Spatial dynamics of the bearded goby and its key fish predators off Namibia vary with climate and oxygen availability

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ABSTRACT

Hypoxia [$O_2 < 2.0$ mL L^{-1} (87 μmol kg^{-1})] and severely hypoxic water masses [$O_2 < 0.5$ mL L^{-1} (21.8 μmol kg^{-1})] are increasing in coastal marine ecosystems due to eutrophication and warming. Here, we investigate the response of the suboxic-tolerant endemic fish, *Sufflogobius bibarbatus*, to variations in the thermal and oxygen environment, as well as to predation pressure, using 22 yr worth of satellite and *in situ* data. We show that environmental variation and predation pressure affect the goby population, which has expanded over the last decade while that of horse mackerel has contracted. These changes co-occurred with a general warming in the north and central shelf areas (north of 24.5°S). Spring warming positively affected both goby and hake abundances, but not the horse mackerel, suggesting different responses to surface temperature. The goby habitat contracted when predators were abundant, particularly in the north, which is the fringe of its distributional area. The implications of the differential tolerance of gobies and their predators for climate variations are discussed.

INTRODUCTION

Oxygen is a major limiting environmental factor in aquatic systems (Wu, 2002) and the expansion of severely hypoxic water masses [<0.5 mL L^{-1} O_2 [87 μmol kg^{-1}]] has become a major cause of concern (Diaz and Rosenberg, 2008), not least because it compresses the habitable area for many marine organisms. A reduction in dissolved oxygen concentration leads to a decrease in the growth rate and feeding activity of fishes (Chabot and Claireaux, 2008), and may alter behaviour and trophic relations, as well as generating shifts in the abundance and accessibility of commercially exploited species (Stramma *et al.*, 2012; Gilly *et al.*, 2013).

Off Namibia, 9000 km^2 of the shelf is hypoxic and in January 2004, 7000 km^2 were suboxic (<5 μmol kg^{-1} O_2) and sulphidic (Lavik *et al.*, 2009). The sea bed under these conditions is typically covered by giant sulphur-oxidizing bacteria (Schulz *et al.*, 1999). Most of the latter areas are situated over the central part of the Namibian shelf (between 20.5° and 24.5°S), where the shelf is broadest and because the slope is less steep than areas further north or south, sedimentation of surface production is higher (Rogers and Bremner, 1991; Emeis *et al.*, 2009). Further north (20.5–17°S) the shelf becomes narrower and steeper and the oxygen concentrations somewhat higher, but still hypoxic [0.5–2.0 mL O_2 L^{-1} (21.8–87.0 μmol kg^{-1})] in the deep waters (Gammelsrød *et al.*, 1998). The southern part of the Namibian shelf (24.5–29°S) is characterized by strong winds, high offshore advection and strong turbulent mixing, and a continuous strong upwelling that circulates nutrients to the surface and well ventilates the deep water masses (Boyer *et al.*, 2000).

The extensive suboxic environment off central Namibia is shaped by a combination of locally produced oxygen-poor water, resulting from the decomposition of the surface production precipitated to the sea

bed, and by the superimposed effect of the seasonal (austral summer) advection of hypoxic tropical surface- and mid-water from across the Angola Benguela Front (ABF; Rouault *et al.*, 2007; Rouault, 2012). This influx of oxygen-poor water (Monteiro *et al.*, 2008) is triggered by a relaxation of the trade winds in the tropical Atlantic (Rouault, 2012) and is accompanied by an increase in sea surface temperature (SST). The warming has two effects on the environment: (i) it reduces the solubility of oxygen; and (ii) it reduces the ventilation of deep water masses (Gammelsrød *et al.*, 1998; Boyd *et al.*, 1987). Indeed, temperature variation has been used as a proxy for variation in the influx of hypoxic waters over the shelf in the northern Benguela (Monteiro *et al.*, 2008; Rouault, 2012). In 1994/1995, a strong Benguela Niño year, positive temperature anomalies were measured at 30 m depth along the entire Namibian coast (Gammelsrød *et al.*, 1998), but were detectable at a depth of 80 m over the northern shelf (a maximum of 8°C at 30–50 m depth), where suboxic and hypoxic waters extended to shallower depths than in normal years (Gammelsrød *et al.*, 1998).

Advection across the ABF is highly variable both on bi-annual (Rouault, 2012) and geological (Meisel *et al.*, 2011) time scales. Paleo-ecological studies of fish scales and proxies for environmental factors in sediment cores suggest that the presence of advected waters has been associated with large fluctuations in fish abundance and changes in community structure over the last 3200 yr (Struck *et al.*, 2002), which probably reflects differences in species-specific responses to hypoxia.

One of the endemic fish species off Namibia is the numerous bearded goby, *Sufflogobius bibarbatus*. This fish species can cope better with low oxygen than other species such as horse mackerel (*Trachurus trachurus capensis*) and Cape hake (*Merluccius capensis*; e.g., Ekau *et al.*, 2010; Utne-Palm *et al.*, 2010). Its main distributional area coincides with that area of the Namibian shelf where sea-bed oxygen levels are <1 mL O$_2$ L^{-1} (43.5 μmol kg^{-1}). It is adapted to diurnal changes in oxygen concentrations and adult fish appear to shuttle between the suboxic sea bed, where they remain during the day, and the more oxygen-rich pelagic layers at night (Utne-Palm *et al.*, 2010). Unlike their predators, these fish can remain alert even after 7–9 h in complete suboxia (<0.007 mL O$_2$ L^{-1} (0.3 μmol kg^{-1}); Salvanes *et al.*, 2011) and can cope with gradual changes in oxygen concentrations as well as with sulphide shocks (Salvanes *et al.*, 2011). Following the decline of clupeid populations in the late 1960s, and their subsequent collapse in the 1980s, higher predators off

Namibia have been increasingly supported by the bearded goby prey (Crawford *et al.*, 1987). For example, on the mid-shelf, which is main distributional area of juveniles (Burmeister, 2001; Gordoa and Duarte, 1991), over 90% of juvenile hake fed on gobies in April 2008; further offshore, alternative prey were more important (A.G.V. Salvanes & P.E. Grung-Berle, unpublished). This little fish is thus contributing indirectly to the economy through predator–prey relationships (Utne-Palm *et al.*, 2010).

In this paper we use 22 yr worth of satellite and *in-situ* data from the northern Benguela upwelling ecosystem to explore the impacts of environmental variation and predation pressure on the abundance and distribution of gobies and their predators. First, we analyse data from the entire ecosystem (17–29°S) to identify the main distributional area of the bearded goby and to determine how goby abundance varies along the Namibian shelf with respect to depth and bottom oxygen concentrations. Next, we divide the data set into three main sub-areas, which in differ the concentration of dissolved oxygen (Fig. 2): north (17–20.5°S), central (20.51–24.5°S) and south (24.51–29°S). We analyse detailed survey and satellite data of SST, focusing specifically on (i) spatial and temporal variation, and the effect of spring warming events on the distribution and abundance of gobies and their predators (horse-mackerel, and Cape hake) and (ii) the predator–prey dynamics. We expect to find the largest effects of environmental variations on the distribution and abundance of the populations in the fringe/margin of their main distributional areas (Rijnsdorp *et al.*, 2009). We show that the three fish species respond to the intrusion of warm water from the north differently: the Cape hake and bearded goby appear to respond to dissolved oxygen in a way that likely reflects their different tolerances, whereas the horse mackerel tends to follow the warm waters as they intrude and retract southwards.

MATERIAL AND METHODS

Fish sampling

Demersal fish samples have been collected in the northern Benguela off Namibia using a standardized survey design on-board the *RV Dr. Fridtjof Nansen* (1990–99) and the commercial vessel *Blue Sea* (2000–2011). Fuller details of the gear and survey designs can be found in Johnsen and Axelsen (this volume). Only day-time hauls (between 06:00–17:00 h local time), and only hauls shallower than 325 m depth are included. Data are stored in the Nansis Database at the National Marine Information and Research

Centre (NatMIRC) of the Ministry of Fisheries and Marine Resources, Namibia.

Environmental data

We have used Reynolds SST data (1° × 1° resolution) derived from daily merged *in situ* and high-resolution (9 km) infrared satellite observations from the AVHRR (advanced very high resolution radiometer) instrument on board NOAA satellites (Reynolds *et al.*, 2002). Information on *in situ* oxygen, and temperature by depth and latitude were collected on all surveys and has also been included. These data were collected using regularly calibrated Seabird 911plus or Seabird 19plus CTD-O instruments. The instruments were lowered to 5 m above the sea bed.

Spring warming index

Indices for 'spring warming' are estimated for each sampling year (1990–2011) and each sub-area (north, central and south) as the slope of the monthly average change in Reynolds SST data (Reynolds *et al.*, 2002) over the 3 months October, November and December (austral spring) prior to each survey. This index is used as a proxy for advection of hypoxic water across the ABF and onto the Namibian continental shelf.

The calculated mean anomalies from seasonal climatology for each sub-area over the same 3 months are based on six measurements of SST per month. For each SST index, an anomaly from seasonal climatology is calculated by subtracting the mean of October, November and December from the climatology of the same months and then dividing the result by the standard deviation for that period. The mean of these anomalies is used as an effect variable in our data analysis.

Fish fauna

To identify the relative abundance of the different fish species, we have used the 22 yr of data collected during the demersal research surveys, covering the entire northern Benguela between 17° and 29°S. Only survey data collected in January–May, and spanning the depth range of 20–325 m have been included. These data were used to calculate an index of relative importance, %IRI (Pinkas *et al.*, 1971; Kolding, 1989), using the PASGEAR program (Kolding, 1989), for each of the three shelf areas. This index uses the relative catch composition per species from all hauls by numbers per h, weight (kg) h^{-1} and frequency of occurrence per stations relative to the total. The mean distribution (catch per hour in kg) of gobies, hake and horse mackerel for 10 × 10 nautical mile squares was calculated

from the pooled data set in ARCMAP (ESRI ArcMap 10.1).

Data analysis

The data set was analysed using R version 2.15.1 (R development Core Team, http://www.r-project.org) to understand how the distribution and abundance of gobies, hake and horse mackerel vary with respect to bottom oxygen concentration, latitude and depth, and, in the case of gobies, what effect predators might have on same. To ensure temporal and spatial matching between fish and *in situ* environmental measures, data were stratified into areas of 0.25 × 0.25 *degrees*. We checked for collinearity among the three predictors included in the GAM model (bottom oxygen, latitude and depth). First, we checked the correlation among the sets of predictor variables to be included in the model and found none of the correlation to be extreme. Next, we checked the variance inflation factor (VIF; Zuur *et al.*, 2007). Normally a VIF of above 3 is an indication of a problem resulting from stronger collinearity. In this, none of the VIF was higher than 1.5. Our treatment of these as independent explanatory variables is thus not expected to bias the predictions.

We analysed the survey and satellite data for each of the northern, central and southern shelf areas using general additive modelling (GAM) in two steps (Zuur *et al.*, 2009). The first step was to analyse the presence/absence data of gobies and horse mackerel using logistic GAMs assuming a Bernoulli distribution for estimating how the probability of occurrence change with the explanatory variables. The probability of occurrence reflects the distribution of the species: a decrease meaning that the species occurred on fewer stations (i.e., distributional area shrinks), and an increase meaning a range expansion.

In the second step we analysed only those data with positive goby and horse mackerel stations – assuming a Gaussian distributed errors – and estimated how abundance (catch per hour, in kg) varied with explanatory variables. The logistic GAM analysis could not be used on the hake data, as hake occurred on more than 98% of the trawl stations and none of the predictors were significantly important, and we were therefore able to analyse the complete data set including the zero catch stations for hake assuming a Gaussian distributed error. All models started out by including all the explanatory variables: year, spring warming index prior to each year, spring mean anomaly in SST (mean SSTanomaly), and abundance of the other species on log scale, i.e., ln (species catch + 1). We then sequentially removed

the non-significant terms and present only the effects that were significant. Model selection was based on the Akaike information criterion (AIC), and from the sets of models the most parsimonious model was that with the lowest AIC: in cases when the difference in the AIC between successive models was less than 2, we further checked whether the differences in the residual deviance between these modes were significant. When the difference in deviance was found to be insignificant we kept the simplest model: in cases where the difference was significant, we retained the model with the smallest residual deviance.

No over-dispersion was found for the binomial deviance, which is expected to have a unit dispersion. All the diagnostic checks of the models fitted indicated that none of the assumptions of homogeneity of variance and normality was violated for the continuous model (Zuur *et al.*, 2009).

RESULTS

Temperature and wind speed vary along the Namibian coast (Fig. 1), and in the last two decades there has been a general warming off Angola and Namibia

Figure 1. Mean AVHRR Pathfinder sea surface temperature from November to March and corresponding mean Quickscat wind stress in N m^{-2} (arrow).
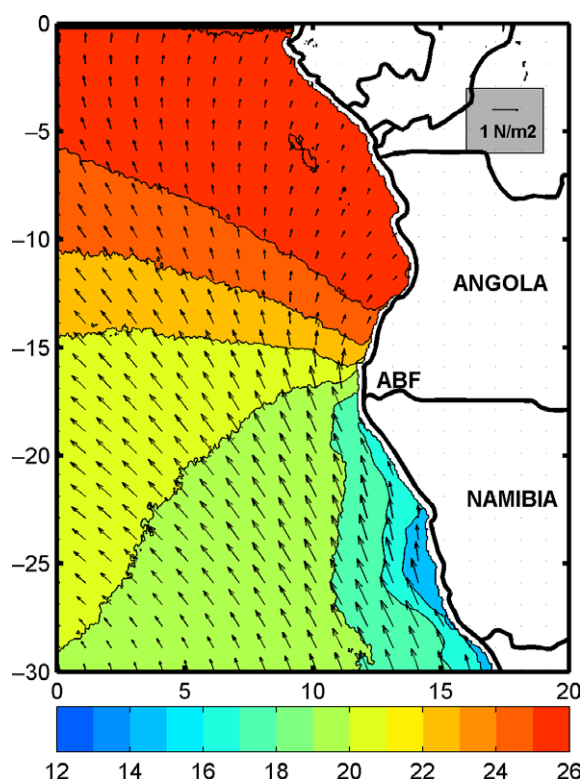
(Fig. 2; Rouault *et al.*, 2009). The warming has been most pronounced (both measured as the spring warming index and the mean anomaly during the austral spring) in the north (Fig. 2). Warming is also visible in the central and southern shelf areas, but to a much lesser extent (Fig. 2). The largest area with severely hypoxic and hypoxic bottom oxygen is found off central Namibia, which is where the goby population is most widely distributed (Figs 3a,b and 4b). That said, some high density patches of gobies are noted in the southern shelf area (Fig. 3b), where severely hypoxic conditions are regarded to occur less frequently than further north (Fig. 3a). Goby abundance appears to decrease when the concentration of dissolved oxygen in the bottom water masses increases (GAM; $F = 9.72$; $P \ll 0.0001$; Fig. 4c). Cape hakes are distributed across the entire central and northern shelf area, and the main distributional area overlaps with that of the bearded goby (Fig. 3b,c). Hake and goby have the highest and second highest %IRI values, respectively, in the central and southern shelf areas (Fig. 5b,c). The main area for horse mackerel is in the north (Figs 3d and 5a), which is the sub-area closest to tropical waters, and this is the area where the horse mackerel %IRI is highest (Fig. 5a). The north appears to be a marginal area for gobies (Fig. 3b), where it represents a relatively unimportant component of catches (Fig. 5a).

Concurrent with the warming trend of the northern Benguela (Fig. 2), the goby has in recent years extended its distributional range over a larger area of the northern, and to some degree also of the central, Namibian shelf (north: $\chi^2 = 45.18$, $P \ll 0.001$; central: $\chi^2 = 20.81$, $P < 0.001$; Table 1, Fig. 6a,b). By contrast, in the south the goby distribution has been more variable, with peaks in the mid-1990s and mid-2000s ($\chi^2 = 33.09$, $P \ll 0.001$; Table 1, Fig. 6c). Interestingly, the distributional extent of horse mackerel has decreased in the north and increased recently in the central area (north: $\chi^2 = 21.96$, $P \ll 0.001$; central: $\chi^2 = 36.40$, $P < 0.001$; Table 2, Fig. 6d,e). During events of strong spring warming, goby abundance increased in the north ($\chi^2 = 3.73$, $P = 0.002$; Table 1, Fig. 7a) but showed a more variable pattern over the central shelf ($\chi^2 = 2.0$, $P = 0.038$; Table 1, Fig. 7b). In the south, spring warming had no effect on goby abundance ($P = $ NS), although if the mean spring SST anomaly was high, abundance tended to decrease ($\chi^2 = 3.77$, $P = 0.006$; Table 1, Fig. 7c).

Horse mackerel and hake responded differently to spring warming. In the north, warming had no influence on the distribution or abundance of horse mackerel. However, in the central shelf area, horse mackerel used somewhat less space when the spring
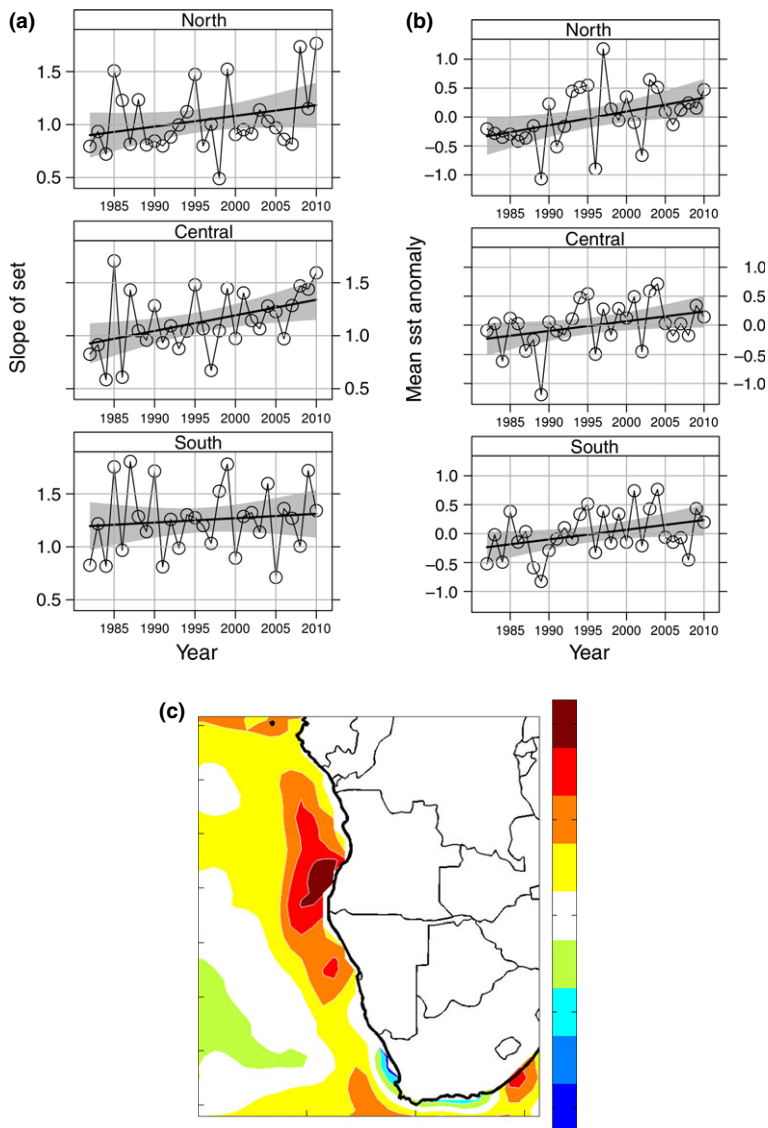
Figure 2. Annual variation and means of the spring warming index (a) and anomaly (b) in northern (17–20.5°S), central (20.5–24.5°S) and southern (24.5–29°S) Namibian shelf areas. The map (c) shows the linear trend from 1982 to 2010 of optimally interpolated Reynolds sea surface temperature in degrees per decade estimated from merging satellite remote sensing and observations. The year in X, specifies that the year corresponds to the preceding spring year, i.e., for X = 1995, the value refers to spring months October, November and December 1994.

warming indices increased ($\chi^2 = 4.13$, $P = 0.042$; Table 2, Fig. 8a), and abundance was somewhat higher ($\chi^2 = 2.68$, $P = 0.035$; Table 2, Fig. 8b).

In the case of Cape hake, the spring warming index had a positive effect on abundance in the northern and central areas (north: $\chi^2 = 3.46$, $P = 0.006$; central: $\chi^2 = 3.53$, $P = 0.011$; Table 3; Fig. 9a,b). When the SST anomaly was very strong, hake appeared to be more abundant in the north, but decreased somewhat over the central shelf (north: $\chi^2 = 2.63$, $P = 0.02$; central: $\chi^2 = 6.27$, $P = 0.013$; Table 3, Fig. 9c,d). A high abundance of both goby predators in the north (horse mackerel and Cape hake) co-occurred with a contraction of the area gobies occupied there (horse mackerel: $\chi^2 = 63.56$, $P \ll 0.0001$; Cape hake: $\chi^2 = 28.53$, $P \ll 0.001$; Table 1, Fig. 10a,d), whereas

in the south, the goby's response to hake catch rate was more variable ($\chi^2 = 51.95$, $P \ll 0.001$; Table 1, Fig. 10e).

DISCUSSION

Recent decades have been characterized by a global warming rate of approximately 0.2°C per decade (Fréon *et al.*, 2009). This can affect the intensity of the upwelling (Bakun, 1990; Narayan *et al.*, 2010), the vertical distribution of marine organisms, as well as the structure and functioning of the whole food web (Hutchings *et al.*, 2009). Previous studies in the region have shown that warming events, in particular Benguela Niños (Shannon *et al.*, 1986), are associated with a drop in the concentration of dissolved oxygen

Figure 3. (a) Distribution of severely hypoxic [<0.5 mL L^{-1} O$_2$ (<21.8 μmol kg^{-1})] and hypoxic water masses [0.5–1.0 mL L^{-1} O$_2$ (21.8–43.5 μmol kg^{-1})] in bottom waters on the Namibian shelf (modified from Bartholomae and van der Plas, 2007). Main spatial distribution of the bearded goby (*Sufflogobius bibarbatus*) (b), Cape hake (*Merluccius capensis*) (c), and horse mackerel (*Trachurus capensis*) (d) measured as average catch per hour for each of 10 × 10 nautical miles. The data represent the average distribution over the years 1990–2011 and are on a semi-logarithmic scale.
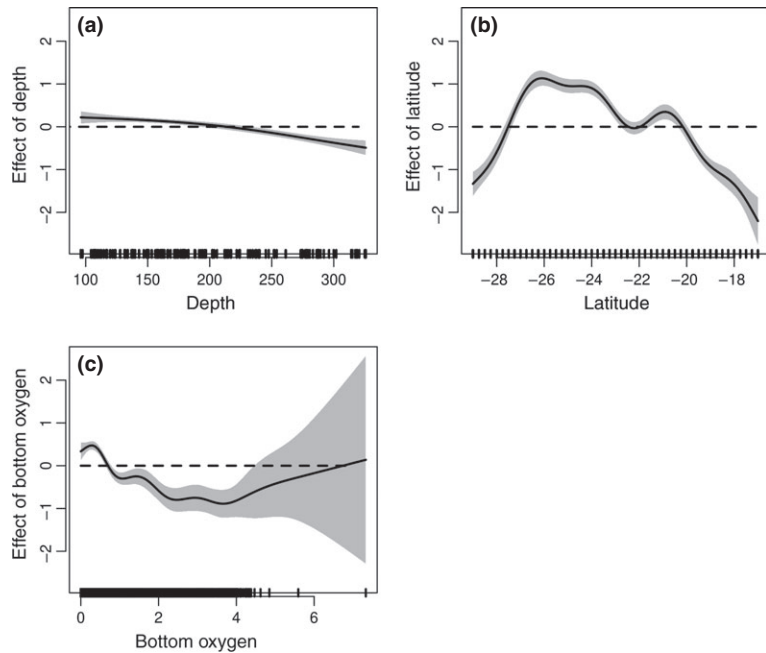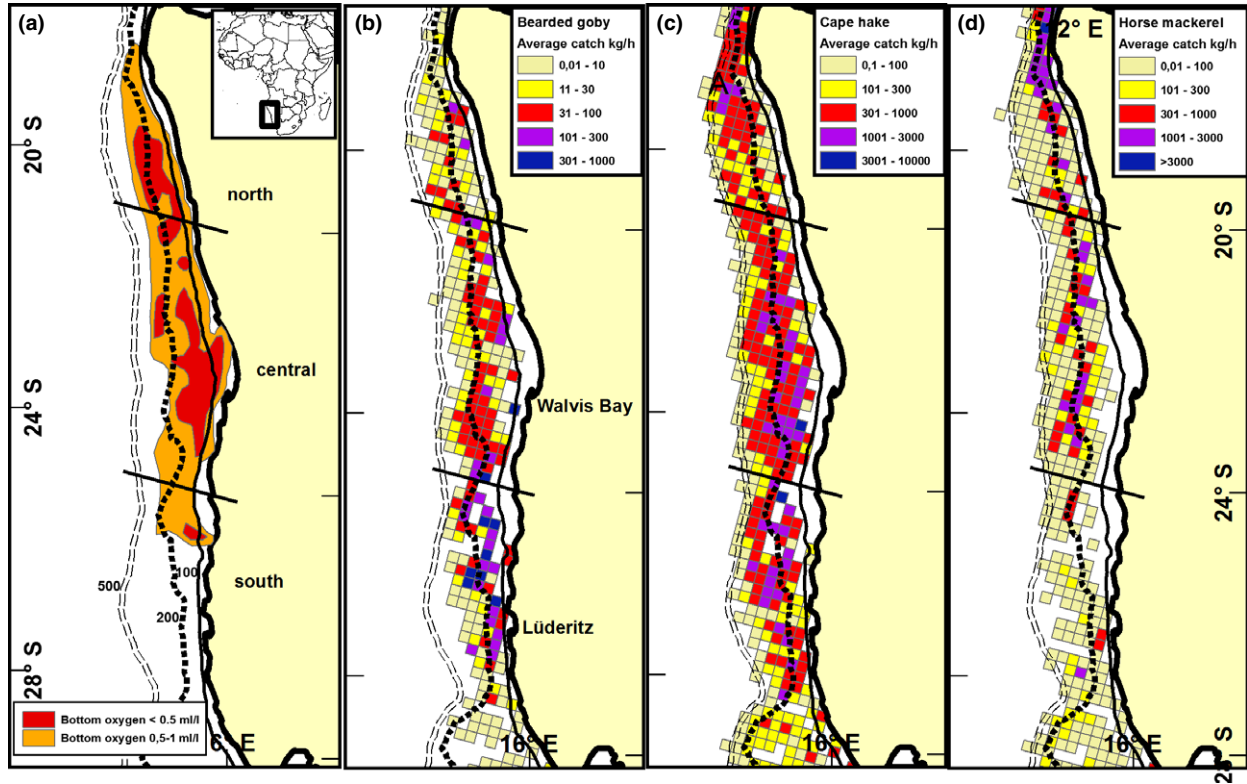
Figure 4. Model predicted goby abundance (measured as catch per hour – panels on logit-scale) with (a) depth (m); (b) latitude (°S), and (c) bottom oxygen (mL L^{-1}) for the entire northern Benguela ecosystem (17–29°S) predicted from general additive modelling. The stippled lines represent 95% confidence bands. R^2 (adj) = 0.442. Deviance explained is 42.8%. All *P*-values ≪0.001.
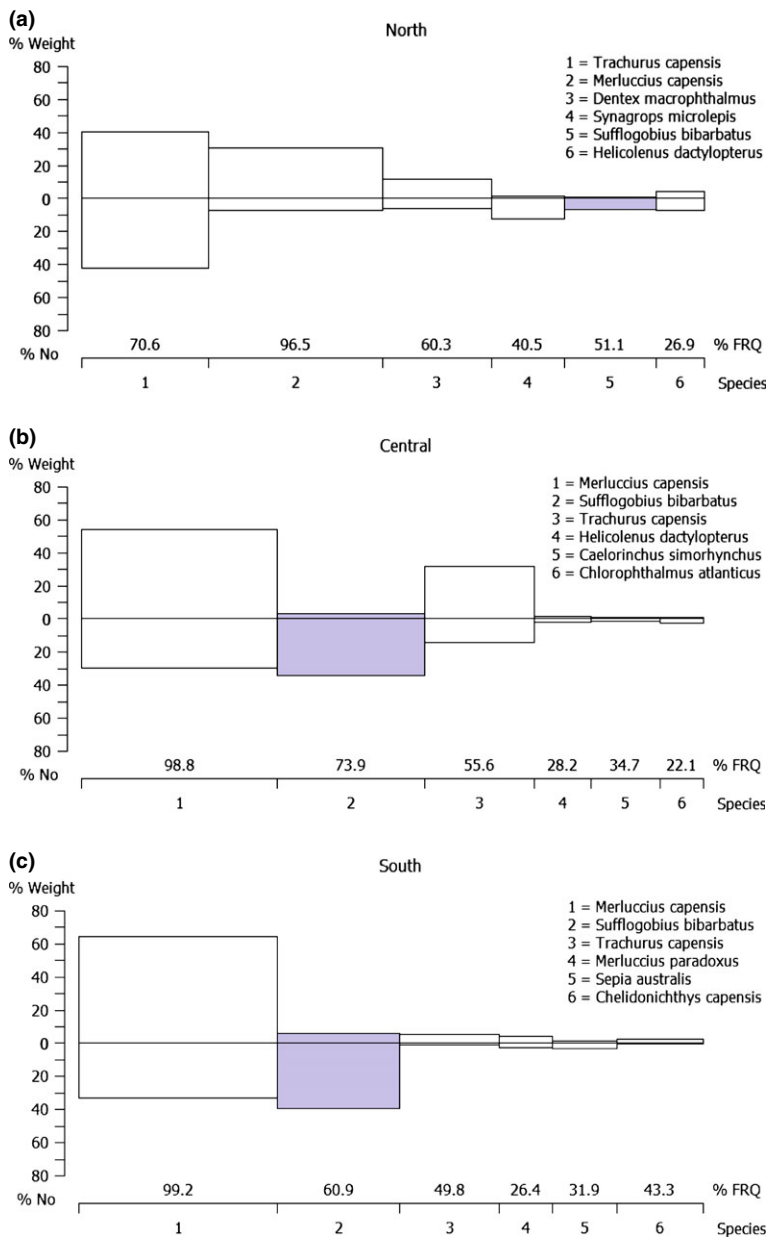
Figure 5. Index of relative importance (%IRI) of major fish species in (a) northern (17–20.5°S), (b) central (20.5–24.5°S) and (c) southern (24.5–29°S) Namibian shelf area. The calculations are based on the pooled catch data in weight and numbers during the hake surveys from 1990 to 2011 and thus represent the average over 22 yr. The shaded boxes reflect the bearded goby. %IRI accounts for catch% composition in weight and length, and the proportion of stations the species were captured (FRQ%).

and an increase in the volume of suboxic and hypoxic deep waters over the shelf (Gammelsrød *et al.*, 1998). This is caused by advection of hypoxic waters from north of the ABF (e.g., Boyd *et al.*, 1987; Gammelsrød *et al.*, 1998; Shannon *et al.*, 1988; Rouault *et al.*, 2007; Rouault, 2012). Our data show that the habitats occupied by the three species studied in the present paper differ in respect to the spring warming, which we use as an index for the advection of low oxygen water. We suggest that it is linked to behavioural responses based on physiological constraints. Further, their unequal tolerance to hypoxic water masses is likely to create different responses to climatic events,

such as Benguela Niños. Young horse mackerel are mainly pelagic and mesopelagic, whereas adults go deeper (Shannon *et al.*, 1988; Namwandi, 2002; Axelsen *et al.*, 2004). On the mid-shelf, gobies undertake DVM and shuttle between the severely hypoxic seabed during the day and more oxygen-rich mesopelagic water masses at night (Utne-Palm *et al.*, 2010). In contrast, hake are mainly demersal (Hamukuaya *et al.*, 1998). Of the three species examined here, gobies cope best with oxygen depletion as they have the lowest critical value for oxygen requirement (5.3% = 0.3 mL L^{-1} = 13.1 μmol kg^{-1}; Utne-Palm *et al.*, 2010) and can even tolerate suboxia of

Table 1. Estimated effects of spring warming (s(Slope)), mean SST anomaly (s(mSSTAnom)), horse mackerel abundance [s (log(HorsCatch+1)], Cape hake abundance [s(log(HakeCatch+1)], and year [s(year)] from general additive modelling on bearded goby distribution (using presence–absence data) and abundance (using positive catch data) for northern (17–20.5°S), central (20.5–24.5°S) and southern (24.5–29°S) Namibian shelf area. Catch is measured as kilo per hour trawling. If predictors are not listed for a shelf area, this reflects that it was not significant. The table provides the smooth terms of the final model. Model selection was based on its AIC values and the test of deviance between successive models.

Model terms	Estimated df	χ^2	P-value	Proportion of deviance explained
North shelf area - distribution				27.168
s[log(HakeCatch + 1)]	2.414	28.530	≪0.001	
s[log(HorsCatch + 1)]	1.899	63.564	≪0.001	
s(year)	3.587	45.183	≪0.001	
North shelf area - abundance				32.240
s(Slope)	4.317	3.730	0.002	
s(mSSTAnom)	6.394	1.699	0.108	
s(year)	4.457	9.557	≪0.001	
Central shelf area - distribution				6.725
s[log(HakeCatch + 1)]	4.729	18.622	0.004	
s[log(HorsCatch + 1)]	1.000	3.781	0.051	
s(year)	3.351	20.807	<0.001	
Central shelf area - abundance				12.169
s(Slope)	8.141	2.005	0.038	
s(mSSTAnom)	1.918	2.594	0.069	
s(year)	2.392	12.574	≪0.001	
South shelf area - distribution				20.077
s[log(HakeCatch + 1)]	5.490	51.946	≪0.001	
s[log(HorsCatch + 1)]	1.977	29.259	≪0.001	
s[year]	7.313	33.094	≪0.001	
South shelf area - abundance				30.800
s(mSSTAnom)	3.123	3.770	0.006	
s[log(HakeCatch + 1)]	2.628	14.729	≪0.001	
s[log(HorsCatch + 1)]	2.480	9.994	≪0.001	
s(year)	3.167	2.588	0.039	

0.12% oxygen (= 0.3 μmol kg^{-1}) for more than 4 h (Salvanes *et al.*, 2011). The critical value for horse mackerel is 10% (*cf.* Table 2 of Ekau *et al.*, 2010), which is equivalent to the range 0.59–0.47 mL L^{-1} (25.8–20.6 μmol kg^{-1}) depending on temperature in the range 13–25°C. Hence, the hypoxic refuges of gobies will likely be avoided by horse mackerel, whereas the gobies will visit the horse mackerel habitat as they ascend to mid-water at night. The critical value for Cape hake is not known but experimental data have shown that the excised hearts of Cape hakes were permanently damaged after exposure to anoxia for 20 min, whereas those of the goby recovered (Utne-Palm *et al.*, 2010), indicating a lower tolerance of Cape hake to low oxygen conditions. However, Cape hake clearly tolerates lower concentrations of oxygen than the horse mackerel. Sundby *et al.* (2001)

observed that live hake eggs and larvae were abundant at oxygen concentration down to 0.3 mL L^{-1} at depths between 200 and 300 m over the central Namibian shelf, and Hamukuaya *et al.* (1998) found juvenile hake down to depths with oxygen concentrations of 0.5 mL L^{-1} (87 μmol kg^{-1}). During the Benguela Niño event in 1994, when hypoxic water masses covered the central and northern sub-areas down to 250 m depth off Namibia, both horse mackerel and juvenile Cape hake were displaced (Hamukuaya *et al.*, 1998; Gammelsrød *et al.*, 1998; Woodhead *et al.*, 1998), thus relaxing predation mortality on the gobies. This is also indicated in our data, with the distributional area of gobies increasing when predator abundances were low (Fig. 10e).

The data reported here also suggest that there are spatial differences in how the gobies and their
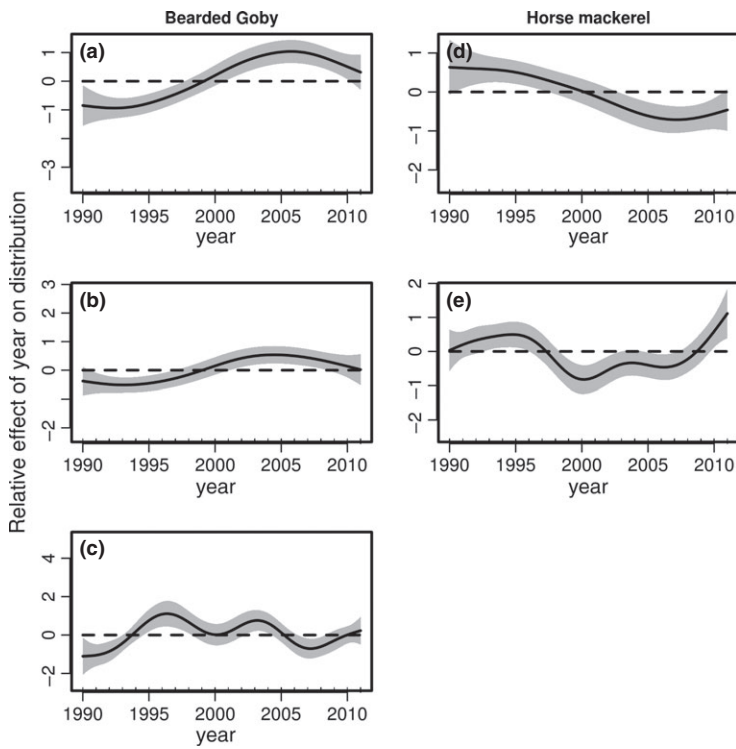
Figure 6. Change in distribution of bearded goby and horse mackerel, respectively, in the north (a, d panels), central (b, e) and southern Namibian shelf (c for gobies) estimated from logistic GAM analysis. The lines represent the annual effect relative to the average and the shaded areas the 95% confidence bands. The stippled horizontal line is the mean over the years.

Table 2. Estimated effects of spring warming (s[Slope]), mean SST anomaly (s(mSSTAnom)), Cape hake abundance (s(log(HakeCatch+1)], and year (s(year)] from General Additive Modelling on horse mackerel distribution (using presence absence data) and abundance (using positive catch data) for northern (17–20.5°S), central (20.5–24.5°S) and southern (24.5–29°S) Namibian shelf areas. Catch is measured as kilo per hour trawling. If predictors are not listed for a shelf area, this reflects that it was not significant. The table provides the smooth terms of the final model. Model selection was based on its AIC values and the test of deviance between successive models.

Model terms	Estimated df	χ^2	P-value	Proportion of deviance explained
North – distribution				13.183
s[log(HakeCatch + 1)]	1.000	8.036	0.005	
s(year)	3.126	21.961	≪0.001	
North – abundance				31.527
s[log(HakeCatch + 1)]	6.950	3.973	≪0.001	
s(year)	1.000	16.915	≪0.001	
Central – distribution				10.531
s(Slope)	1.000	4.131	0.042	
s[log(HakeCatch + 1)]	1.954	29.078	≪0.001	
s(year)	6.313	36.404	≪0.001	
Central – abundance				31.290
s(Slope)	3.275	2.678	0.035	
s(mSSTAnom)	4.354	2.441	0.033	
s[log(HakeCatch + 1)]	1.948	36.901	≪0.001	
s(year)	8.136	2.857	0.004	
South – distribution				14.848
s(mSSTAnom)	2.771	9.870	0.029	
s[log(HakeCatch + 1)]	2.415	9.472	0.025	
South – abundance				13.473
s[log(HakeCatch + 1)]	1.000	22.759	≪0.001	

Figure 7. Effect of spring warming index on abundance of bearded goby in the (a) northern and (b) central Namibian shelf; and (c) the effect of mean SST anomaly on the goby abundance in the southern Namibian shelf estimated from GAM analysis. The lines represent the annual effect relative to the average and the shaded areas the 95% confidence bands. The stippled horizontal line is the mean over the spring warming indices.
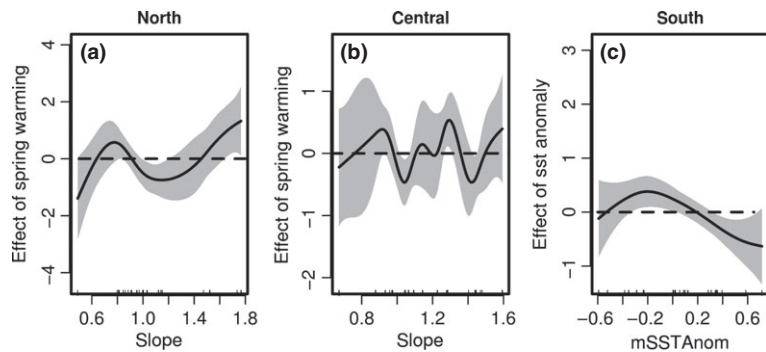
Figure 8. Effect of spring warming index and mean SST anomaly on the (a) distribution (logistic GAM analysis) and (b) abundance (GAM analysis) of horse mackerel of the central shelf area. The lines represent the annual effect relative to the average and the shaded areas the 95% confidence bands. The stippled horizontal line is the mean over the spring warming indices and anomaly.
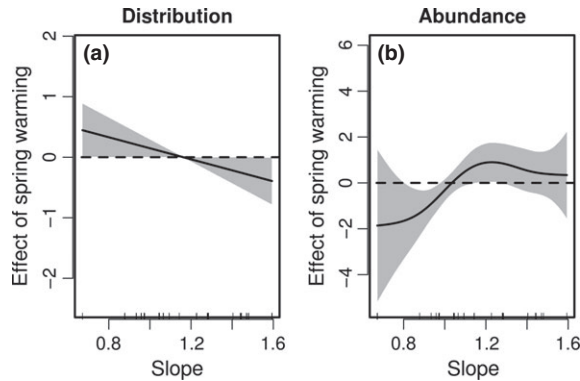

predators responded to environmental changes. The expansion of the goby's range and the contraction of horse mackerel in the north during the last decade (Fig. 6a,d) co-occurred with a general warming in the northern and central shelf areas (Fig. 2), whereas the pattern was less clear in the south (Fig. 6c). This is likely linked to the different oceanographic features in the central and northern areas, which are located downstream of the strong upwelling cell in the south at Lüderitz (26°S), where this upwelling cell contributes to separate the northern (Namibian) and southern (South African) Benguela regions (Hutchings *et al.*, 2009). The northernmost part of the ecosystem is influenced by the seasonal advection of warm-water that varies in intensity on inter-annual time scales (Rouault, 2012). South of the strong upwelling cell, the ecosystem is to a larger extent impacted by short-term wind variability (Shannon and Nelson, 1996), and the dynamics of Agulhas rings from the east (Schouten *et al.*, 2000). The higher environmental

Table 3. Estimated effects of spring warming [s(Slope)], mean SST anomaly [s(mSSTAnom)], horse mackerel abundance [s(log (HorsCatch+1)] and year [s(year)] from general additive modelling on Cape hake abundance for northern (17–20.5°S), central (20.5–24.5°S) and southern (24.5–29°S) Namibian shelf area. If predictors are not listed for a shelf area, this reflects that it was not significant. The table provides the smooth terms of the final model. Model selection was based on its AIC values and the test of deviance between successive models.

| Model terms	Estimated df	χ^2	*P*-value	Proportion of deviance explained
North shelf area				21.544
s(Slope)	4.070	3.459	0.006	
s(mSSTAnom)	4.821	2.631	0.020	
s[log(HorsCatch + 1)]	2.589	10.186	<0.001	
s(year)	7.436	3.492	0.001	
Central shelf area				20.847
s(Slope)	2.812	3.531	0.011	
s(mSSTAnom)	1.000	6.267	0.013	
s[log(HorsCatch + 1)]	1.518	45.905	<0.001	
s(year)	8.510	5.777	<0.001	
South shelf area				21.861
s[log(HorsCatch + 1)]	1.808	3.620	0.023	
s(year)	4.913	3.913	0.001	

Figure 9. Effect of spring warming index and mean SST anomaly on Cape hake abundance of northern (a, c panels) and central (b, d panels) Namibian shelf estimated from GAM analysis. The lines represent the annual effect relative to the average and the shaded areas the 95% confidence bands. The stippled horizontal line is the mean over the spring warming indices and anomaly.
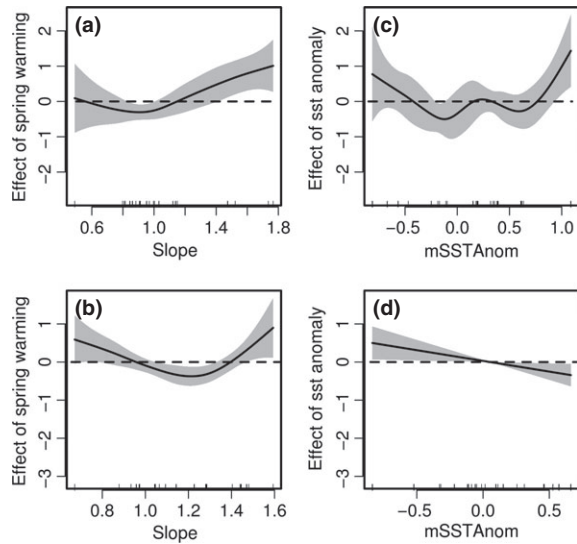

variability in the south compared with the central and northern shelf area off the Namibian coast may explain the latitudinal differences in the spatial dynamics of the bearded goby and its key predators.

In Fig. 11 we outline a conceptual model of the vertical distributions of the three fish species with, and without, an intrusion of warm water from north. The distributions are overlapping but each of the three species has their individual depth-dependent centres of gravity: the mesopelagic horse mackerel is found highest in the water column. Cape hake is better adapted to low oxygen concentrations and is distributed below horse mackerel, with its lower range of distribution controlled by the depth of the suboxic water layer. As the most low-oxygen tolerant species, bearded gobies are found nearest to the sea floor, where they can use the anoxic habitat as a refugee during the day, as noted earlier (Utne-Palm *et al.*, 2010). During Benguela Niños, the oxygen concentration in the entire water column declines, and bottom waters are less well ventilated, which results in the development of a thick layer of low-oxygen water near the sea bed, especially in the central area. This not only increases the volume of refuge for the bearded goby, which reduces predation pressure from hake, but also forces the hake to move northward into waters that are not anoxic (Fig. 9). Again, this alleviates predation pressure on the goby population. Horse mackerel seem to be decoupled from this hake–goby interaction, as it occurs higher in the water column and (mainly) further north, only shifting southwards following the warm water intrusions.

In Fig. 12 we present a conceptual model for the response of the three species to the Benguela Niños warming events (*cf.* Gammelsrød *et al.*, 1998). As
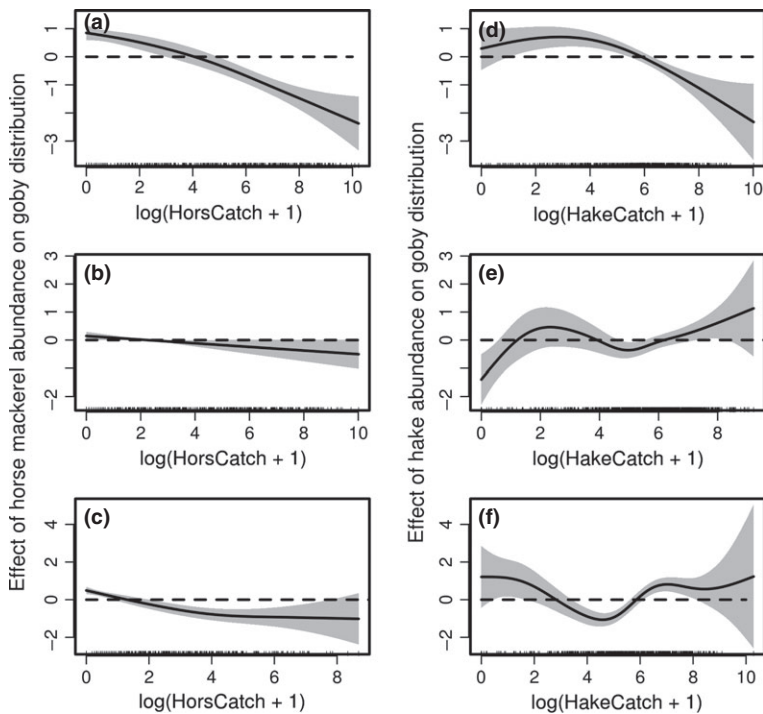
Figure 10. Effect of the predator abundances (horse mackerel and Cape hake) on bearded goby distribution estimated from logistic GAM analysis. The lines represent the annual effect relative to the average and the shaded areas the 95% confidence bands. The stippled horizontal line is the mean over the ln(predator abundance+1). (a, d) Northern, (b, e) central, and (c, f) southern Namibian shelf area, respectively, for horse mackerel and Cape hake.
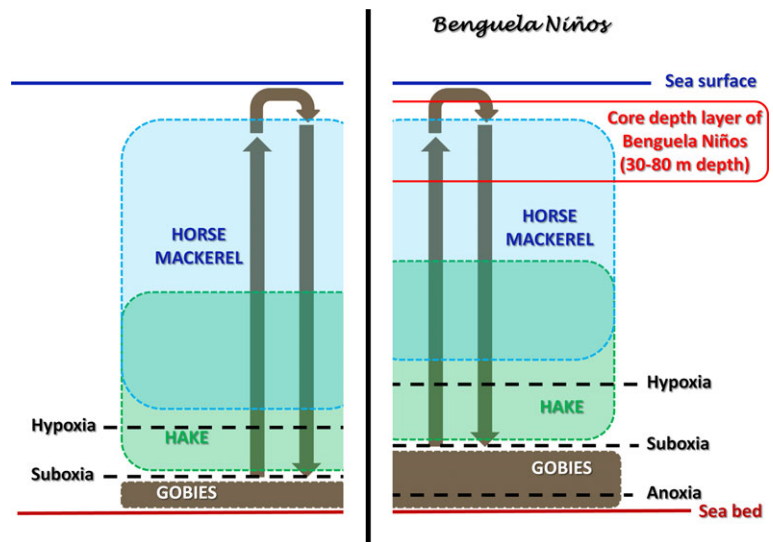
Figure 11. Conceptual model for vertical distributions of bearded goby, horse mackerel and Cape hake. The dark green mid-section of the figure indicates the overlapping depth range of horse mackerel and hake. The brown vertical arrows refer to diel vertical migration of the gobies.
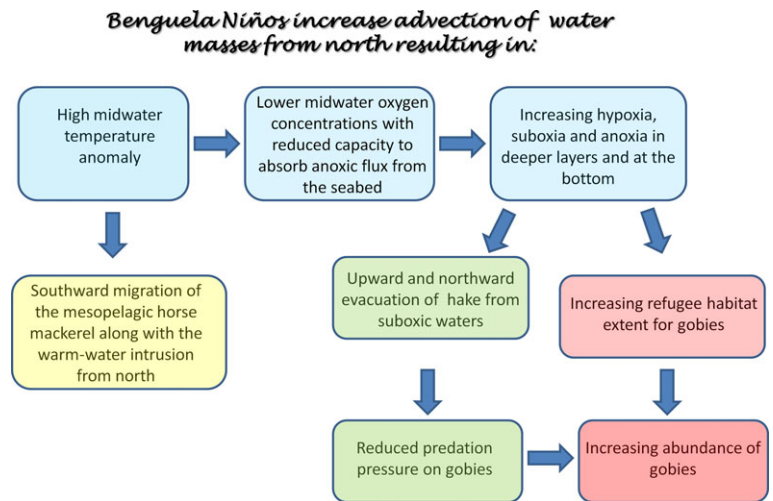
Figure 12. Conceptual model for the impact of Benguela Niños on the distribution and abundance of horse mackerel, Cape hake and bearded goby.

horse mackerel belongs to a family known for preferring warmer water, it has a possibility to extend its distribution southwards to the central area during warm-water intrusions from north. Because it is an actively swimming pelagic and mesopelagic species, and likely has a high oxygen demand, the volume of habitable water in the central area is comparatively limited, as not only is the advected water low in oxygen but relaxation of local wind reduces upwelling and the ventilation of deep waters (e.g., Boyd *et al.*, 1987). This is compounded off central Namibia by the high levels of local production and surplus decay (this region already has the lowest routine levels of dissolved oxygen), resulting in a compression of suitable habitat and forcing horse mackerel to occur at shallower than normal depths. This is supported by data of Namwandi (2002) indicating that during the Benguela

Niño in 1995, annual catches of horse mackerel from the pelagic purse seine fishery increased 50% from 1994 to 1995, whereas catches from the mid-water fleet decreased during the same period, suggesting a higher catchability of the species in shallower waters. However, such environments will be favourable for gobies, which have an extreme tolerance for suboxic and sulphidic environments (Utne-Palm *et al.*, 2010; Salvanes *et al.*, 2011). Our data show that the goby's distribution increased both in the central (main distributional) and (especially) in the (otherwise marginal) northern areas during years when warming occurred, and that abundance was high in the north following extreme spring warming events (Fig. 7a).

Bakun (1990) has hypothesized that global warming will lead to increasing atmospheric pressure differences between land and ocean which, in turn, cause

increased coastal upwelling. This is supported by observations over a 40-yr time series from all of the major eastern boundary upwelling systems (Narayan et al., 2010). Climate change has the potential to increase the already high primary production in upwelling systems, which in turn can further increase oxygen stress and negatively affect food web structure, and fisheries. But off central Namibia, events of suboxia and hypoxia relax predation pressure on gobies which temporarily could increase biomass to higher trophic levels by increased goby abundance. This could, in turn, become available for predation by hake when environmental conditions improve.

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