 compared to a population without cannibalism (Figure 9a). As   increases, $Z_{y,a}$ rates decrease for all ages > 4 years with little to no change in mortality rates occurring around the 3 year age class. As the rate of cannibalism increases within the model, the rate of   decreases for all age classes. When high cannibalism proportions (0.8 to 0.9) are used,   drops close to zero for ages ≥ 13 years. Therefore the total mortality experienced by the non-cannibalized portion of the population is inversely proportional to the   value (Figure 9 and Equation 16).

With an increase in   there is a decrease in the number of fish dying that are older than 3 years, which also accounts for the decrease in the total biomass of dying fish in the population (Figure 9b and c). Fish aged between 1 to 4 years have the highest mortality rate due to cannibalism. There is increased cannibalism on the young fish by the remainder of the population due to the high encounter rates with the early age classes. Therefore the numbers of fish that recruit into the fishery also decrease. The overall recruitment into the model population remained fixed at 419.6×10^{6} because there was no fishing, and the increased cannibalism rates did not affect the ability of the spawner biomass to produce less than the maximum capped value.
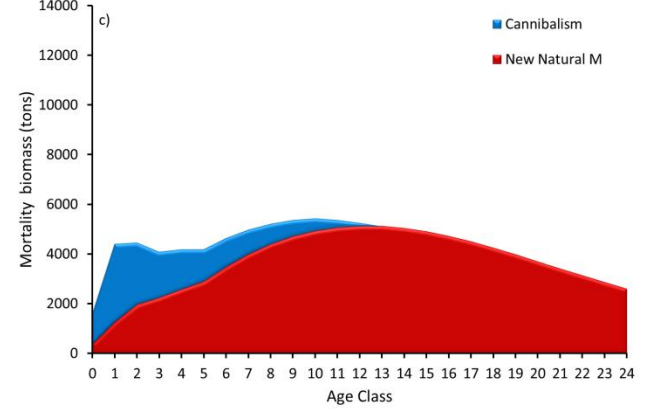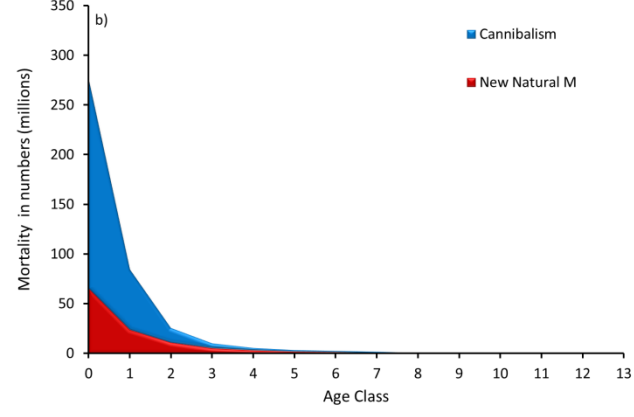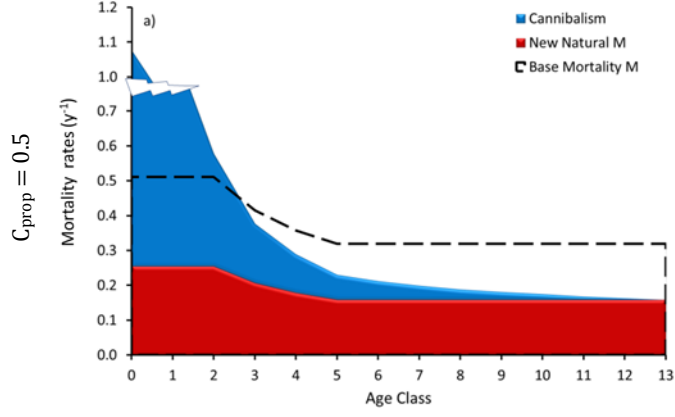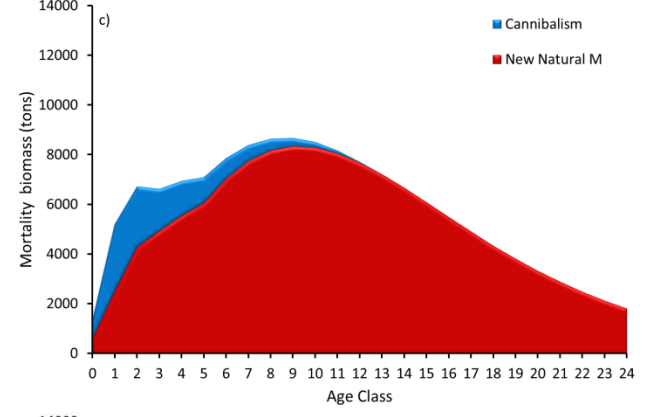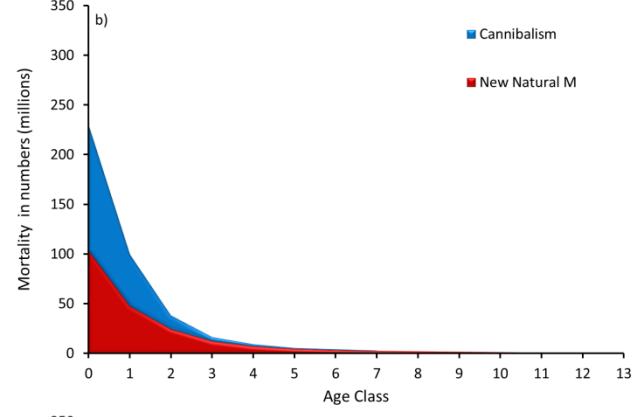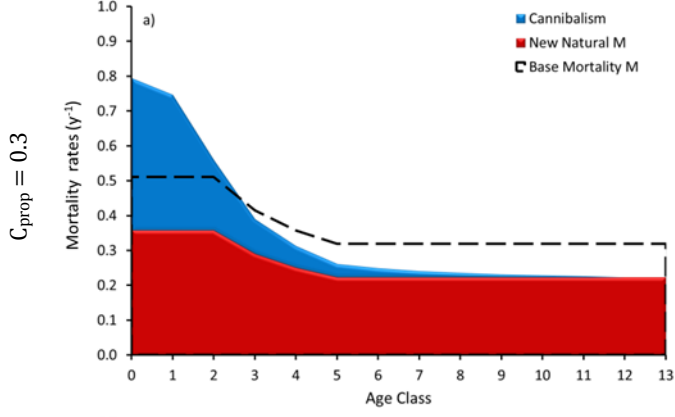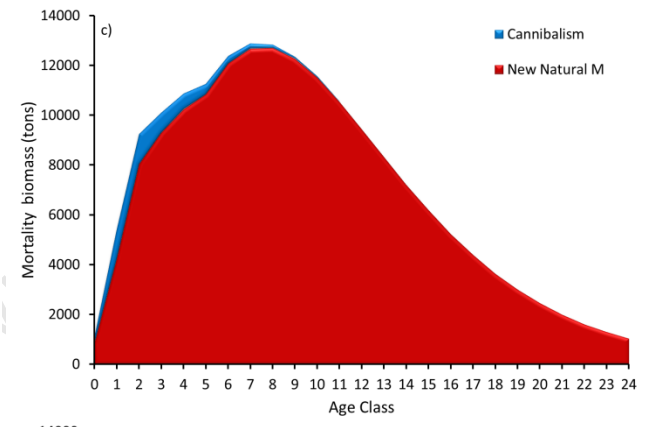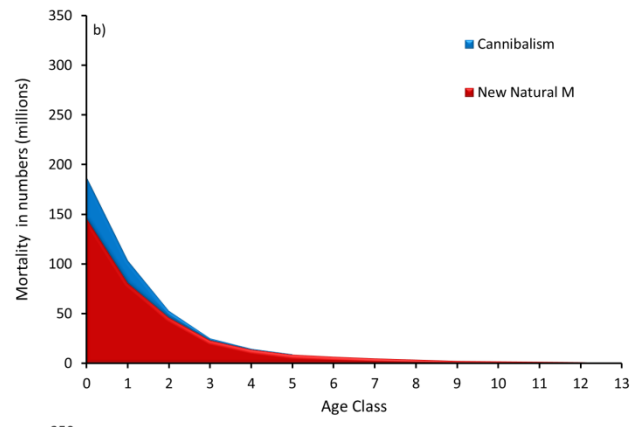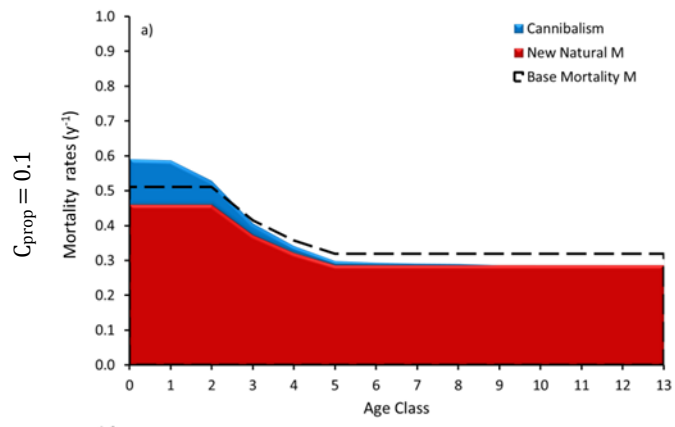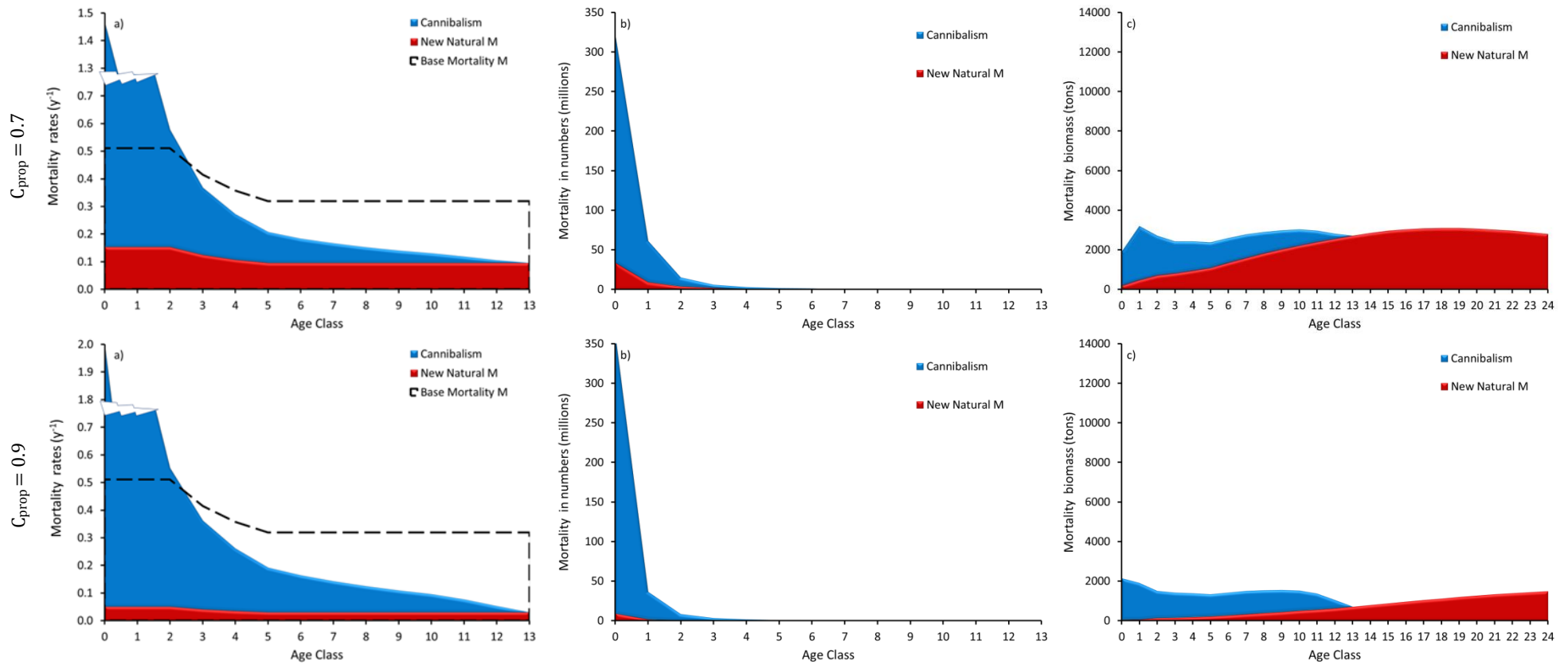
Figure 9. Cumulative stack graphs showing the effect of changing , the contribution of cannibalism to total mortality per age class (a) relative magnitudes of adjusted natural mortality rates (y⁻¹) and cannibalism mortality rates (y⁻¹) for each age class, (b) relative numbers in each age classes dying through adjusted natural mortality rates (y⁻¹) and cannibalism mortality rates (y⁻¹) and (c) relative biomass (tons) for each age class dying with different selected cannibalism proportions and all using a fixed recruitment (419.4 x 10^6 y⁻¹) without fishing.

Effects of differing levels of cannibalism on population structure

The age structure of the population with no fishing, a fixed spawner biomass (599 000 tons) and varying levels of cannibalism are presented in Figure 10a and 10b.
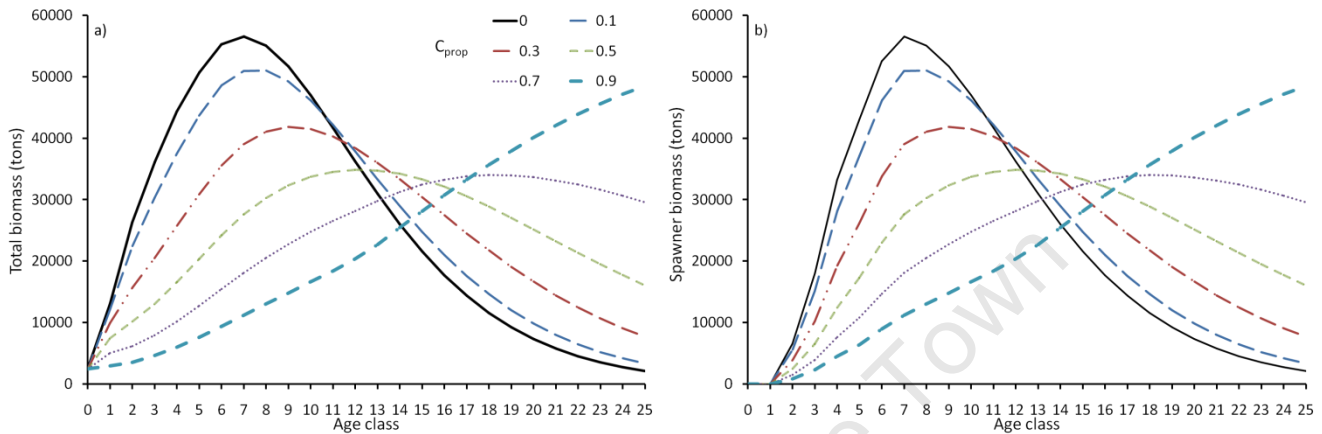

Figure 10. The distribution of (a) total biomass and (b) spawner biomass across age classes for different proportions of cannibalism   as a component of natural mortality.

The population without cannibalism is dominated by younger fish (mode = 7 year age class), and as cannibalism is introduced the mode of the distribution shifts to the older age classes. At a   = 0.9 the mode of the distribution is at a maximum value of 25 year olds, with successive decreasing biomass in each of the younger year classes.

Estimating C_{prop} for M. paradoxus

Using the estimates of percentage of small hake in the diets of large hake (Shannon et al. 2003), a of value of 0.1 gave the closest results (Table 4), even though it overestimated the percentage death of the young year classes (0 to 2 year olds). Due to the weak effect produced by such a low

value, a value of 0.2 was used in the remainder of the model to enhance the   effect on

resulting population age structure.

Table 4. Percentages of total biomass mortality attributed to cannibalism for two age groups (0 to 2) and (3 to 25). Shannon et al. (2003) gives estimated percentage mortalities due to cannibalism from the 1980-90s in the southern Benguela population which has been truncated by fishing at F = 0.2 y^{-1}.

0.1	16 %	1 %
0.2	28 %	2 %
0.3	41 %	4 %
Shannon et al. (2003) Estimate	15 %	2 %

Understanding BOFFFF and Beverton – Holt recruitment sensitivities.

The model was run to identify at what fishing mortalities, for both longlining and trawling, BOFFFF-based recruitment decreased below the maximum value. It was found that, in the longlining scenarios, the BOFFFF recruitment function resulted in decreasing recruitment (< 419.4 x 106 recruits) at F ≥ 0.51 y^{-1} without cannibalism and at F ≥ 0.43 y^{-1} with cannibalism.   At F ≤ 0.55 y^{-1} BOFFFF-based recruitment was less than that which was produced from the Beverton – Holt recruitment model for both cannibalistic and non-cannibalistic functions.

Similar results were found when testing the trawl scenarios. BOFFFF-based recruitment functions resulted in decreasing recruitment at F ≥ 0.35 y^{-1} without cannibalism and at F ≥ 0.4 y^{-1} with cannibalism. The recruitment resulting from the Beverton – Holt function was smaller than that from the BOFFFF-based function for F ≤ 0.47 y^{-1} with cannibalism and F ≤ 0.37 y^{-1} without cannibalism. For

fishing mortality values greater than these thresholds, the BOFFFF-based recruitment was smaller than that estimated using the Beverton – Holt model .

c) Testing Lleonart's hypothesis

When comparing the age structures resulting from application of the two different recruitment functions (Figure 11), both result in decreases in biomass in each age class as fishing mortality increases, as would be expected. The BOFFFF recruitment function results in greater biomasses than the Beverton-Holt function in all age classes when F=0.3 y^{-1}. This situation is reversed when F = 0.6 y^{-1} (Figure 11). The peak biomass shifts towards younger fish for both fishing selectivities.
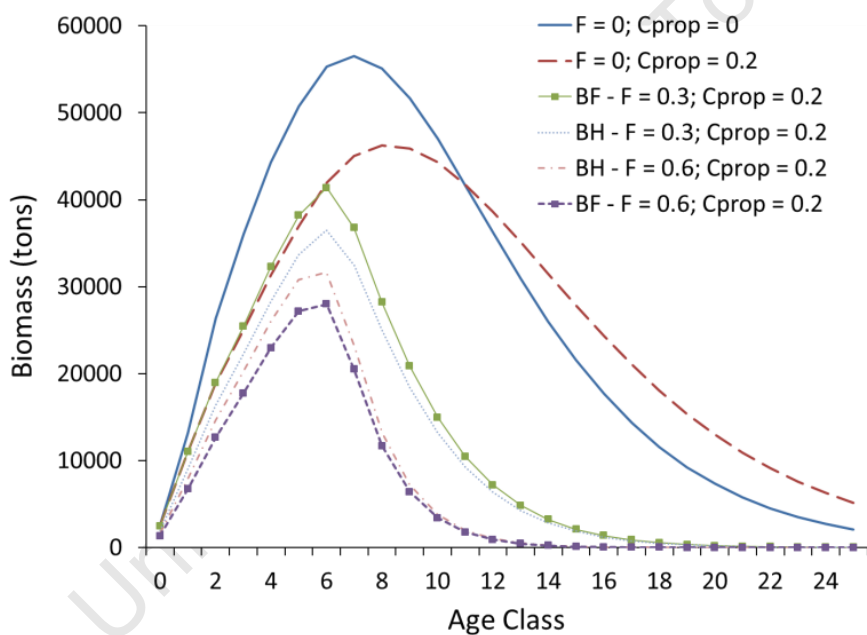

Figure 11. Resulting age structures for cannibalistic populations using longline fishing selectivites and the two recruitment functions. Line 'F = 0; Cprop = 0' and line 'F = 0; Cprop = 0.2' are both at a maximum carrying capacity of 599 999 tons. F = fishing mortality rate (y^{-1}); BF = BOFFFF recruitment function; BH = Beverton – Holt recruitment function.

To test Lleonart's hypothesis, a comparative study was made with different levels of   and

potential BOFFFF recruitment (by removing recruitment cap) at different fishing mortalities for both

longlining and trawling (Figure 12).
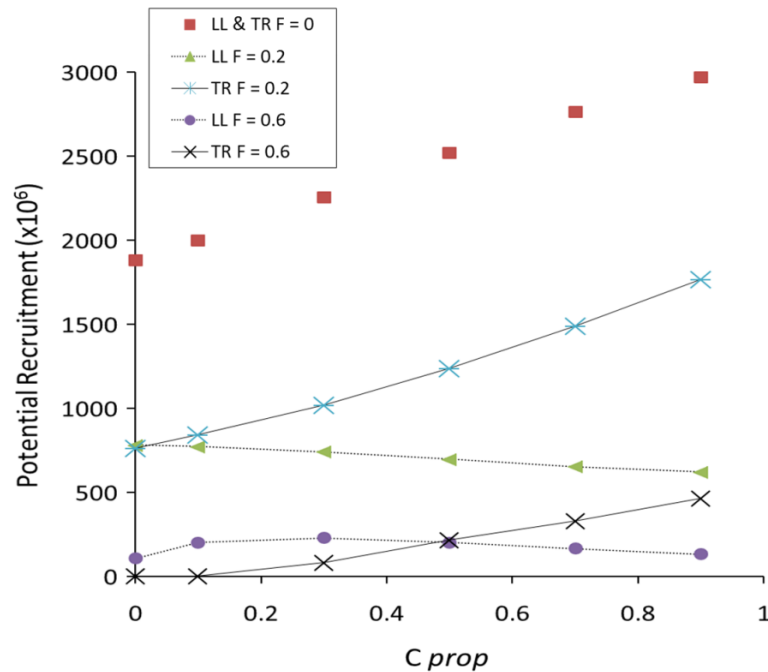

Figure 12. Resulting scatter-plot showing potential recruitment (x 10^6) and the proportion of cannibalism (at different

fishing rates(F = 0 y^{-1}; 0.2 y^{-1}and 0.6 y^{-1}) for both trawling and longlining (in 99th year). LL = Longlining; TR = Trawling;

F = Fishing mortality rate.

Without any fishing, as the level of   increased, the overall potential recruitment for the

population also increased. This was similar for different F values when trawling. As the

increased at a fixed F value, the potential for recruitment in the population also increased. The inverse

was found for longlining. As the   was increased at a fixed F value, the potential recruitment

decreased. Trawling a population at F = 0.6 y^{-1} and a   ≤ 0.1 resulted in substantially reduced

recruitment, but values of   > 0.1 resulted in increased potential recruitment. In contrast,

longlining at F = 0.6 y^{-1} resulted in peak recruitment for small values of C_{prop}, with recruitment

decreasing as C_{prop} values increase. Heavy fishing on large cannibalistic fish was thus found to decrease potential BOFFFF-based recruitment over the long term, refuting Lleonart's hypothesis.

Resulting spawner age-structures at F = 0.6 y^{-1} for different values of   are presented in Figure 13. As   increases, the trawl selectivity allows for greater survival of old BOFFFF individuals (> 12 year olds) when compared to longlining, enhancing numbers of 3 to 5-year-old fish.
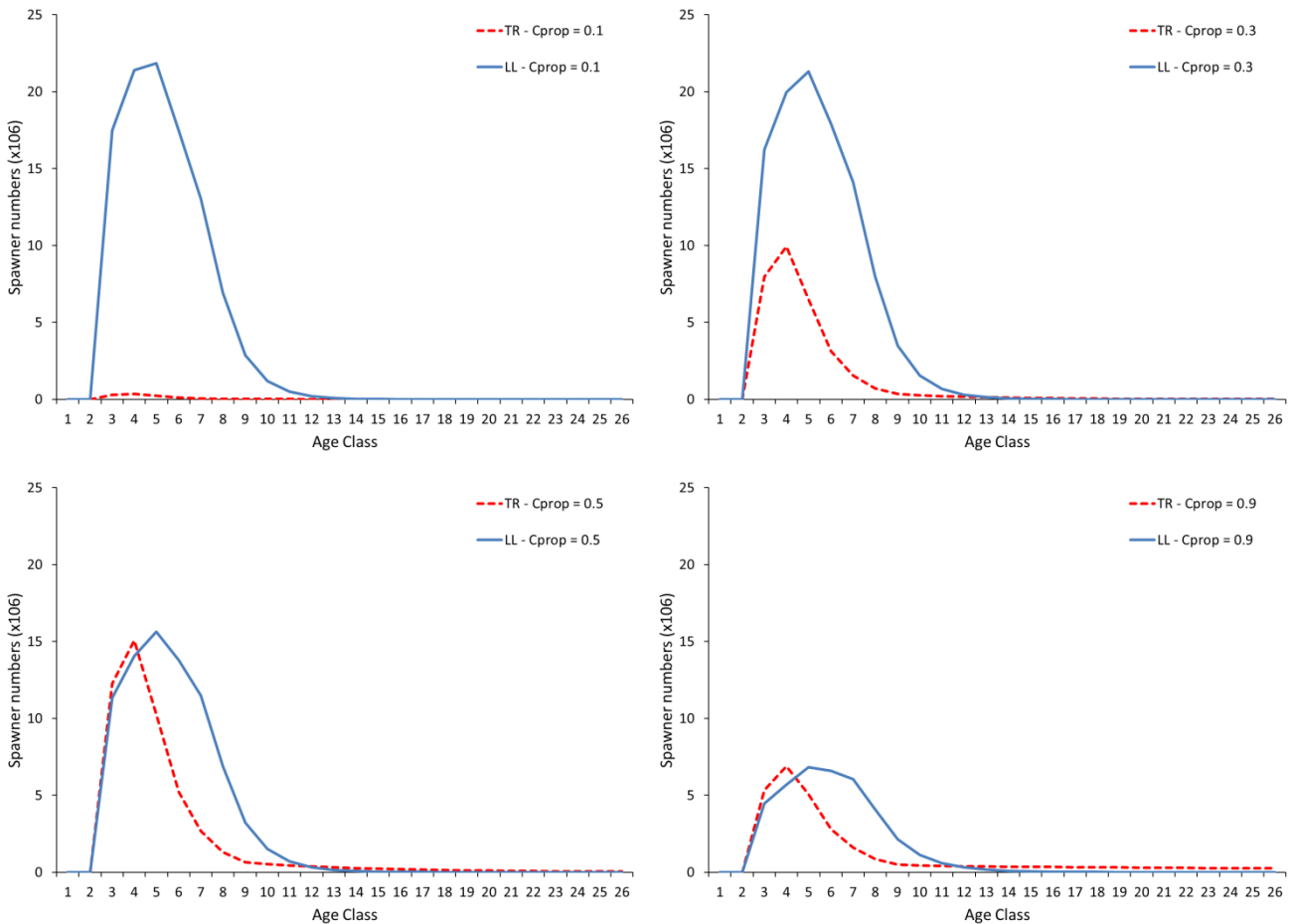

Figure 13. Resulting spawner numbers (x10^6) showing age structure (in 99th year) at different levels of   for trawling and longling at F = 0.6 y^{-1}. L = Longlining; TR = Trawling.

d) Comparing the effects of different fishing selectivities

An MSY of 20 268 tons was achieved with trawl selectivity at $F = 0.32$ y^{-1}. This was 56 % lower than the MSY of 34 822 tons potentially available when using the longline selectivity at $F = 0.35$ y^{-1}. Figure 14 shows the spawner biomass (tons) and resulting age structure at MSY for the longline and trawl selectivity.
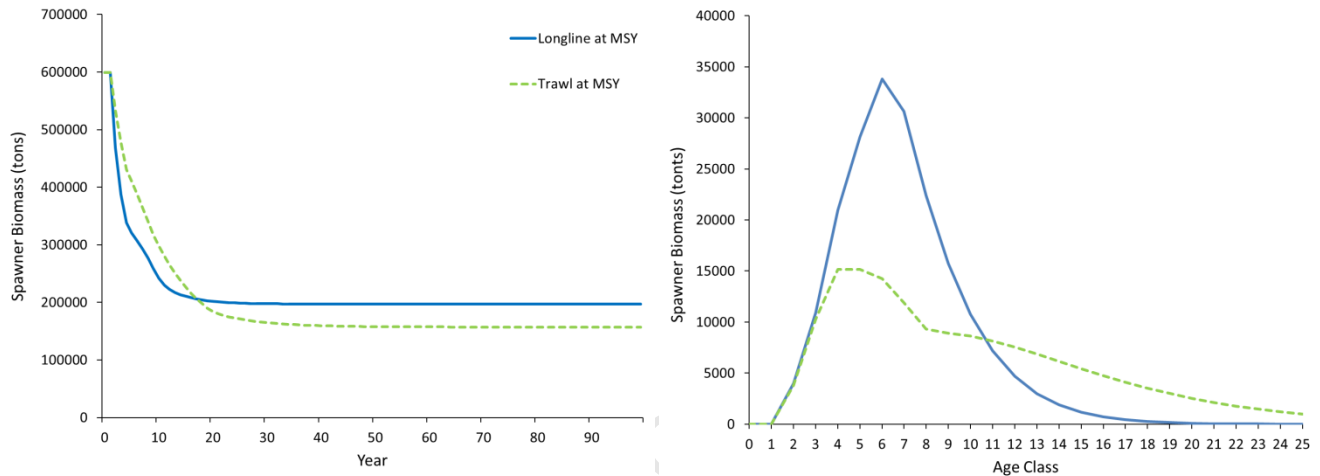

Figure14. a) Spawner biomass (tons) and (b) age structure (tons) for year 98 at MSY for both selectivies in a cannibalistic population (($F = 0.32$ y^{-1}) and ($F = 0.35$ y^{-1}) from using a fixed maximum recruitment.

Trawl selectivity at MSY results in a lower sustainable spawner biomass when compared to using longline selectivity, even though the longline selectivity allows for a greater total yield (Figure 14a). The resulting age structure from trawling has more large fish in the population (> 11 year olds), thereby increasing the overall potential recruitment (as discussed above). Fishing using longline selectivity allows for a larger number of young fish (< 11 year olds) but results in depletion of the old age classes (> 17 years) (Figure13b).

Comparing the effects of changing the fishing selectivity of a heavy fished population with cannibalism and Beverton-Holt recruitment

Figure 15a compares how the spawner biomass adjusts to the introduction of two fishing selectivities after a population with cannibalism was initially fished using a trawl selectivity at MSY for 30 years ($F = 0.32$ y^{-1}). Figure 15b shows how fishing using longline selectivity or a combined longline and trawl selectivity results in an age structure which has more fish in each age class when compared to initial fishing conditions (only trawling at $F = 0.32$ y^{-1}).

The initial scenario of trawling at MSY kept spawner biomass at 150 700 tons, only 25 % of K_{sp} (spawner biomass at pristine levels). When the catch of 20 700 tons was equally shared between both fishing selectivities (trawl and longline) after the 30 years, there was an increase in the spawner biomass to about 370 000 tons (60 % of K_{sp}) because of enhanced recruitment resulting from the removal of large, cannibalistic fish. The third scenario was to completely remove trawling and allow the full catch to be caught by longlining. This gave the strongest positive response to the spawner biomass and allowed the population to recover to 70 % of K_{sp} (430 000 tons) while still obtaining the same fishing yield as the initial trawling. This result indicates that removing large fish enhances the survival of small fish, but it ignores the effects of BOFFFF on recruitment.
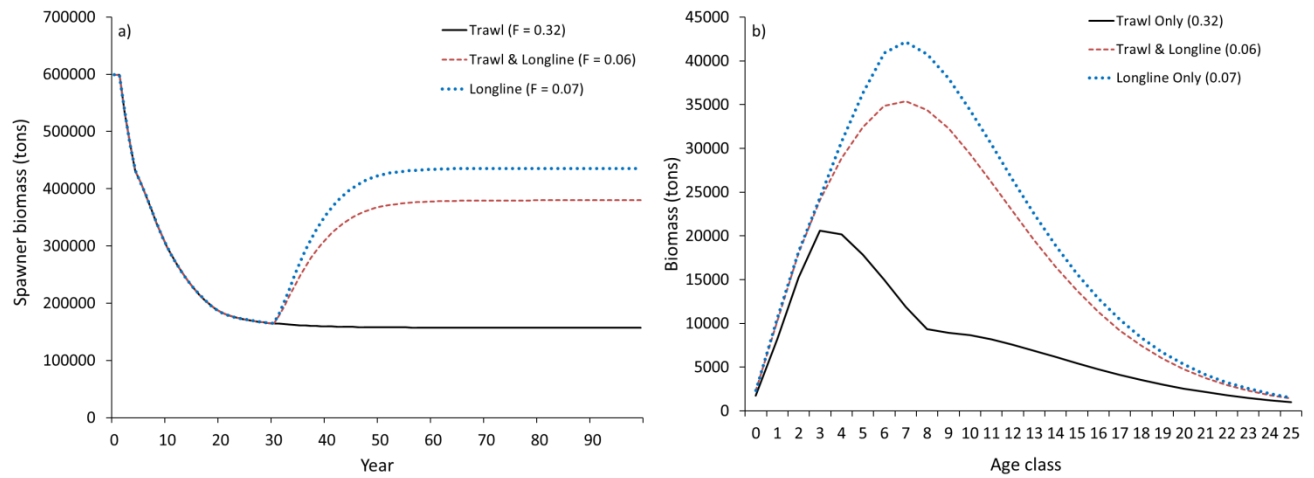
Figure 15 The (a) spawner biomass (tons) and (b) resulting age structure (tons) at equilibrium under Beverton-Holt recruitment. Three differing fishing strategies were applied to the population after it had been fished using a maximum sustainable trawl fishing yield of 20 300 tons for 30 years (F = 0.32 y^{-1}). The first strategy was to keep trawling as before, secondly the longline fishery was included in the fishery, with longline and trawl each catching 50% of the catch and thirdly, the trawl fishery was removed and only a longline fishery was introduced at a F = 0.07 y^{-1} to catch the same yield as originally caught by trawling.

Discussion

Encounter index

The encounter index was developed assuming a density-dependent relationship between cannibal and prey, as is observed in various cannibalistic species (Polis 1981, Claessen et al. 2003). The "Estimated" encounter index allowed for a dynamic value of Z_y, dependent upon age structure and the prey cannibal numbers for each age class. Certain difficulties were experienced during the development of the "Estimated" encounter index due to insufficient data on the feeding habits of different age classes and the cannibalistic behavior of *M. paradoxus.* Even though there has been much research undertaken on the feeding habits of Cape hake around southern Africa (Lleonart et al. 1985, Payne et al. 1987, Traut 1996), the available data are not in a format which is usable for a dynamic and density-dependent cannibalism function within an ASM. Certain assumptions were made in the development of the encounter index, such as cannibalism within *M. paradoxus* being density dependent and knife-edged size-selective feeding of the cannibals.

The method of developing the encounter indices within the ASM did not account for changes in density effects due to environmental factors, such as variation in distribution due to the movement of low dissolved oxygen waters or changes in upwelling intensity along the western coast of South Africa (Macpherson et al. 1991*).* It is believed that, as the low oxygen waters move closer inshore, it would force a greater degree of overlap between cohorts, and thereby increase expected cannibalism. In contrast, as low oxygen water moves further offshore, so cannibalism rates are expected to drop due to increased available spacing between cohorts (Macpherson et al. 1991, Macpherson and Gordoa 1994**).** The model was developed as a single-species model and is not influenced by changes in

availability of other prey or predators such as *M. capensis*. Even with such limitations the encounter index met the requirements of the ASM to simulate a dynamic and age-specific cannibalism effect on the population, representative of interactions in nature.

Effects of C_{prop} on total mortality

It was shown that with an increasing value of   in the population, the mortality rate on early age classes (≤ 2 years) also increases, whereas the mortality rate for fish > 4 years decreases. This continual feeding on young fish can lead to a capping mechanism which prevents new recruitment into a fishery (Claessen et al. 2004). This recruitment capping effect therefore results in the mode of the population biomass age structure shifting towards the old fish. As the BOFFFF in the population increase, so the potential recruitment of the population also initially increases. Although there is an increase in the potential recruitment index for cannibalistic populations, it is unlikely to be available to the fishery due to high levels of cannibalism on the young. It is believed that this is likely to only occur in a population with cannibalism levels well above the values experienced by *M. paradoxus.* Low levels of cannibalism were not found to make a significant difference to the overall recruitment, and resulted in slightly increasing mortality of the younger size classes (< 2 years) and decreasing the mortality of older (> 4 years) age classes.

In the establishment of a dynamic mortality per age class, a model artifact was that as the level of cannibalism increased, the   for the non-cannibalized age classes tended towards zero. To curb the unbalanced increase of the non-cannibalized fish, a coefficient called   was introduced to ensure that the resulting total spawner biomass didn't exceed a K_{sp} of 599 000 tons in an unfished population. This artifact could lead to an unrealistic population age structure resulting from high levels

of cannibalism, but was negated by using relatively low cannibalism rates when running the experiments.

Choosing a C_{prop} value for *M. paradoxus*

A cannibalism mortality rate of 0.1 y^{-1} was estimated from Shannon et al. (2003), but due to the low effect produced by such a low value of   a value of 0.2 y^{-1} was chosen for *M. paradoxus.* This approximation is within the range estimated by Payne et al. (1987), but higher than estimates by Traut (1996). Previous studies reveal a large range of expected cannibalism rates for *M. paradoxus*, and very little information is available for size-specific estimates. Shannon et al. (2003) and Payne et al. (1987) estimate that approximately 18 to 20 % of the natural mortality of *M. paradoxus* can be explained by cannibalism, while other studies undertaken in the last few years don't show any significant rates of cannibalism (< 5 %) (Traut 1996). The diet study by Traut (1996) reveals that cannibalism in *M. paradoxus* in the last few years has dropped by approximately 15 % when compared to the studies undertaken by Payne et al. (1987).

Lleonart's hypothesis

Lleonart's hypothesis, which states that catching big fish benefits recruitment into the hake fishery in a cannibalistic population, was tested for both Beverton - Holt stock-recruitment and maternal-based BOFFFF recruitment. Lleonart's hypothesis was partly supported within this study for Beverton-Holt recruitment but not if BOFFFF-based recruitment was used. As the fishing rates were increased, the number of spawners and therefore recruitment and fish in each pre-fishery class also decreased (Figure 11). These decreases in annual recruitment, due to decreasing total spawner biomass and

increases in total mortality, were responsible for the decreasing numbers in each year class in the population (Figure 11a). It can be expected that the number of deaths in the early age classes was moderated by the decreased cannibalism mortality experienced by the young age classes as fishing rates were increased.

When comparing maximum potential maternal-based BOFFFF recruitment and different values of for the different fishing selectivities, it was found that as the C_{prop} increased at fixed trawl fishing rates the potential recruitment also increased. The potential recruitment dropped with increasing values of when using longlining at a fixed value. The reason that trawling seems to boost potential recruitment as increases is that the trawl selectivity favours an older population age structure (as discussed above, see Figure 10) and allows for a greater survival rate of old BOFFFF individuals when compared to longlining.

It was also noted that, even though the trawl selectivity had potentially higher recruitment into the population at different F values, complete stock collapse also occurred sooner than when longlining at low levels of . As values of were increased the population became viable again and resulted in potentially producing more recruits than longlining. These results are the opposite to those predicted by Lleonart et al. (1985), therefore no supporting results were found using this ASM with BOFFFF-based recruitment to substantiate Lleonart's hypothesis.

Evaluating trawl and longline selectivity

When spawner biomass and age structure were compared between the use of trawl- and longline-selectivities, at a fishing pressure which results in MSY and using Beverton-Holt recruitment, similar results to Cochrane et al. (1997) and Jayiya (2001) were found. The longline selectivity was found to be superior to the trawl selectivity for potential fishery yield and on a spawner-biomass per recruit basis.

Figure 15 represents a situation that could mimic the history of *M. paradoxus* catches in southern Africa. It illustrates a fish population that has been intensely harvested for many years using trawl selectivity. The model has illustrated that by changing the fishing selectivity towards something more similar to longlining, it is possible for spawner biomass to recover to levels double in number to that of trawling and allow for a larger MSY.

CHAPTER 3

Conclusions

Cannibalism-induced mortality in *M. capensis* was initially assessed by Lleonart et al. (1985), but including cannibalism in population models has been one of the chief problems affecting population calculations (Punt et al. 1992, Macpherson and Gordoa 1994). This study was focused on trying to understand and explore various ways in which cannibalism can be incorporated into an ASM, and to develop a dynamic total mortality for each age class. The model was built as a single-species model to be able to get a better understanding of the effect cannibalism has within a population. The model did not include the potential effects of other predators or alternate prey types, and further development of the model gives opportunity to include these functions.

According to Field et al. (2008), BOFFFF theory suggests that the more the age structure of a population tends towards the older individuals of a population, the greater the potential recruitment that population can provide. Field et al. (2008) suggest that the hake fisheries should be targeting equally across the entire age structure of the population, while Lleonart et al. (1985) suggested selective fishing of the older and more cannibalistic portion of the population should optimize recruitment. In a cannibalistic population, there is an increase in potential recruitment experienced by the population as the age structure shifts to the more mature individuals (Figure 10), but the mortality incurred by the younger ages classes (< 3 years olds) also increases (Figure 11a and b). The increasing potential recruitment was only found to occur when fishing with trawl selectivity and BOFFFF-based recruitment, indicating weak support for Lleonarts hypothesis.

The heavily fished model population using trawl selectivity was able to respond positively in both spawner biomass recovery and in potential maximum fishery yield by changing over to a longline selectivity based fishery. The use of longline selectivity has been shown by the model to be favorable for MSY, K_{sp} and resulting recruitment when compared to using trawl selectivity, with similar results being found in various other studies (Japp and Wissema 1999, Jayiya 2001). However, this result ignores the effect of BOFFFF-based recruitment.

Final remarks

Lleonart's hypothesis, which suggests that decreasing the number of large cannibals in a population (such as by using a longline selectivity) would result in an enhancement effect on the number of pre-fishery recruit age classes, was only partly supported, and only when using the Beverton-Holt stock-recruit function at moderate fishing mortality. The study by Field et al. (2008) indicates that BOFFFF are important for successful recruitment in *M. paradoxus*, and their survival in a cannibalistic population (when trawling) was seen to boost recruitment potential.

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"The Heavens declare the glory of God, the sky proclaims his handiwork" Psalm 19:1

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