**Aquatic
Living
Resources**

Cultivation, Allee effect and resilience of large demersal fish populations

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Abstract – In the marine environment, small forage species can predate on, or compete with, the pre-recruits of their larger predators. The "cultivation effect" hypothesis proposes that this mechanism can slow down the recovery of depleted populations of large demersal fishes by creating Allee effects that lower their recruitment success. Using an individual based fish community model applied to the southern Benguela ecosystem, we simulate situations of potential cultivation effect on a population of shallow water hake *Merluccius capensis*. We search for evidence of Allee effects due to cultivation and investigate how complex trophic interactions could influence their underlying mechanisms and impact. The resilience of the shallow water hake population was measured by following the variations of the ratio R/S (the number of recruits over the number of spawners) when population size decreases and the predators and competitors of shallow water hake pre-recruits were identified. Simulations suggest that cultivation effects are likely to emerge within the fish community of the southern Benguela ecosystem. Our twelve species model emphasizes that cultivation effects result from complex influences of predation and competition on the different pre-recruit stages, whose trophic role depends on both body size and geographical distribution. For realistic linkages between forage species and shallow water hake pre-recruits, cultivation effects occurring in the limits of the southern Benguela fish community are predicted to delay population recovery by several decades. These significant delays are not characterized by a decrease of R/S at low stock size, which is the sign usually tracked when looking for Allee effects. Our study suggests that cultivation effects could play a major role in the dynamics of overexploited large demersal fish populations and pleads for the development of improved detection techniques for these processes.

Key words: Marine ecosystem dynamics / Fishery exploitation / Recruitment / Spawning abundance / Fish competitors / Predators / Model / Benguela system

Résumé – « Cultivation », effet Allee et résilience des populations de grands poissons prédateurs démersaux. Dans l'environnement marin, les petites espèces-fourrages peuvent se nourrir des juvéniles (pré-recrues) de leurs prédateurs plus grands, ou entrer en compétition avec eux. L'hypothèse de l'effet de « cultivation » suppose que ce mécanisme peut ralentir le recouvrement de populations effondrées de grands poissons démersaux en créant des effets Allee qui diminuent le succès de leur recrutement. Grâce à un modèle individu-centré de communauté de poissons appliqué à l'écosystème du sud-Benguela, nous simulons des situations d'effet de « cultivation » potentiel au sein d'une population de merlu *Merluccius capensis*. Nous cherchons des preuves de la présence d'effets Allee et étudions comment des interactions trophiques complexes peuvent influencer leurs mécanismes sous-jacents et leur impact en terme de dynamique des populations. La résilience de la population de merlu est mesurée en suivant les variations du rapport R/S (le nombre de recrues sur le nombre de femelles prêtes à pondre) lorsque la taille de la population décroît et les prédateurs et compétiteurs des pré-recrues de merlu sont identifiés. Les simulations suggèrent que des effets Allee, tels que ceux décrits par l'hypothèse de l'effet de « cultivation », sont susceptibles d'émerger dans la communauté de poissons de l'écosystème du sud-Benguela. Notre modèle montre que ces effets résultent d'influences complexes de la prédation et de la compétition sur les différents stades de pré-recrues, dont le rôle trophique dépend à la fois de la taille corporelle et de la répartition géographique. Pour des intensités d'interaction trophique réalistes, les effets Allee apparaissant dans les limites de la communauté de poissons du sud-Benguela retardent le recouvrement de la population de merlu de plusieurs décennies. Ces délais significatifs ne sont pas caractérisés par une diminution du rapport R/S, ce qui est le signe habituellement considéré comme symptomatique d'un effet Allee. Notre étude suggère que les effets Allee peuvent jouer un rôle majeur dans la dynamique des populations surexploitées de grands poissons démersaux et plaide pour le développement de méthodes de détection améliorées de ce processus.

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1 Introduction

Large demersal predatory fish species have often been major targets for fisheries. During the second half of the 20th century, many of these fish populations presented strong decreasing trends of their biomass and several of them have collapsed (Casey and Myers 1998; Hutchings 2000; Christensen et al. 2003; Myers and Worm 2003). Large demersal predators exert top-down control on marine food webs (Cury et al. 2003) and trophic cascades have been observed as a consequence of their decline, leading to new regimes dominated by lower trophic level species (Fogarty and Murawski 1998; Carscadden et al. 2001; Frank et al. 2005). Years after these sudden changes in ecosystem structure, evidence for recovery are scarce, even when drastic reductions of fishing mortality were imposed (Hutchings 2000). These situations have given credit to the regime shift theory, which assumes that ecosystems can have multiple stable states, swapping from one to another depending on environmental conditions (Collie et al. 2004). The theory predicts that the responses of marine ecosystems to environmental changes are not always reversible (Scheffer et al. 2001) so that getting back to low fishing efforts would not necessarily result in retrieving high biomass of large demersal fish.

Understanding the mechanisms responsible for the non recovery of large demersal fish populations is crucial to preserve fish resources and restore depleted fish stocks, both tasks that Nations are required to fulfill by 2015 (World Summit on Sustainable Development, Johannesburg 2002). Several hypotheses have been evoked, including genetic responses to exploitation (Hutchings 2005; Walsh et al. 2006) environmental changes (Beaugrand et al. 2003) and changes in species interactions (Hutchings 2000; Bundy and Fanning 2005). Among the latter category, it has been suggested that the collapse of demersal fish populations caused the reorganization of the trophic webs in which they were embedded with major consequences for recruitment. Walters and Kitchell (2001) proposed that the ecological success of large demersal fish species in unexploited systems is partly due to "cultivation", i.e. a high predation pressure exerted by adult stages on their pre-recruits' competitors and predators, often called "forage species". According to this trophic triangle conceptual model (Fig. 1A), when the abundance of large demersal species' adults decreases under high fishing effort, the abundance of the smaller forage species increases, leading to enhanced competition and/or predation mortality of large demersal species' pre-recruits. This "cultivation/depensation effect" (hereafter referred to as "cultivation effects" only) may induce long term recruitment failures, thereby considerably reducing the ability of the demersal population to recover from depletion. As all Allee effects (Liermann and Hilborn 2001), cultivation effects manifest themselves through the decline of at least one component of individual fitness as population size decreases toward zero (Gascoigne and Lipcius 2004).

The hypothesis of detrimental trophic relationships affecting the recruitment of large demersal fish species is supported by a strong theoretical background. Indeed, both competition (Cushing 1990) and predation (Bax 1998) are important sources of mortality for fish pre-recruits. Yet, little is actually known about the functioning of cultivation effects and their impact on the recovery of depleted fish populations.
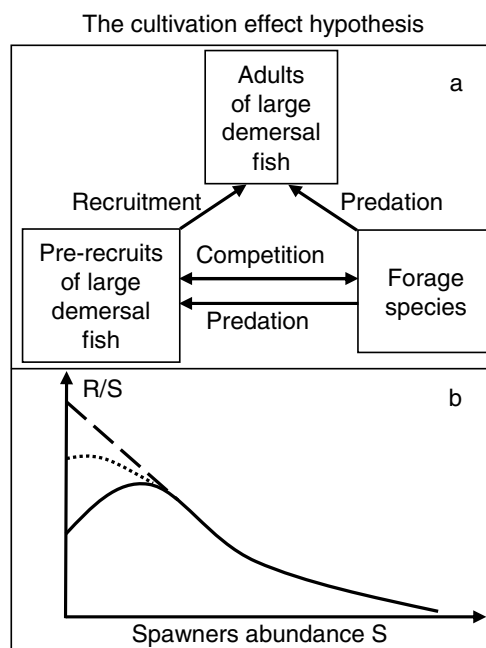
The cultivation effect hypothesis

Fig. 1. (A) "Trophic triangle" involved in cultivation (modified from Walters and Kitchell 2001). (B) Number of recruits R per spawner (R/S) against spawners abundance S. R/S is related to the resilience of a population. Three types of responses to low abundance levels are represented: demographic Allee effects (solid line), component Allee effects (dotted line) and classic compensation (broken line).

Walters and Kitchell (2001) described the cultivation effect in a simplified context where both adults and pre-recruits of large demersal fish species are strongly connected to forage species. However, natural marine ecosystems are complex trophic webs in which multiple interactions with other organisms are likely to interfere with the trophic triangle involving demersal and forage species, and could therefore dampen the role of cultivation effects. In this paper, we propose to explore cultivation effects within a complex structure of trophic interactions. Using the individual-based model OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) (Shin and Cury 2001) applied to the southern Benguela ecosystem, an increasing fishing mortality of a large demersal species, the shallow-water hake *Merluccius capensis*, is simulated under different trophic conditions. We search for evidence of cultivation effects within the modeled fish community and identify their underlying mechanisms.

2 Material and methods

2.1 Allee effects

Allee effects affect average individual fitness at low population size. Assuming a constant survival from recruit to spawner, fitness can be expressed as the ratio R/S, the number of recruits produced by each spawner in one generation, with R the number of juveniles entering the exploited stock at one given year and S the number of spawners (Myers et al. 1995).

In that context, individual fitness comprises only two components: pre-recruits' survival relative to predation and pre-recruits' survival relative to starvation (competition for food). If pre-recruits suffer high predation and/or competition mortalities, then R will be low compared to S and consequently fitness will be low. The size of exploited populations is usually approximated by S (Shelton and Healey 1999). At very low population size, R/S measures the ability of depleted populations to recover.

The nitty-gritty of Allee effects is explained through Figure 1B. We apply to the specific case of cultivation the Allee effect terminology defined by Stephens and collaborators (1999) and Liermann and Hilborn (2001). The assumption of compensatory dynamics, that is, better reproductive success at low population size, underlies fisheries management (Rose et al. 2001). Cultivation effects are "demographic" (solid line) if the negative influence of forage species on pre-recruits' survival offsets compensation and leads to depensatory dynamics i.e. fitness R/S decreases at low population size. In the case of a "component" Cultivation effect (dotted line), compensation occurs but increasing forage species biomass alters some of the fitness components and results in overall fitness values lower than in the purely compensatory situation (dashed line).

2.2 Model description

The southern Benguela upwelling ecosystem is located off the western south-African coast (26–38°S, 16–28°E). It is exploited by both pelagic and demersal (mostly hake) South-African fisheries. To explore the potential impacts of cultivation effects in this ecosystem, we use OSMOSE, an individual-based model dedicated to the study of the dynamics of exploited fish communities, in its first version described by (Shin and Cury 2001; Shin and Cury 2004). OSMOSE relies on the hypothesis that predation is an opportunistic process based on body size, i.e. any fish is potentially a predator or a prey of any other one depending on their relative sizes. The main processes that rule the fish life cycle are taken into account: predation, growth, reproduction and mortality due to predation, starvation and fishing. The interaction unit is the school, i.e. a group of fish belonging to the same species, moving together and having the same size so that they share the same potential prey and predators. OSMOSE is structured into a hierarchy of interacting classes. Each class is a template characterized by a list of attributes (biological parameters) and functions (e.g. growth, mortality) from which objects that are part of the simulated system are built. Hence, each species is an object created from the class "species". A species is characterized by a number of cohorts created from the class "cohort". Similarly, a cohort is represented by schools which are objects of the class school.

In marine ecosystems, larger organisms feed at higher trophic levels (Jennings et al. 2002) so that adults of the largest fish species are mainly piscivorous. On the contrary, adults of small fish species are likely to feed on both fishes, including fish eggs and larvae, and plankton, which is represented implicitly in the model by the carrying capacity. These "mixed diet" species are determined from the literature. The proportion of fish in the diet of each cohort is approximated

from previous studies. For each of these age classes, we create strictly piscivorous and strictly planktivorous schools, their relative number reflecting the average diet we defined previously.

At each iteration, fish schools sequentially experience the processes of foraging, predation, starvation mortality, growth, fishing mortality and finally reproduction, which is simulated by adding fish eggs into the system. Schools interact in a two-dimensional grid of square cells, within the limits of their distribution areas which are given in input of the model at each time step for each life stage of each species.

In the model, the carrying capacity represents the maximum biomass of non-piscivorous fish that the system can sustain. At each time step (semester or six-months period), and in each cell, if the biomass of non-piscivorous fish is higher than the carrying capacity, non-piscivorous fish suffer starvation until their biomass reaches the carrying capacity level. In a given cell, the loss of biomass due to starvation is distributed uniformly between non-piscivorous schools.

At each semester, piscivorous fish schools move to feed in the adjacent cell where the amount of potential prey is the highest. When the predation process is completed, a coefficient of predation efficiency ξ is calculated for each school as the ratio between the food biomass it consumed and the maximum food biomass it can ingest during one time step.

The Von Bertalanffy (1938) model is used to calculate mean annual growth rates in length. At each time step, these rates are re-adjusted such that schools that have consumed more food than others can allocate more energy to growth. A critical coefficient of predation efficiency ξ_{crit} is defined as the maintenance level beyond which the energy provided by food intake is allocated to growth. For a school i, if $\xi_i \geqslant \xi_{crit}$, the growth rate in length varies linearly with ξ_i such that: (i) for $\xi_I = \xi_{crit}$, the rate is null, (ii) for $\xi_I = (\xi_{max} + \xi_{crit})/2$, with $\xi_{max} = 1$, the rate equals the mean rate $\Delta L_{s,a}$ calculated from the von Bertalanffy model. Thus, the growth rate in length $\Delta L_{s,a,i,t}$ of a school i, of age a, of species s, and at time t, follows the expression:

$$\begin{cases} \Delta L_{s,a,i,t} = 0 & \text{if} \quad \xi_{i,t} < \xi_{crit} \\ \Delta L_{s,a,i,t} = \frac{2\Delta L_{s,a}}{1-\xi_{crit}}(\xi_{i,t} - \xi_{crit}) & \text{if} \, \xi_{i,t} \geqslant \xi_{crit}. \end{cases}$$

When $\xi_i \leqslant \xi_{crit}$, the school i experiences starvation mortality expressed as a negative linear function of predation efficiency. The following equation is applied, with $M_{\xi\,max}$ the maximal starvation mortality rate:

$$M_{\xi_i} = -\frac{M_{\xi_{max}}}{\xi_{crit}}\xi_i + M_{\xi_{max}}$$

Fishing mortality is applied as a species and age specific annual rate.

Reproduction in OSMOSE occurs through a single annual spawning event for each species. The number of eggs produced is proportional to the spawning biomass and the relative fecundity of a given species. The recruitment level emerges from the diverse sources of pre-recruits mortality represented in the model.

2.3 Parametrization of the model

The 1990s is the period chosen for the state of reference of the system (Travers et al. 2006). The twelve fish species that dominated at the time the Southern Benguela system (Shannon et al. 2003) are explicitly modeled. Anchovy *Engraulis capensis*, sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi*, horse mackerel *Scomber japonicus*, chub mackerel *Trachurus trachurus capensis*, shallow-water hake *Merluccius capensis*, deep-water hake *Merluccius paradoxus*, kingklip *Genypterus capensis*, snoek *Thyrsites atun*, silver kob *Argyrosomus inodorus*, and two mesopelagic species, lanternfish *Lampanyctodes hectoris* and lightfish *Maurolicus muelleri* represented in the 1990s at least 76.2% of the fish biomass and 93.8% of all fish catches; they were also responsible for 84% of the total food consumption by fish species and top predators and 72% of the small pelagic fish production (Travers et al. 2006).

For each species, growth, reproduction and survival parameters are defined at model initialization (Travers et al. 2004). The minimal predator/prey size ratio (in length) is taken as 3.5 for all species (Froese and Pauly 1998). It is estimated that a fish should annually consume at maximum 3.5 g of food per body gram (Shin et al. 2004).

The southern Benguela ecosystem is modeled as a square grid of 40×40 cells. The twelve populations differ in their age specific distribution areas (Travers et al. 2004) and interact where these distributions overlap. As 1+ age classes of chub mackerel and snoek migrate out of the southern Benguela ecosystem during the first semester (Crawford 1989), they interact with other species in the model during the second semester only.

Adults of anchovy, sardine, round herring, horse mackerel, lanternfish and lightfish can feed on both the explicitly modeled early fish stages and the planktonic organisms represented by the carrying capacity (Shannon et al. 2003). These small pelagic species have spatial distributions that overlap to some extent with the distribution of adult shallow water hakes and are then potential prey (Travers et al. 2004). They are also potential predators and competitors of shallow water hake pre-recruits regarding the partial overlap of their respective spatial distributions and the ratio of their sizes. Therefore, they are liable to undergo an increase of their biomass in reaction to hake depletion and may then induce a high mortality of shallow water hake pre-recruits. They will be referred to as forage species hereafter.

Levels of piscivory in the diet of forage species were set to represent the great variability of situations observed in the field. Indeed, individual fish diets strongly fluctuate due to the spatiotemporal variations of local food availability. For instance, during the 1990s, Armstrong et al. (1991) reported that the diet of anchovy was mainly composed of zooplankton among which fish eggs represented a small contribution at the scale of the southern Benguela ecosystem (Verheye et al. 1998). However, Valdés et al. (1987) observed that within an area of intensive spawning, cannibalism could be responsible for 70% of the egg mortality of the South African anchovy, which implies locally very high levels of piscivory. To cover the wide range of piscivory levels observed in the diet of forage species, three increasing piscivory levels were determined.

Estimating levels of piscivory among fish is practically impossible from current data because stomach content analyses usually do not discriminate ichtyoplankton from mesozooplankton and macrozooplankton categories. Verheye et al. (1998) reported that crustaceans represented on average more than 97% of zooplankton in the southern Benguela system so we roughly approximated the average contribution of fish eggs and larvae to be 3% of the meso and macrozooplankton categories of fish diets. As mean meso and macrozooplankton contributions to fish diets are well documented for the Benguela ecosystem, we were able to calculate a minimum piscivory level of 2% for anchovy (Armstrong et al. 1991), 6% for horse mackerel (Jarre-Teichmann et al. 1998; Pillar and Barange 1998), 3% for the two mesopelagics (lanternfish and lightfish) and for round herring (Shannon et al. 2003) and 1% for sardine (Armstrong et al. 1991; Van Der Lingen 2002). A medium and a maximum piscivory levels were obtained respectively by multiplying 10-fold and 30-fold the minimum values.

For each set of piscivory percentages, the model was tuned by allowing an additional larval and juvenile (classes of age 0) mortality term to vary, reflecting the highly fluctuating mortality experienced by these stages in real ecosystems (Shin et al. 2004).

2.4 Simulations

To test the presence of cultivation effects, we consider a scenario where shallow-water hake *Merluccius capensis* is submitted to an increasing fishing mortality F until the population reaches a depleted state, arbitrarily defined as 1% of its reference size. The piscivory levels in the diet of forage species determine the proportion of early fish stages (eggs, larvae) in the diet of age 1+ fish and therefore measure the intensity of potential cultivation effects. Indeed, increasing piscivory of forage species may enhance predation on early hake stages. The largest (2 and 3 year old) hake pre-recruits are exclusive piscivorous and may also suffer from an enhanced competition on ichtyoplankton. The overexploitation of the shallow water hake population is simulated for each piscivory level. Each simulation describes the ecosystem dynamics through a two hundred year period for a given fishing mortality. For each run, the system is left to stabilize for the first hundred years. Final results are means calculated over the last 100 years for sets of 30 simulations.

Our simulation plan is designed as a two-stage process. We first merely search for evidence of cultivation effects. In our model, three conditions must be met for such an effect to occur. i) The simulated collapse of the shallow water hake population triggers a strong increase in the forage species biomass. ii) Increasing piscivory in forage species diet is accompanied by an increasingly negative effect on shallow-water hake's recovery. Effects on recovery are illustrated for each piscivory level by simulating a moratorium situation ($F = 0$) following a period of strong overexploitation. Complete recovery is achieved when the population reaches its reference level for the 90's in the southern Benguela ecosystem (around one million tons). iii) Fitness patterns show evidence of Allee effects. Demographic Allee effects are detected by tracking declining R/S

values when S decreases (Myers et al. 1995). We seek component Allee effects by comparing systematically R/S curves for the three piscivory levels: if compensation occurs in two different scenarios but R/S values are lower in one case, one can conclude this is the consequence of the negative influence of one or several component cultivation effects.

The second step of our simulation plan aims at understanding how a complex trophic structure can influence the mechanisms underlying the cultivation effects that could exist in the southern Benguela ecosystem. In order to do so, patterns of R/S curves are explained further by disentangling the processes affecting the two components of fitness we evoked in Sect. 2.1: pre-recruitment survival regarding predation and pre-recruitment survival regarding starvation. Shallow water hake pre-recruits grow immensely in size from the larval stage to the moment they enter the exploitable stock aged 3 and consequently assume a vast range of different trophic roles. To reflect this variety, we focus on the predation and starvation mortality patterns of the two potentially most different pre-recruit stages modeled in OSMOSE: the small, strictly planktivorous zero-to-six-month old pre-recruits and the large, strictly piscivorous three-year old individuals that enter the spawning stock. The main sources of predation mortality for these pre-recruit stages, hereafter called respectively early pre-recruit stages and late pre-recruit stages, are identified using the average virtual diets produced by the model for each age class of each simulated species.

3 Results

3.1 Cultivation effect and impact on shallow water hake resilience

Responses of forage species to increasing exploitation of the shallow water hake population are presented in Figure 2. Variations in the diet of forage species influence both the way shallow water hake reacts to increasing fishing effort and the biomasses reached by forage species at low shallow water hake abundance. However, an overall increase of the forage species biomass is always observed with decreasing biomass of shallow water hake. Consequences for the R/S patterns of the shallow water hake population are shown in Figure 3. No depensatory dynamics are observed, therefore demographic cultivation effects can be ruled out. At small shallow water hake population size, increasing piscivory levels in the diet of forage species results in lower R/S values. This shows that the dynamics of shallow water hake is affected by one or more component Allee effects that strengthen with increasing forage species piscivory. After a prolonged period of overexploitation, the shallow water hake population recovers its reference biomass under moratorium regime in all three simulated trophic situations, but this is a much faster process when the piscivory level in the diet of forage species is the lowest (Fig. 4). In that latter case, biomass steeply increases almost immediately after the beginning of the fishing ban, whereas the first signs of a slower recovery are delayed by approximately thirty years for medium and maximum piscivory levels.
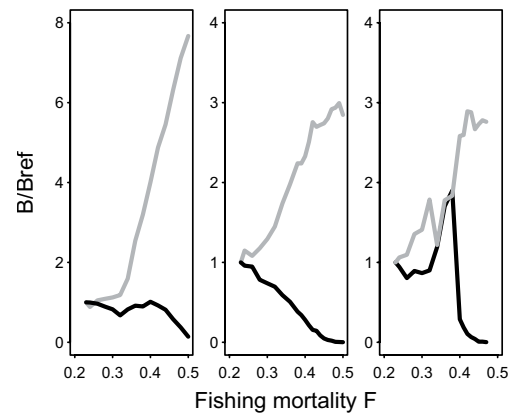

Fig. 2. OSMOSE simulation of the effect of increasing fishing mortality of shallow water hake on the biomass of hake (black line) and on the biomass of forage species (grey line) from left to right the minimum level of piscivory, the medium level and the maximum level. Results are expressed in relative biomass (Biomass B/reference biomass B_{ref} during the 1990s).
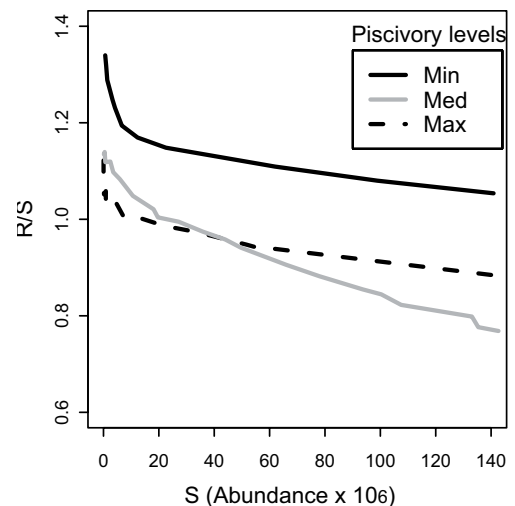

Fig. 3. Shallow-water hake R/S curves for the three piscivory levels in the diet of small pelagic fish. R and S are the numbers of recruits and spawners respectively

3.2 Predation and starvation mortality patterns

The effect of a decrease of shallow water hake population size on pre-recruits' predation and starvation mortality rates are presented for each of the three piscivory levels we simulated (Fig. 5). The observed variations can be explained through the shifts in the main sources of predation experienced by pre-recruits when population size plummets (Fig. 6). The latter are shown for the minimum piscivory level only because results were qualitatively equivalent for all piscivory levels.

Early pre-recruit stages

Early pre-recruit stages experience simultaneously decreasing predation and increasing starvation when the size of the shallow water hake population declines from its reference state to low levels. The simulations suggest that more
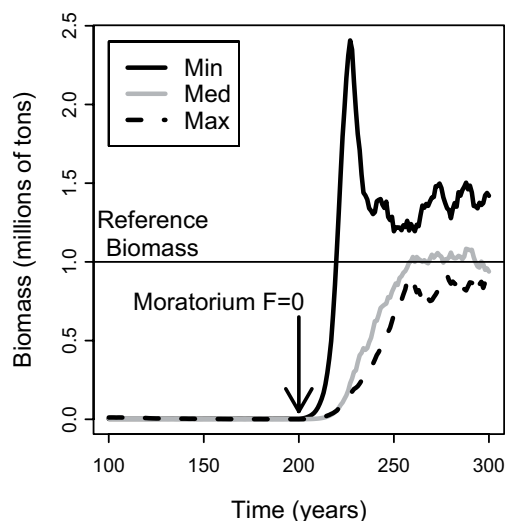
Fig. 4. Shallow-water hake recovery times for the three piscivory levels. A situation of moratorium (fishing mortality rate $F = 0$) is simulated after a prolonged period of overexploitation. Resilience is defined as the speed at which the hake population returns to 1 million t, its reference biomass in the 1990s.
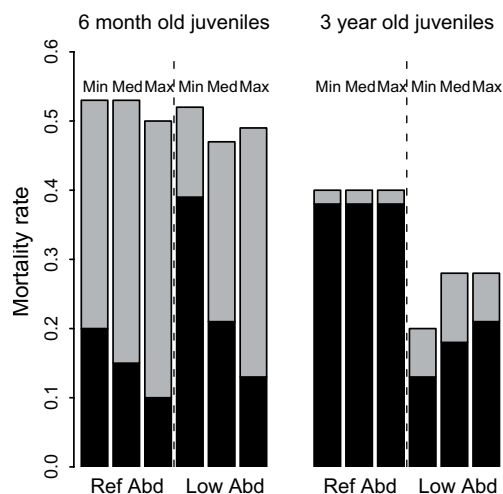

Fig. 5. Effect of a decrease of the abundance (Abd) of hake on the predation (dark grey) and starvation (black) mortality rates experienced by 6 month old juveniles of hake and 3 year old juveniles of hake, for three piscivory levels in the diet of small pelagic fish (minimum, medium, maximum). Low abundances represent 1% of the reference abundance of hake

Fig. 6. Main contributors to predation mortality of 6 month old juveniles and 3 year old juveniles of hake at reference state and under strong overexploitation for the lowest level of piscivory: Shallow water hake (black), Forage species (light grey), Kingklip (white) and Others (dark grey).

because increasingly more piscivorous species do not compete as strongly with the planktivorous early pre-recruits whose survival regarding starvation improves. This lower competition for food compensates for the higher predation mortality predicted by the model and the overall mortality of early pre-recruits remains nearly unaffected by increasing forage species piscivory. This result suggests that the negative effect of increasing forage species piscivory on shallow water hake recovery is not due to processes affecting the earliest pre-recruit stages.

Late pre-recruit stages

A first component Allee effect appears as predation mortality increases when shallow water hake population size declines toward low levels. Late shallow water hake pre-recruits are large organisms and the virtual diet we obtained in output show that the small forage species do not feed on them. At the reference state, adult shallow water hakes are the main predators of their late pre-recruit stages and contribute to 35% of the predation mortality. When the abundance of adult shallow water hakes declines under high fishing effort, predation mortality due to kingklip gradually increases. The contribution of this large demersal species to the predation mortality of late pre-recruits reaches 90% at low shallow water hake population size.

Increased piscivory levels have a global negative effect on the survival of late pre-recruit stages at low population size, the overall mortality rate varying from 0.21 for the minimum piscivory level to 0.28 for the maximum level. This negative effect is due to another component cultivation effect whose intensity at low population size strengthens when the proportion of fish eggs and larvae in the diet of forage species increases. In the model, late shallow water hake pre-recruits are represented as strictly piscivorous and higher piscivory levels in the diet of forage species means they experience stronger competition

than 50% of the predation mortality suffered by early shallow water hake pre-recruits at the reference state is due to older conspecifics. The prevalence of cannibalism explains why predation on early pre-recruits becomes less intense when the size of the exploited shallow water hake population declines. The enhanced starvation of early pre-recruits at low stock size corresponds to a component cultivation effect due to the higher competition for planktonic food exerted by the increasing forage species biomass. This particular cultivation effect weakens when the piscivory level in the diet of forage species increases and therefore cannot explain the associated slower recovery of the shallow water hake population. This is
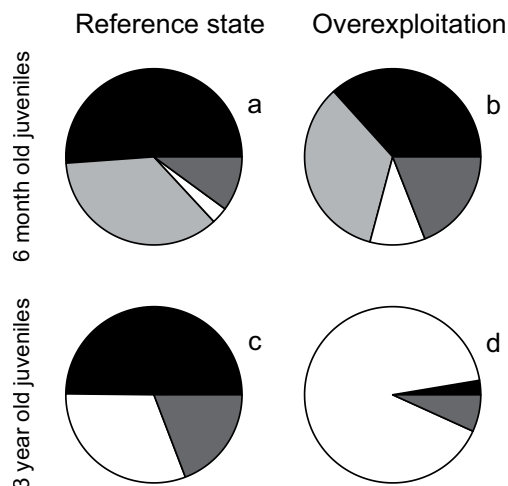
for fish food and higher starvation mortality. This component cultivation effect is then at least partly responsible for the predicted erosion of the shallow water hake resilience for increasing levels of piscivory in the diet of forage species.

4 Discussion

As assumed by the cultivation effect hypothesis, the simulated depletion of the shallow water hake population triggers a major increase of the biomass of forage species. Our simulations also show that the shallow water hake population recovers later and slower when the level of piscivory in the diet of forage species increases.

Cultivation effects rely on strong negative correlations between the abundances of large demersal species adult stages and their prey. These are well reproduced by our model but one could question their realism and generality in Nature. Indeed, marine trophic webs have been shown to display considerably higher connectance than their freshwater and terrestrial counterparts (Link 2002), suggesting that the decline of major predatory species could be compensated by favoring the rise of functionally redundant organisms. Empirical observations show that this is often not so. Evidence for strong top down controls are numerous (Pace et al. 1999; Reid et al. 2000; Worm and Myers 2003) and the extreme case of trophic cascades (Choi et al. 2004; Frank et al. 2005; Daskalov et al. 2007) has been increasingly documented. Mirroring natural marine ecosystems, OSMOSE is itself a trophically permissive system. In the model, trophic interactions are strengthened by specific geographic distributions defined from observations (Travers et al. 2004). Through the interplay between trophic looseness and species niche overlap, our results suggest that no fish species could compensate for the local extinction of shallow water hake in the southern Benguela. Strong negative correlations between predators and prey in natural trophic webs are also made more likely by the use of non-selective fishing gears that affect both large demersal and alternative predators of similar size (Kennelly 1995).

The second trophic condition that has to be met to create a cultivation effect is predation or competition of forage species on the pre-recruits of large demersal species. OSMOSE predicts an increasingly negative effect of small pelagics on the recovery of shallow water hake when the piscivory percentages in their diet increases.

The seemingly very high piscivory levels we used in the model are not unusual in the diet of forage species in areas where they overlap with pre-recruit stages. As an example, Ellis and Nash (1997) measured a 36 to 97% portion of planktonic fish eggs in stomach contents of sprat and herring in a spawning area east off the Isle of Man. Bax (1998) also provided several examples of fish massively feeding on fish eggs and larvae. In natural systems, these periods of overlapping are limited in time however, giving piscivory percentages in the diet of forage species a highly variable character that is not represented in the model. The quantitative impact of forage species on the shallow water hake recruitment would therefore depend on how frequent and long are these encountering periods as well as on the period of the year during which they occur. Drapeau et al. (2004) measured averaged (from 1988 and

2001) annual spatial overlaps between the distributions of thirteen key species in the southern Benguela. The distribution of sardine, anchovy and round herring appeared to strongly overlap the distribution of shallow water hake, with an 80% overlap in the case of sardine. A strong decrease of the biomass of shallow water hake in that system could then trigger a significant cultivation effect. In another highly productive system, the Georges Bank, Garrison et al. (2000) assessed qualitatively the overlap of the spatial distributions of small pelagic fishes and larvae of haddock, a population that collapsed in the early 1990s. They found an excellent match in both time and space between the distribution of herring and the distribution of haddock larvae in the Bank and proposed that the predation of forage species on haddock larval stages could be responsible for the observed low recovery of the population.

OSMOSE allows taking a first step in estimating the impact of the coexistence of forage species with shallow water hake pre-recruits in the southern Benguela. However, models of fish community ignore some potentially important ecosystem compartments and their quantitative predictions in terms of resilience can only be considered where their simplified structure reflects accurately the main trophic relationships at stake. For example, age two and three shallow water hake pre-recruits are not entirely piscivorous and also feed on euphausiids in the southern Benguela system (Payne et al. 1987; Ware 1992). From a purely quantitative point of view, OSMOSE merely suggests that in the absence of major trophic relationships linking shallow water hake with organisms outside the fish community, cultivation effects due to small pelagic fish species would delay strongly its recovery in the southern Benguela ecosystem. Regardless of the number of compartments in the model, it remains true that forage species coexisting with pre-recruit shallow water hake stages can compete with them for similar resources or feed on them depending on their relative size. This is at the heart of OSMOSE, and does not modify the nature of the mechanisms underlying cultivation effects.

Literature and results from OSMOSE suggest that both top down control of large demersal species on small pelagics and interactions between small pelagics and pre-recruits of shallow water hake are potentially significant in the southern Benguela ecosystem. A finer analysis of the trophic relationships at stake in the model shows how multiple trophic interactions can influence the simple triangle scheme described in the cultivation effect hypothesis.

Our simulations show that what seemed to be at first a straightforward output – increased piscivory in the diet of forage species leading to lower shallow water hake pre-recruitment survival – actually results from various cross effects of both predation and starvation on the different shallow water hake pre-recruit stages. In accordance with other studies (Valdés et al. 1987; Bax 1998), cannibalism is predicted to be positive density dependent in OSMOSE and as a consequence compensates to some extent cultivation effects. This prediction is likely to be often verified in Nature as numerous empirical studies have underlined the importance of predation by older conspecifics in hake (Pitcher and Alheit 1995) and in many other demersal species (Juanes 2003). Counter intuitively higher levels of predation on early pre-recruit stages

have negligible effects on their overall survival because of simultaneous competition release. No field method is currently available to measure such complex processes but their potential importance would require further investigation.

Increased starvation mortality of late pre-recruit stages appears to be the main cultivation effect responsible for the erosion of shallow water hake resilience with increasing piscivory levels. For each of the three piscivory levels, R/S values are higher at low stock size, but the combination of component Allee effects we identified dampens the prevalent compensation effect, therefore leading to lower resilience of the hake population when piscivory of forage species increases.

Until now, most empirical studies conducted to explain the absence of recovery of demersal fish populations have focused on the search for demographic Allee effects in R/S data sets, with few concluding results. Demographic Allee effects first appeared to be scarce (Myers et al. 1995), but the controversy in their occurrence in small size populations has recently been revived as new pieces of work stressed out the low quality of the analyzed data (Shelton and Healey 1999) and the existence of underestimated bias (Frank and Brickman 2000). Our results show that component cultivation effects could also significantly affect the recovery of large demersal fish species, suggesting one cannot rule out the significance of cultivation even in the absence of obvious demographic Allee effects. In theory, component cultivation effects cause smooth regime shifts (Collie et al. 2004), where the return to high large demersal fish biomasses is slowed down but not prevented. However, OSMOSE shows that component effects can also delay recovery, thereby mimicking discontinuous shifts to alternative stable states.

5 Conclusion

Although the potential role of cultivation effects in lowering the resilience of depleted large demersal fish populations has been underlined by several studies (Swain and Sinclair 2000; Garrison et al. 2002; Bundy and Fanning 2005), their actual impact has not been proven empirically. Our simulations show that significant cultivation effects could be easily "missed" by current methods, which focus on detecting demographic Allee effects only and leave aside their component counterparts. The complexity of real ecosystems makes it difficult to understand the role of cultivation effects in the slow recovery of demersal fish stocks. It is then essential to better quantify the trophic role played by fish pre-recruits (eggs, larvae, juveniles) and consequently, to promote means and techniques for refining stomach content analyses. This should served as a base to fisheries managers to develop an improved policy of stock rebuilding that takes heed of the major role of trophic interactions in the dynamics of exploited populations.

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