

**Comments on the “River model” (de Moor and Butterworth 2014):
Bounding exploitation rate, estimating escapement for critically dependent predators, or
understanding the interactions between anchovy and penguin demographics?**

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Summary

The “River model” presented in de Moor and Butterworth (2014:MARAM/IWS/Peng/B5) builds on assumptions relating to time and space that are not explicitly tested. This document argues that, in order for the river model approach to be useful in adequately estimating escapement of anchovy for seabirds feeding on them at the west coast, the temporal resolution has to be finer, spatial dynamics need to be modelled explicitly, and consequences of “bad years” need to receive particular attention. Furthermore, the consequences of the assumption that all anchovy in the water are available to breeding penguins needs testing, as do any remaining assumptions on shoal variability in view of the birds’ feeding dynamics once an appropriate temporal and spatial resolution has been chosen.

Introduction

The African penguin (*Spheniscus demersus*) population has decreased substantially in the last century and is currently at its lowest recorded level with fewer than 18 000 breeding pairs at all South African colonies combined (Crawford et al. 2014). The decline in population numbers and localised differences in breeding success are believed to be closely related to the scarcity of food (Crawford et al. 2008, 2011, 2014).

Within this discussion, the main question addressed here is: Are commercial purse-seine fisheries having a negative effect on the breeding penguin population (and populations of other seabirds) by competing directly for food?

Since the late 1990s, anchovy (*Engraulis encrasicolus*) in the southern Benguela is generally regarded as only having been exploited lightly to moderately, where exploitation rates (F/Z) have not exceeded 10%, and total catch relative to (“May”) survey recruitment biomass has stayed below 50% (Astor 2014). Most recently, these indicators generally point to moderate, rather than light, exploitation in the years 2005 to 2011.

A model aiming to estimate the impact of fishing on the amount of anchovy available to west coast penguin colonies during the months April to September for the years 1987-2011 has been presented by de Moor and Butterworth (2014). Model results are used to suggest low impact of fishing on anchovy and, consequently, little reduction in availability to predators, such as penguins. Plots of May survey results are used to argue that anchovy distribution, generally, is appropriate for breeding penguin feeding in the vicinity of Dassen and Robben islands.

In the following, we highlight some crucial points related to the design of (assumptions underlying) the model presented in de Moor and Butterworth (2014). We suggest that, in order for this model to be useful in relating to penguin foraging dynamics and demographics, additional analyses would need to be carried out. We provide contextual information which supports this request, and underline the likely need for a redesign of the model if it should contribute to improve our understanding of the interactions between the anchovy-directed small pelagic fishery and penguin demographics.

Context

Anchovy

Anchovies spawn on the eastern, central and western Agulhas Bank during austral spring and summer, from October through to February, with a peak in November and December. The bulk of the eggs and larvae are transported westwards and northwards onto the west coast, where they metamorphose and move shorewards onto the shelf. Pre-recruits have been found as far northwards as the Orange River (29°S), with the area around Hondeklip Bay (30°S) representing the northernmost regular major nursery ground. This journey takes them in the order of five to eight weeks, plus another two to three months from the offshore pre-recruit grounds up against the coast.

Where they come inshore depends on a) where they were spawned, b) how fast the transport in the jet current was, and c) their survival on the pre-recruit grounds off the west coast, where they are, *inter alia*, preyed upon by snoek (*Thyrssites atun*), yellowtail (*Seriola lalandi*) and albacore (*Thunnus alalunga*). Small recruits are also found further south, i.e., might move directly into St Helena Bay, and even inshore on the western Agulhas Bank, i.e., south of Dassen and Robben islands.

Once inshore, shoals of anchovy recruits move southward at 10-20 km per day in summer (Hutchings 1992; Figure 1), feeding largely on meso-zooplankton. They are consumed by seabirds, mammals, fish and the fishery, typically leaving very little to die of "M0", i.e., old age or disease. Based on models such as those underlying the analyses in Smith et al. (2011), predatory fish and cephalopods represent the largest source of mortality for anchovy and sardine, followed by fisheries, marine mammals and seabirds. Hutchings et al. (2012) point out that this ranking applies even in view of the increase in marine mammal numbers in the southern Benguela in recent years. Consequently, how many anchovy recruits will pass seabird colonies at the west coast depends on spawning date, transport speed in the currents, their growth rate and migration rate southwards, as well as on predation and fishing.

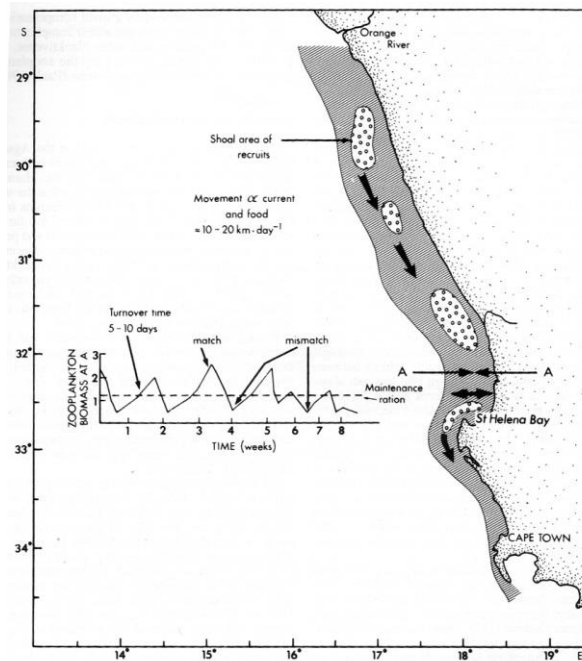


Figure 1 Movement of anchovy juveniles and recruits southwards (from Hutchings, 1992).

Assuming small recruits arrive in Hondeklip Bay (30°S) and using 10-20 km/day as migration rate, it would take them ca. 3.5-7 months to St Helena Bay (32.5°S). As an example, then, an egg spawned on the western Agulhas Bank in October could arrive as recruit in St Helena Bay by the end of April/May, and off Robben Island another two to four months later, i.e., around the end of June. An egg spawned in late December might only arrive as a pre-recruit in Hondeklip Bay in April, as a recruit in St Helena Bay in July, and another 2-4 months later (i.e., late August/September) at Robben Island. On the other hand, anchovy recruits have been found inshore in the northern St Helena Bay in March (van der Lingen & Huggett 2003). These would arrive in Table Bay in the beginning of July.

Seabirds

Birds are expected to adjust the timing of breeding to when environmental conditions are favourable and food is abundant so that their reproductive success is maximized (Lack 1954). Generally, the length of the breeding season correlates negatively with latitude (Sharp 1996). The higher the latitude, the greater is the seasonal variation in food supply and the shorter the time window for breeding (Croxall and Gaston 1988). Birds breeding in temperate regions show rhythms of reproductive activity which are typically synchronized to the pattern of optimal availability of food to ensure that breeding occurs at the appropriate time of year (Lack 1954, 1967, Furness and Monaghan 1987, Sharp 1996). The uncertainties around the timing of anchovy availability to breeding African Penguins is likely the reason for their prolonged breeding season, from ca. March to the end of September for Robben Island, and even more extended on Dassen Island (Wolfaardt et al. 2009).

In addition to temporal restrictions, the proximity and predictability of the food supply is crucial, particularly during breeding when birds are central place foragers (*sensu* Orians and Pearson 1979).

While albatrosses and petrels can cover hundreds of kilometres on their foraging trips (Weimerskirch et al. 1993, Waugh et al. 2002) and thus may exploit food sources distant from their breeding sites (Davis and Cuthbert 2001), penguins' foraging capabilities and hence foraging ranges are much more reduced (Wilson 1985, Wilson & Wilson 1990; 1995, Petersen et al. 2006, Ryan et al. 2007, Pichegru et al. 2009; 2010; 2012). To raise their chicks successfully, an African Penguin foraging trip should last no longer than on average 1-2 days. In this time they have to catch enough food to compensate for the high energetic cost of getting the food, to ensure their own survival, and to feed the chicks (Boersma and Rebstock 2009).

Predictability is dependent on the spatial and temporal scale considered, especially in the marine habitat. Prey is clustered from fine to large scale and it is important to take this spatial scale into account when linking a predator's foraging behavior to its prey. In temperate area at large and meso-scales, seabirds appear to have a good knowledge of the location and concentrations of patches and generally use a commuting type of trip to reach their foraging zones. Relying on such predictability, individuals head in a particular direction from the colony to reach favoured habitats of known productivity (e.g. Irons 1998, Patrick et al. 2014). Once there, animals generally use an area-restricted search behaviour to search for patches and swarms at finer scales (Weimerskirch 2007).

Questions concerning the River model as presented by de Moor and Butterworth (2014/B5)

1) What are the consequences of the assumptions about the monthly time step?

De Moor and Butterworth discuss the monthly time step chosen and suggest that a smaller time step might be more appropriate in view of the high variability of the availability of anchovy recruits to foraging seabirds as documented, *inter alia*, in the small scale surveys around penguin colonies. Studies of chick condition suggest that this trait seems to be sensitive to changing conditions on about a two-week time step (L. Waller, Cape Nature, pers. comm). Penguin chicks would not survive a month with very little food (Boersma and Rebstock 2009, Boersma et al. 1990). We therefore recommend a two-weekly time step as minimum temporal resolution.

2) What are the consequences of disregarding the spatial characteristics of the west coast system?

In the Benguela system off the west coast the movement of pre-recruit fish inshore is highly variable temporally and spatially. Most of the fishing takes place north of Dassen and Robben islands, and in the first half of the year, concurrent with (or preceding) the peak breeding season of seabirds.

Natural differences in the speed of the southward migration of anchovy recruits, potentially different shoal characteristics after fishing and environmental conditions add to the variability of food availability and predictability. These possibly aggravate the direct consequences of the reduced biomass due to predation and fishing in and around St Helena Bay. It is further assumed that all biomass passing the islands is within the foraging range of breeding birds, disregarding the foraging distance limitations of breeding penguins (see above), which were the motivation for the radii of the experimental closures.

3) What are the consequences of the assumption that all anchovy in the water are available to penguins?

As mentioned above, the fishing industry has recently complained about reduced availability of anchovy for being "hard on the ground". This implies that only a fraction of the anchovy in the water

is available to the fishery. However, this fraction can also be assumed to be outside of the range of penguins, which tend to forage mainly in the upper 50 m (Crawford and Whittington 2005). While they are physiologically able to dive deeper than 50 m, doing so will entail a greater expenditure of energy through diving to a greater depth and a longer search time to find prey as their usual cues for locating fish (other diving seabirds and the scent of dimethyl sulphide) are likely reduced. The ratio of anchovy catch/TAC may be an appropriate approximation for this reduced availability. The consequences for spatial and temporal characteristics of the reduced availability need careful testing.

4) What are the effects of particularly "bad" years?

When food is so scarce that adults are at risk of starvation, breeding is generally not attempted in long-lived species (e.g., Schreiber and Schreiber, 1984) as adults favour their own survival and potential for future reproduction. There is a substantial range of food availability in which most birds are still unable to breed, but manage to maintain adult survivorship. Breeding success, however, varies in closer relation to increasing food supply (Cairns 1988, Cury et al. 2011). Species with multiple clutches, such as the African Penguin, are likely to show stronger links between food supply and reproductive output at moderate to good levels of food availability (Cairns 1988).

Apart from years with below-median anchovy recruitment, such as 2011, there are years where the number of recruits calculated from the anchovy operating model behind the OMP for May differ markedly from the observations in the recruitment survey. For example, in 2006, the May survey produced an estimate that was only 17% of the model-prediction, in 2007, 49%. The effect of fishing on the birds will be underestimated in the current version of the river model. The consequences of such negative discrepancies between recruitments survey estimates and model outputs for breeding penguins need testing.

As one would expect, the effect of fishing on available food is particularly notable in years with low food biomass. The Robben Island Penguin Pressure Model (Weller et al. 2014) defines a feeding zone for breeding birds which is scaled to roughly correspond to the area experimentally closed to purse seine fishing during 2011-2013. Figure 2 illustrates the relatively large impact that fishing in the area can have on the biomass of food (anchovy and sardine combined) available to breeding penguins, e.g. during the years 1991-1992 and 2006-2007. In the absence of small scale surveys around the island to ascertain food availability, sensitivity testing for thresholds of minimum required food ("escapement") at each time step during the modelled breeding season needs to be carried out.

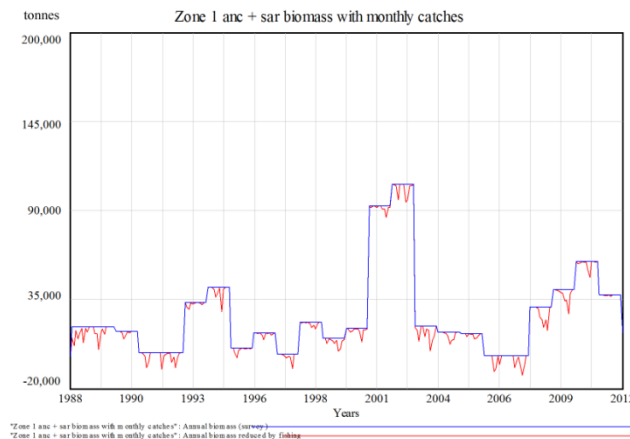


Figure 2. Small pelagic catches (anchovy and sardine combined) during the period April-October, 1988-2012, in the “inner food zone” off Robben Island (Weller et al., 2014), overlaid recruit biomass from the pelagic recruit survey in May of the corresponding year (DAFF, courtesy of Dr Carl van der Lingen). The latter were downscaled from estimates for survey stratum B (Cape Columbine to Cape Point) (Coetzee et al. 2008). The blue line indicates anchovy biomass as detected by the survey and the red line is the biomass reduced by fishing. Note potentially large impact of small pelagic catches in the foraging zone for breeding birds in years with low food biomass in this area, e.g., during 2006 and 2007.

5) What are the consequences of smoothing timing and speed of the “river of recruits”?

Anchovy aggregate into shoals, and fishing potentially changes the shoal characteristics and increases the patchiness of food available to breeding birds, including penguins. The travelling speed of the shoals will also depend on the distribution of zooplankton, which in itself shows high seasonal and interannual variability at the west coast (e.g., Huggett et al. 2009). At any spatial scale and time step of the model, the assumptions of the remaining smoothing need careful testing.

Conclusion - Bounding exploitation rate, estimating escapement for critically dependent predators, or understanding the interactions between for anchovy and penguin demographics: what was the question?

Acknowledging all models are wrong, and some models are useful, raises the question of the purpose of the “River model”. As for now, it is not used for management of the anchovy-directed fishery, and it does not need to be used in this way either: The generally low to moderate exploitation in recent years does not warrant more elaborate modelling for purposes of target-resource oriented management (TROM) than is currently carried out.

The “river model” approach is, however, potentially useful in modelling relationships between penguins, other seabirds, anchovy, and anchovy-directed fishing. In addition to closed areas (e.g., Frederiksen et al. 2008), the fishery for sandeel (*Ammodytes sp.*) in the North Sea, as well as for capelin (*Mallotus villosus*) in the Barents Sea are managed based on escapement strategies (e.g., ICES 2014). Models underlying the evaluation of such management strategies need to be designed with appropriate spatial and temporal resolution. It is with this possible purpose in mind that the above questions have been raised, and careful assumption analyses are requested.

In order to increase our understanding of the interaction of breeding penguins at the west coast and their feeding environment and the reduction in fishery, models and observations with even higher resolution are required. It is here that the continuation, and likely intensification, of small scale island surveys will be indispensable, in addition to GPS tracking and vessel monitoring.

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