

Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species

WARREN M. POTTS¹, ROMINA HENRIQUES^{1,2}, CARMEN V. SANTOS³, KATE MUNNIK⁴, ISABELLE ANSORGE⁴, FRANCOIS DUFOIS^{4,5}, ANTHONY J. BOOTH¹, CAROLA KIRCHNER⁶, WARWICK H.H. SAUER¹ and PAUL W. SHAW^{1,7}

¹Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa, ²School of Biological Sciences, Royal Holloway University of London, Egham, United Kingdom, ³Faculty of Science, University of Agostinho Neto, Luanda, Angola, ⁴Department of Oceanography, University of Cape Town, Cape Town, South Africa, ⁵Marine and Atmospheric Research, CSIRO, Floreat, Australia, ⁶(formally)Ministry of Fisheries and Marine Resources, Secretariat of the Pacific Community, New Caledonia, Namibia, ⁷Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, United Kingdom

Abstract

Despite increasing awareness of large-scale climate-driven distribution shifts in the marine environment, no study has linked rapid ocean warming to a shift in distribution and consequent hybridization of a marine fish species. This study describes rapid warming (0.8 °C per decade) in the coastal waters of the Angola-Benguela Frontal Zone over the last three decades and a concomitant shift by a temperature sensitive coastal fish species (*Argyrosomus coronus*) southward from Angola into Namibia. In this context, rapid shifts in distribution across Economic Exclusive Zones will complicate the management of fishes, particularly when there is a lack of congruence in the fisheries policy between nations. Evidence for recent hybridization between *A. coronus* and a congener, *A. inodorus*, indicate that the rapid shift in distribution of *A. coronus* has placed adults of the two species in contact during their spawning events. Ocean warming may therefore revert established species isolation mechanisms and alter the evolutionary history of fishes. While the consequences of the hybridization on the production of the resource remain unclear, this will most likely introduce additional layers of complexity to their management.

Keywords: *Argyrosomus*, climate change, evolution, fisheries management, northern Benguela

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Introduction

Warming oceans have resulted in many fishes shifting their distributions towards higher latitudes (Stebbing *et al.*, 2002; Perry *et al.*, 2005; Masuda, 2008; Last *et al.*, 2011). Together with significant ecological effects (Harley *et al.*, 2006), these shifts have resulted in heterogeneous changes in fish abundance and have significant consequences for fisheries and their management (Cheung *et al.*, 2010). While adaptive measures have been suggested from both resource assessment (Link *et al.*, 2011) and management perspectives (Madin *et al.*, 2012), these are based on the assumption that a change in abundance is the only parameter affected. However, as fishes shift their distributions, the interactions between native species and those colonizing a 'new' environment may have ecosystem consequences (Parmesan & Yohe, 2003), while the secondary contact

between previously isolated species may introduce additional layers of complexity via hybridization.

Although the hybridization of some terrestrial organisms has been linked to climate change (Garroway *et al.*, 2010; Mallet *et al.*, 2011), no studies in the marine environment have yet reported a link between ocean warming and hybridization in fishes. Hybridization between marine fish species is not uncommon, and relatively easy to detect since the advent of molecular techniques (Rao & Lakshmi, 1999; Roques *et al.*, 2001; Nielsen *et al.*, 2003; Morgan *et al.*, 2012). However, attributing the drivers of hybridization to climate change or to ocean warming is seldom possible due to the absence of baseline information (such as historical data) and the possibility of hybridization resulting from other factors such as artificial species introductions (Taylor *et al.*, 2006; Gozlan *et al.*, 2010). Therefore, the evolutionary, ecological and fisheries management consequences of hybridization in warming oceans have not been adequately considered.

Ocean warming hotspots are thought to provide critical early indicators of the expected consequences of climate change (Frusher *et al.*, 2013, Hobday & Pecl, 2014;

Correspondence: Warren M. Potts, tel. +27 46 603 8483, fax +27 46 603 7504, e-mail: w.potts@ru.ac.za

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Potts *et al.*, 2014) and it is in these areas that hybridization amongst closely related marine species may be detected first. The offshore seas of southern Angola are thought to be warming rapidly (Monteiro *et al.*, 2008), leading to the area being recognized as an ocean warming hotspot (Hobday & Pecl, 2014). This region of the South Eastern Atlantic Ocean is dominated by the Angola-Benguela Frontal Zone (ABFZ) (Fig. 1), an ocean current convergence formed by the confluence of the cold, nutrient rich, northward-flowing Benguela Current and the warm, oligotrophic, southward-flowing Angola Current. Although the temperature gradient of the ABFZ provides geographically recognizable boundaries and forms a warm-temperate biogeographic transition zone (Anderson *et al.*, 2012), the boundary locations are not fixed, migrating southwards into central Namibia during the austral summer and northwards into northern Angola during the austral winter (Lass *et al.*, 2000; Lass & Mohrholz, 2005). South of the ABFZ, where the Lüderitz Upwelling Cell forms there is a major, perennial cold water boundary which is thought to limit the southward dispersal of warm-temperate coastal species (Henriques *et al.*, 2014).

The coastal area between central Namibia and northern Angola has two morphologically similar *Argyrosomus* species (Griffiths & Heemstra, 1995). *Argyrosomus coronus* (Griffiths & Heemstra, 1995) is a fast growing, late maturing species distributed in warmer waters from Luanda in northern Angola to northern Namibia (Potts *et al.*, 2010); while *A. inodorus* (Griffiths & Heemstra, 1995) is a slower growing, early maturing species distributed in cooler waters from central to northern Namibia (Kirchner & Holtzhausen, 2001) (Fig. 1). In Angola, *A. coronus* is targeted heavily in the coastal fisheries, both artisanal and subsistence, and there is now a growing recreational fishery (Potts *et al.*, 2009). In Namibia, both species are heavily exploited by an established recreational fishery that operates in the West Coast Recreational Area (WRCA – a 200 km section of coastline between the northern boundary of the Namib Naukluft National Park and the Ugab River), and contributes significantly to the economy of the area (Stage & Kirchner, 2005). While the artisanal and subsistence fisheries in Angola are largely unregulated, bag limits, size limits and Marine Protected Areas provide some protection for *Argyrosomus* species in Namibia.

In this study, we present evidence for ocean warming, a rapid shift in distribution and the hybridization of these two closely related coastal marine fish species in the northern Benguela. This work was initiated after our observations of a rapid decline in catch rate and average size of *A. coronus*, with no apparent declines in the other dominant fish species, in a tourist-based recreational fishery in southern Angola. To investigate

these trends, we analysed changes in coastal sea surface temperature off southwestern Africa (and specifically the ABFZ region) using satellite data since 1982. We examined the size frequency and catch and effort data, and temperature sensitivity derived from these data, for the three dominant species in the southern Angolan recreational fishery from 2005 to 2010 to uncouple the effects of exploitation from distributional shifts. We then used morphological and molecular genetic techniques to compare historical (1994–1995) and contemporary (2009) catch composition of *Argyrosomus* species in the Namibian recreational coastal fishery. Finally, we compared the incidence of hybridization between *Argyrosomus* species at the historical (using published allozyme marker frequencies) and contemporary (using new mtDNA and microsatellite DNA marker data) time points. The results should contribute to our knowledge of the likely impacts of ocean warming worldwide and are relevant to evolutionary and conservation biologists, and fisheries managers

Materials and methods

Study site

The coastal region between Swakopmund (Namibia) and Lucira (Angola) is situated in the Namib Desert (Fig. 1). The Angolan coast (between the Cunene River mouth and Lucira) includes three towns, Tômbwa, Namibe and Lucira, and numerous small villages. The Namibian section of coast is also sparsely populated with the majority of people living in Swakopmund and Hentiesbaai. Due to the arid conditions, coastal populations in this area are almost exclusively reliant on the goods and services provided by the coastal zone. This region boasts unique oceanographic characteristics and is dominated by the ABFZ (Fig. 1) which is the confluence of the cold, eastern boundary Benguela and the warm, southward flowing, Angola currents. The perennial Lüderitz Upwelling Cell is situated south of the study region and forms a distinct and permanent cold water (SST 11–14 °C) biogeographic barrier to coastal marine fauna (Henriques *et al.*, 2014).

Sea surface temperature (SST)

There are limited *in situ* oceanographic data for the coastal zone of the ABFZ. Remote sensing (Meeuwis & Lutjeharms, 1990; Cole, 1999; Cole & Villacastin, 2000; Veitch *et al.*, 2006) has, however, provided a source of environmental data, despite being primarily focussed on the offshore zone. The advanced high resolution radiometer (AVHRR) has been dominant platform used in the region, providing data for over three decades. In the present work, we used the night time SST estimated each day by the Pathfinder v5.2 reanalysis dataset with a spatial resolution of 4 km² between 1982 and 2009. A quality flag of 4, considered the lowest quality level for acceptable data (Kilpatrick *et al.*, 2001), was imposed. Recent

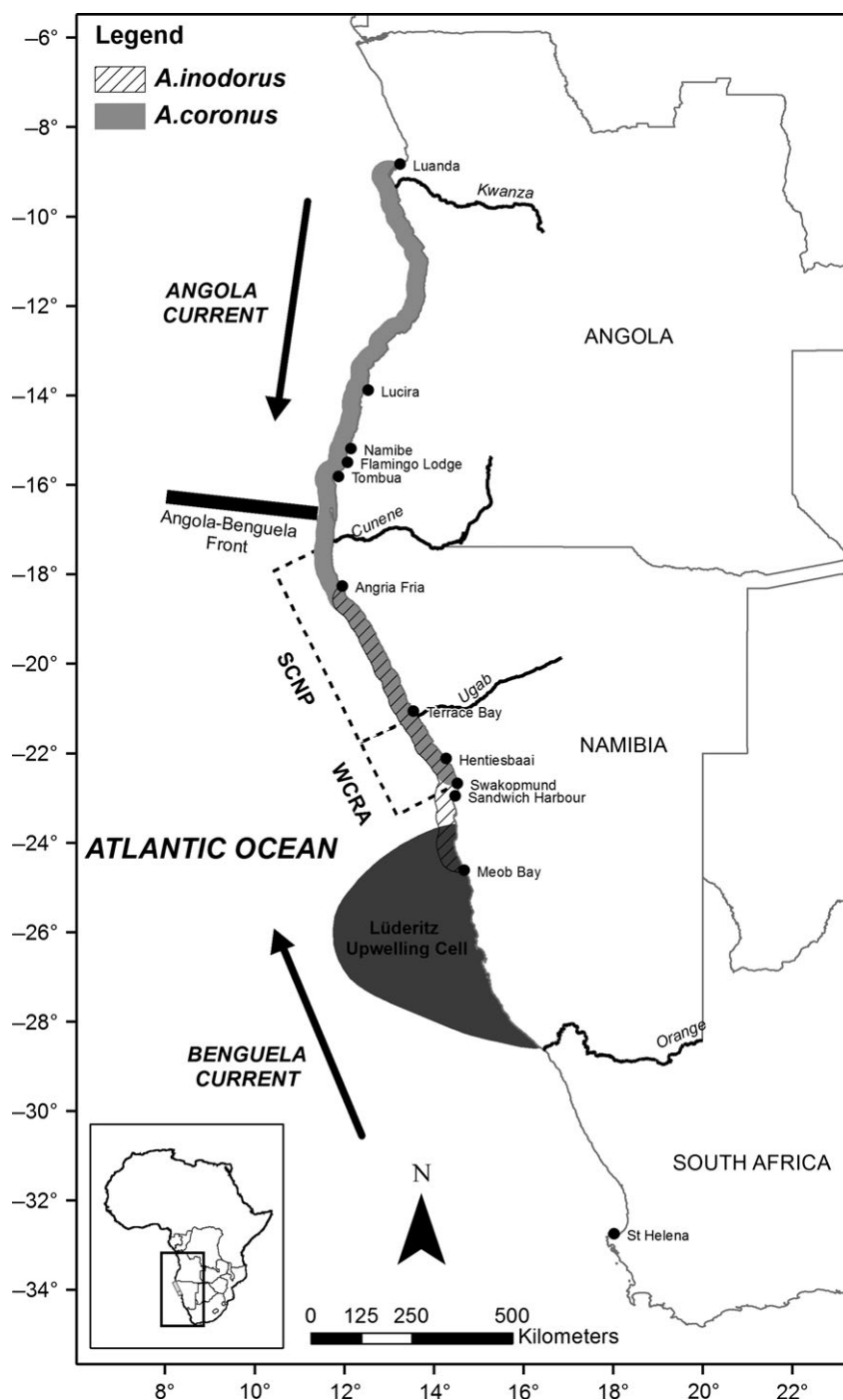


Fig. 1 The southwest African coastline showing the known distribution of *Argyrosomus coronus* and *Argyrosomus inodorus*, position of key oceanographic features, physical features, national parks, recreational areas, major towns and collection sites. SKNP = Skeleton Coast National Park, WCRA = West Coast Recreational Area.

studies (Valente & Silva, 2009; Lee *et al.*, 2010; Blythe & Silva, 2011) have identified the MODIS sensor on board both NASA's Aqua and Terra platforms as more suitable for the estimation of environmental parameters in the coastal zone. Validation of such estimates with *in situ* measurements is considered critical, particularly in areas where the spatial vari-

ability of SST gradients is high, such as in upwelling zones (Dufois *et al.*, 2012). We obtained SST estimates from thermal infrared spectrophotometer data from the MODIS Terra satellite that passes over the region daily (at approximately 10:30 am). The MODIS Terra data, available from 2000 to 2010, have been processed using SeaDAS (<http://seadas.gsfc>).

nasa.gov) at a resolution of 2 km (Dufois *et al.*, 2012). Through a comparison (exact match up days) between satellite-derived and *in situ* daily SST measurements between May 2005 and December 2010 off Flamingo Lodge (S15 34.239, E23 01.128), a standard correction factor for the MODIS SST data was calculated for the region.

Sea surface temperature trend analysis

The trend in the average annual coastal SST data for each pixel in the northern Benguela coastal region was described using a linear regression. The results of this per pixel regression ($^{\circ}\text{C}$ change per decade) for the period between 1982 and 2009 (pathfinder dataset) and between 2000 and 2010 (MODIS Terra data) were plotted for the entire region.

Fishery monitoring

A recreational tourist-based fishery, operating along a 23 km section of coast adjacent to Flamingo Lodge in southern Angola (Fig. 1) was monitored by research scientists for between 185 and 289 days per year from 2005 to 2010. The location of fishing effort (GPS coordinates), number of anglers and the start and end time of each fishing outing was recorded and fishing effort was generally randomly distributed in space and time throughout the zone on each day. All fish that were captured in the fishery were recorded and the majority (>90% were released) as part of the catch and release policy at the lodge. There were three dominant species in the recreational fishery: the west coast dusky kob, *A. coronus*; leerfish, *Lichia amia* (L.); and shad, *Pomatomus saltatrix* (L.). These species are the dominant large predatory teleosts in the coastal waters off southern Angola and the fishing area and methods remained similar throughout the duration of the study. All three species were included in the analysis to assess whether changes in abundance over time were species-specific or a general multi-species community-wide trend. Anglers captured fish using artificial lures and bait. Conventional shore angling tackle, with graphite surf casting rods between 3.0 and 4.5 m long, multiplier or spinning reels, monofilament (0.35 and 0.55 mm diameter) or braided line (0.18–0.30 mm diameter) and hook sizes between 3/0 to 8/0 for all three target species. The target species remained the same throughout the study. When captured, these fishes were measured to the nearest mm on wet PVC vinyl stretchers, fin clipped for DNA analysis, handled with moist cloths, unhooked and released.

Catch per unit effort analysis

Recreational fishery catch rate (CPUE = no. of fish. angler $^{-1}$ h $^{-1}$), calculated as the total number of fish captured per sampling event divided by the effort expended, was calculated for the three fish species as all are caught using the same fishing gear in what can be considered to be a mixed-species fishery. It is therefore hypothesised that if there is a decrease in relative abundance, CPUE, of a species, for example *A. coronus*, compared to two other species, then this decrease is most probably independent of fishing effort. CPUE data were disag-

gregated by life history stage for *A. coronus* and *L. amia*. As few juveniles were captured, *P. saltatrix* CPUE included both juveniles and adults. Species-specific cumulative frequencies of positive (>0) catches as a function of SST were constructed. Pairwise Kolmogorov–Smirnov tests, over the SST range, tested the null hypothesis that catch, by species, was independent of temperature.

A Delta (Δ) model (Aitchison, 1955; Pennington, 1983) was used to examine the effect of environmental and temporal covariates on both the probability of catch (in number), presence-absence and abundance (magnitude of the catch). Delta models are the product of two models; a logistic regression models the zeros, and a second model describes the positive values. These models are also called zero-altered or hurdle models (Maunder & Punt, 2004) as the ‘hurdle’ of a value being nonzero must be overcome before the positive observations, conditional on at least one nonzero observation, can be modelled. The general form of the Delta model is:

$$\Pr(Y|x, y) = \begin{cases} p(x) & y = 0 \\ (1 - p(x)) \frac{f(y)}{1 - f(0)} & y > 0 \end{cases}$$

where x denotes a random binary variable with 0 and 1 assigned to the positive and zero observations, respectively, and $f(y)$ denoting the probability distribution chosen to describe the positive observations. We applied a log-normal distribution (Myers & Pepin, 1990; Ye *et al.*, 2001; Fletcher *et al.*, 2005). The expected mean of the Delta model with log-normally distributed positive observations is $E(y) = (1 - p) \exp(\mu + \frac{\sigma^2}{2})$, where μ and σ are the mean and standard deviation of the natural logarithm-transformed positive observations, respectively (Fletcher *et al.*, 2005).

Mean annual CPUE, per species, was modelled by including year as a continuous independent variable into both the binomial and log-normal models. The effect of temperature and photoperiod were assessed by including year (as a factor), temperature and photoperiod as continuous independent variables. The most parsimonious zero and positive models for each species were determined using a stepwise procedure using Akaike’s Information Criteria (Akaike, 1972). Statistically nonsignificant variables ($P > 0.05$) were excluded.

Argyrosomus fishery species composition

The proportion of *A. coronus* in the ‘*Argyrosomus*’ catch was assessed during two periods (period 1 = 1994–1996, period 2 = 2008–2009) in Namibia and one period (2005–2009) in southern Angola. In Namibia, otoliths and muscle tissue samples were collected from *Argyrosomus* specimens from the recreational fishery throughout the WCRA during period 1, while a fin clip was removed from each sampled fish and preserved in 95% ethanol immediately after capture during period 2. In Angola, fin clips were taken from specimens collected between the Cunene River mouth and Lucira (Fig. 1).

Two procedures were used to differentiate individuals of the two *Argyrosomus* species within the fishery catches. First, an otolith morphometric measurement technique, based on the taxonomic findings for the genus (Griffiths & Heemstra, 1995), was used to identify samples collected during

period 1. This morphological method was validated using a molecular (allozyme) electrophoresis technique (Van Der Bank & Kirchner, 1997) that genetically distinguishes individuals of the two species.

As no permit was available to sacrifice fish in Namibia during period 2, a molecular Polymerase Chain Reaction-based Restriction Fragment Length Polymorphism (PCR-RFLP) DNA approach (which can be applied to nonlethal fin clips taken from catch & release fish) was used to identify to species the sample data collected instead of the destructive otolith morphology approach. Extraction of total genomic DNA was conducted using a standard phenol: chloroform protocol (Sambrook *et al.*, 1989) and PCR amplification of a 700 base pair (bp) region of the mitochondrial cytochrome oxidase I (COI) gene was obtained with the universal primer pair FishF1 and FishR1 (Ward *et al.*, 2005), following the author's protocols. PCR products from known reference individuals of each species were purified with an enzymatic digestion protocol, utilizing 0.5 μ l of Exo1 (New England Biolabs, Ipswich, UK) plus 1 μ l of SAP and 10 \times supplied buffer (Fermentas), and sequenced in both directions using the same PCR primers (Macrogen Inc., Seoul, South Korea). Resulting sequences were aligned with Clustal X (Thompson *et al.*, 1997) in BioEdit, and used to identify endonuclease restriction enzymes that would generate species-specific digestion patterns. The enzyme HaeIII (New England Biolabs) was predicted to cut the COI PCR fragment at four restriction sites (232, 391, 436 and 671 bp from the 5' end) in *A. coronus*, and at three restriction sites (232, 391, and 671 bp) in *A. inodorus*, creating an expected species-specific pattern of five (Profile A: 29, 45, 159, 232 and 235 bp) and four (Profile B: 29, 159, 232 and 280 bp) DNA fragments, respectively. A 6 μ l volume of PCR product was digested for 1 h at 37 °C with 1 U of HaeIII in 1 \times supplied buffer, and digestion terminated with a final step of 80 °C for 20 min. Restricted products were run on ethidium bromide stained 3% agarose gels, and relative size of fragments was established against Hyperladder II size marker (Bioline, London, UK), using the species reference samples as positive controls. COI PCR products from 20 random samples, including all different restriction profiles observed, were sequenced to validate the observed RFLP profile.

Hybridization analysis

Allozymes are codominantly inherited genetic markers. They are considered to be powerful markers to detect hybridization, as species are often fixed for alternative alleles and thus hybrids (F1, F2 or backcrosses) are immediately evident, and allozymes are therefore often used to detect signs of mixed ancestry in fishes (Whitmore, 1990). Data (16 *A. coronus*, and 5 *A. inodorus* from Terrace Bay plus 9 *A. inodorus* from Swakopmund) from the molecular electrophoresis analysis conducted by Van Der Bank & Kirchner (1997) was used to identify any putative hybrid individuals caught during the first period.

Due to the lack of fresh sample tissue from Namibia, an alternative hybridization technique was used during the second period. Firstly, the PCR-RFLP method was used to identify 180 *A. coronus* from sample sites at Luanda, Lucira, Flamingo and

Cunene in Angola and around Hentiesbaai (between Swakopmund and the Ugab River) in Namibia and 40 *A. inodorus* captured around Hentiesbaai (between Swakopmund and the Ugab River). Samples from these specimens were then PCR amplified for mtDNA COI (see above) and six cross-specific nuclear microsatellite DNA markers (UBA5, UBA40, UBA50, UBA91, UBA853 and UBA854 – Archangi *et al.*, 2009) originally developed for *Argyrosomus japonicus*. Optimized PCR mixes for the microsatellites included 1 \times NH₄Cl buffer, 2 mM of MgCl₂, 0.2 mM of dNTPs, 0.5 pmol of each primer, 0.2 U of Taq polymerase (Bioline) and 50–100 ng of extracted DNA in a final volume of 10 μ l. The annealing temperature and the number of cycles were modified (T_a = 48 °C, number of cycles = 35) to obtain specific amplification reactions.

To check for spatial genetic homogeneity within the species (for standardized frequencies for hybridization tests) pairwise genetic differentiation between sampling sites was estimated for both mtDNA and microsatellite datasets, with statistical significance assessed after 10 000 permutations, in ARLEQUIN (Excoffier *et al.*, 2005). Microsatellites may under some circumstances have less power to detect hybrids than allozymes (due to higher allele numbers and much higher potential homoplasy in the former), so allelic frequencies were estimated for each locus/species and a preliminary simulation study conducted to investigate the suitability of the microsatellite dataset to detect hybridization events. Five hybrid states were modeled using HybridLab (Nielsen *et al.*, 2006): pure species, F1, F2, backcross \times pure *A. coronus* (b1), and backcross \times pure *A. inodorus* (b2). For each state 60 hybrids were simulated, using as a starting dataset 30 genotypes confirmed as pure species from each putative parental *Argyrosomus* species (Henriques, 2012). Confirmed pure species genotypes and simulated hybrid genotypes were run in STRUCTURE (Pritchard *et al.*, 2000) to test the accuracy of the software in detecting different levels of hybridization. Five independent iterations were run for two groups ($K = 2$) under the admixture model, with independent allele frequencies, for 50 000 MCMC iterations after an initial burn-in period of equal length. Identification of putative hybrids was based on the posterior probability of assignment (q) of each individual analysed to one or other parental species. A threshold of $q = 0.1$ was chosen to separate parental (pure species) individuals and F1s or hybrids resulting from backcrosses (Vähä & Primmer, 2006). In all analyses thresholds were set to $q \geq 0.9$ for pure *A. coronus* and $q \leq 0.1$ for *A. inodorus*, while individuals with $0.1 < q < 0.9$ were considered hybrids. The Bayesian approach implemented in NewHybrids (Anderson & Thompson, 2002) was used to corroborate the results obtained with STRUCTURE, with the threshold of posterior probability set to $q_i = 0.5$ (Aboim *et al.*, 2010). Analyses were conducted using the Jeffreys prior for mixing and allelic frequencies, and run for 50 000 MCMC iterations. As all analyses conducted using the simulated genotype dataset revealed that both STRUCTURE and NewHybrids could accurately detect F1, F2, b1 and b2 hybrids, assessment of hybridization events and determination of hybrid status were performed on the test samples of 180 *A. coronus* and 40 *A. inodorus* using the run parameters described above.

Results

Sea surface temperature trends

The medium-term AVHRR data showed a significant warming trend (Spearman's rank correlation, $P < 0.05$) of $0.60\text{ }^{\circ}\text{C}$ per decade along the west coast of southern Africa between northern South Africa and central Angola (Fig. 2a). Although the coastal waters (MODIS Terra data) of the study region were warming at a rate of $0.80\text{ }^{\circ}\text{C}$ per decade (Fig. 2b) between 2000 and 2010, this trend was not significant (Spearman's rank correlation, $P > 0.05$).

Relationship between temperature and catch per unit effort (CPUE)

The CPUE data were zero-inflated. The proportion of zeros, those fishing outings with no fish caught, was species-specific with *Pomatomus saltatrix* having the lowest proportion of zeros (30%) and *A. coronus* adults and juveniles the highest (73% and 75% respectively). The observed CPUE appeared to be temperature-dependent for *A. coronus* (Figure S1), with values highest below 22 and $20\text{ }^{\circ}\text{C}$ for juvenile and adult *A. coronus* respectively. In contrast, the CPUE for *L. amia* (juveniles and adults) and *P. saltatrix* appeared to be temperature-independent (Figure S1).

Juvenile ($<890\text{ mm TL}$, Potts *et al.*, 2010) and adult *A. coronus* were mostly (95%) captured when SST was less than 21.0 and $19.0\text{ }^{\circ}\text{C}$ respectively (Fig. 3). In contrast, 95% of the positive catches of the juvenile ($<670\text{ mm FL}$, Potts *et al.*, 2008) and adult *L. amia* were made at temperatures below $24.0\text{ }^{\circ}\text{C}$ and *P. saltatrix* were captured even at the highest water temperatures (Fig. 3). Cumulative catch rate frequency, as a function of temperature, was only different at the species level ($P < 0.05$, Fig. 3) and temperature was only statistically significant ($P < 0.05$) for both adult and juvenile *A. coronus* explaining almost a quarter of the variation in the presence-absence data for this species (Table S1).

Short-term trends in the southern Angolan recreational fishery

The percentage of adult, compared to juvenile, *A. coronus* in the southern Angolan recreational fishery catch dropped from 72% in 2005 to 15% in 2010 (Figure S2). In contrast, the percentage of adult *L. amia* fluctuated between 30% and 80% without any discernible trend with time, while adults dominated the *P. saltatrix* catch (99%) throughout the study period (Figure S2). Adult *A. coronus* were also the only group that exhibited a significant reduction in their average catch rate over time (Figure S3, $P < 0.05$).

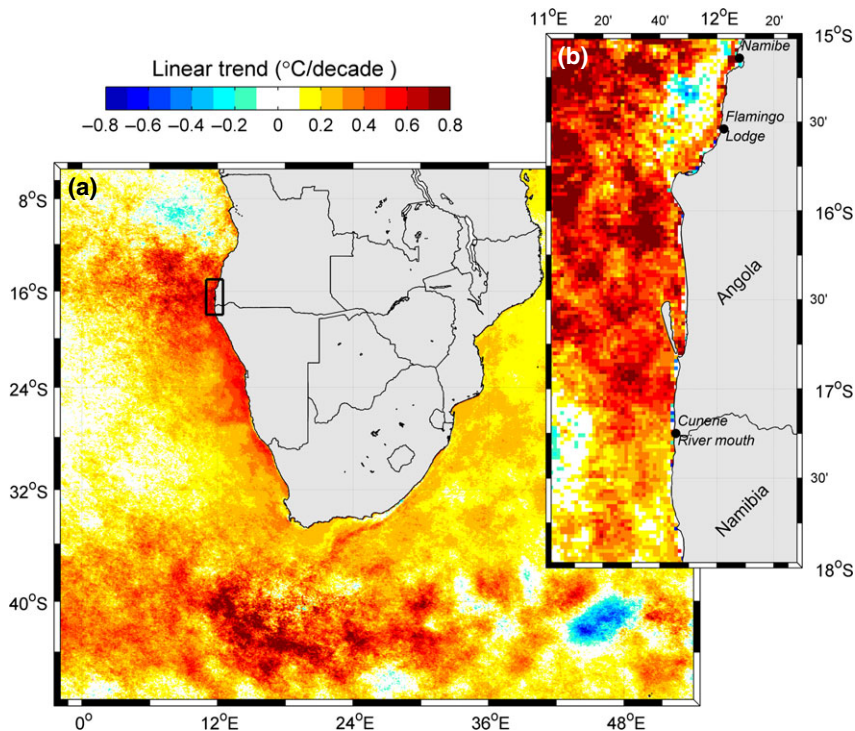


Fig. 2 Sea surface temperature trend ($^{\circ}\text{C}$ per decade) based on (a) the Pathfinder (1982–2010) 5.2 night time dataset and (b) the MODIS Terra ($2 \times 2\text{ km}$ resolution) data for the orthern Benguela region (2001–2010).

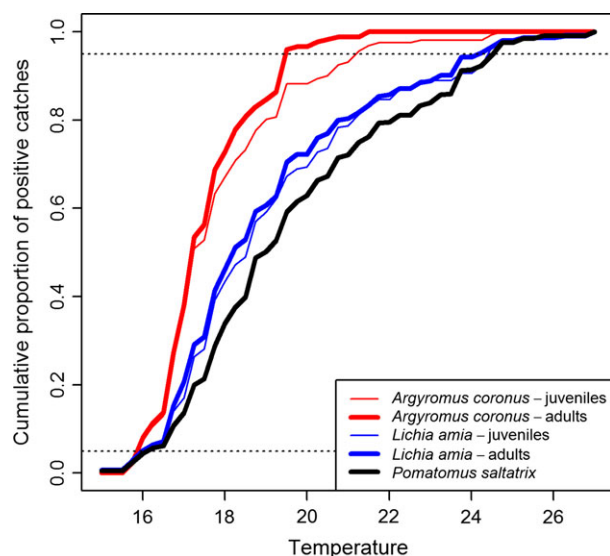


Fig. 3 Cumulative relative proportions of positive catches as a function of temperature for juvenile and adult *Argyrosomus coronus*, juvenile and adult *Lichia amia*, and *Pomatomus saltatrix*. Horizontal lines denote the 5th and 95th percentiles.

Argyrosomus species composition in the coastal fisheries

Based on the validated otolith morphological analysis, *A. coronus* comprised only 8% of the *Argyrosomus* catch in the WCRA during period 1 (1993–1995, Table 1). In contrast, the PCR-RLFP analysis indicated that *A. coronus* dominated the *Argyrosomus* specimens captured in the WCRA during period 2 (2005–2009, Table 1). *A. coronus* dominated the catch (99%) at the Cunene River mouth, at the border between Namibia and Angola, during period 1 (99%) and period 2 (100%) (Table 1).

Hybridization

The allozyme electrophoresis method identified fixation for alternative alleles at seven loci (out of 34 screened)

for the 16 *A. coronus* and 13 *A. inodorus* samples collected in central and northern Namibia during period 1. Based on this, the probability that individuals of the two species were from the same gene pool was estimated to be approximately zero, i.e. they are genetically distinguishable species (Van Der Bank & Kirchner, 1997). These data indicated no evidence for the presence of hybrids (i.e. no heterozygotes, or linkage disequilibrium, at the seven species-specific loci) between the two species in these samples.

After identification and removal of putative hybrid individuals (see below) the combined mtDNA sequencing and nuclear DNA microsatellite analysis from the *Argyrosomus* samples collected during period 2 (2009) also revealed clear species-level separation between *A. coronus* and *A. inodorus*, with population genetic divergence estimated at $F_{ST} = 0.99$ ($P < 0.001$) for mtDNA and $F_{ST} = 0.16$ ($P < 0.001$) for microsatellites. The assessment of microsatellites identified pronounced allele frequency differences between the species, and a number of alleles private to both *A. coronus* and *A. inodorus* in all six loci. When tested with the simulated hybrid dataset, the STRUCTURE analysis accurately detected all F1 and F2 hybrids, but lost precision in the detection of backcrosses in 50% of cases. The number of incorrect assignments was reduced when the Bayesian approach implemented in NewHybrids was used, with only 13% of the backcrosses to *A. coronus* and 5% to *A. inodorus* not identified. This suggested that the microsatellite dataset was powerful enough for hybridization inference. Analysis of the test (sampled) dataset in STRUCTURE (corroborated the results of NewHybrids), combined with morphological evidence and mtDNA haplotypes, identified admixed species origins for five of 180 *A. coronus* (plus one further identified by NewHybrids alone) and two of 40 *A. inodorus* individuals (Fig. 4 and Table 2). The two *A. inodorus* 'hybrid' individuals displayed *A. inodorus* phenotype and mtDNA haplotype but were assigned

Table 1 Percentage of *Argyrosomus coronus* (numbers sampled in parentheses) in the catch composition of the 'kob' (*Argyrosomus*) fishery in, from south to north, the West Coast Recreational Area (WCRA) and Skeleton Coast National Park (SCNP) in Namibia, at the Cunene River mouth (the border between the two countries) and at Flamingo Lodge, Lucira and Luanda in Angola. Samples were all collected between June and August

	NAMIBIA			ANGOLA		
	WCRA	SCNP	Cunene River mouth	Flamingo Lodge	Lucira	Luanda
1993–1995*	8 (237*)	15 (325*)	99 (258*)	–	–	–
2005–2007†	–	–	100 (45†)	100 (100†)	–	–
2008–2009	57 (146† + 18‡)	–	100 (12‡)	100 (78† + 12‡)	100 (41† + 12‡)	100 (44† + 12‡)

*Electrophoresis validated otolith morphometry.

†Molecular Polymerase Chain Reaction-based Restriction Fragment Length Polymorphism.

‡MtDNA sequencing.

as *A. coronus* on nuclear genotype, whereas the six *A. coronus* 'hybrids' all displayed *A. coronus* type mtDNA and were identified as backcrosses with *A. coronus* according to their nuclear genotypes (Table 2).

Discussion

The short-term MODIS Terra dataset indicated extremely rapid recent warming over the study area. Although such results might be interpreted as a cyclical decadal signal, which has been reported for the northern Benguela (Hutchings *et al.*, 2009), the similar warming trend (0.60 °C/decade) identified in the medium-term (three decade) analysis (Fig. 2a) and in the offshore zone (Monteiro *et al.*, 2008; Hutchings *et al.*, 2009) was far greater than the global mean (1960–2009) of 0.07 °C/decade (Burrows *et al.*, 2011), and higher than other ocean warming 'hotspots' such as the Antipodean region that has been warming at a rate of 0.2 °C per decade since 1944 (Ridgway, 2007). Our findings suggest that the coastal waters of the ABFZ is a key study area, both from an oceanographic perspective to understand its role in the regional ocean environment, and from a biological perspective where the response of animals such as fishes may provide an indication of changes that are likely to occur globally in areas that are warming at a slower rate.

One of the main observed consequences of ocean warming has been a latitudinal distributional shift of fishes (Perry *et al.*, 2005). Oxygen limitation has been identified to be the primary mechanism driving these distributional shifts in migratory fishes (Pörtner & Knust, 2007), while other factors such as 'reproductive scope' may drive the distributional shifts of resident species (Potts *et al.*, 2014). Theoretically, as fish grow the limitation of oxygen required to maintain their basic metabolic rate (Cheung *et al.*, 2011) often triggers a movement response to cooler, oxygen rich waters. While complex linkages between the environment and their physiology drive shifts in the movement behaviour of fishes (Hinch *et al.*, 2006), oxygen limitation is

the most likely explanation for the observed temperature sensitivity in *A. coronus*, as the resident juveniles become oceanadromous at maturity, with their migration patterns closely correlated with seasonally changing temperatures in the region (Potts *et al.*, 2010). Temperature sensitivity was also evident when one examines the catch of the co-occurring species as a function of temperature (Figure S1). Here we show that *A. coronus* was generally captured at lower temperatures than the other two coastal species.

Decreasing length frequency distributions and catch per unit effort for *A. coronus* in the southern Angolan recreational fishery suggests that adult *A. coronus* have undergone a recent distributional shift out of southern Angola in response to warming SST in the region. Alternatively, these observations may be interpreted as a consequence of overexploitation (Maunder & Punt, 2004; Shin *et al.*, 2005) or a deeper water/offshore migration, such as that observed in the demersal fish fauna in the North Sea (Perry *et al.*, 2005; Dulvy *et al.*, 2008). However, the stable catch rate for juvenile *A. coronus*, adult and juvenile *L. amia* and *P. saltatrix* during the same period, all of which are exposed to the same fishing pressure in southern Angola coastal fisheries, therefore suggests that exploitation is not the primary driver for the observed changes.

While there was no historical length frequency and catch per unit effort data from Angola during the first period, the results of both the otolith morphometry and genetic analyses indicated that there was a substantial increase (3–57%) in the presence of *A. coronus* in the central Namibian (WCRA) *Argyrosomus* fishery between 1993–1995 and 2009. As fishermen are unable to distinguish between these two morphologically similar species, and have maintained similar capture techniques since 1993, these results have provided evidence to suggest that at least a portion of the *A. coronus* population has shifted alongshore south from southern Angola into central Namibia (Table 1). This large overlap also suggests that *A. inodorus* have not responded to warming conditions with a concomitant

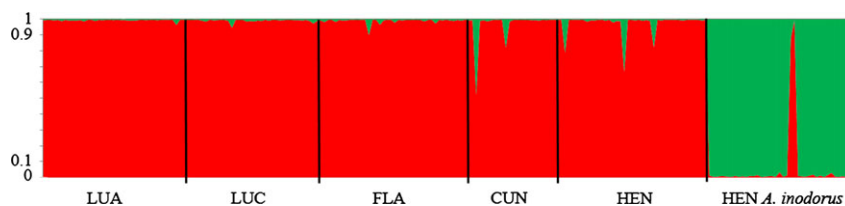


Fig. 4 Multilocus genetic assignment tests performed on 220 'kob' individuals sampled in 2009, using STRUCTURE for hybrid identification based on six microsatellite loci: red vertical bars indicate *Argyrosomus coronus* type individuals, green bars indicate *Argyrosomus inodorus* types. Dashed lines indicate probability of assignment to each species: $q > 0.9$ = pure *A. coronus*; $q < 0.1$ = pure *A. inodorus*; $0.1 < q < 0.9$ = putative hybrid. Sample sites for *A. coronus*: LUA – Luanda; LUC – Lucira; FLA – Flamingo; CUN – Cunene River Mouth; HEN – Hentiesbaai. Sample sites for *A. inodorus*: HEN – Hentiesbaai.

Table 2 *Argyrosomus coronus* (KNA = Namibia and KA = Angola) and *A. inodorus* (KN) individuals showing evidence for introgressive hybridization as diagnosed by morphology, mtDNA COI sequence and nuclear microsatellite genotypic assignment using STRUCTURE and NewHybrids

Individual	Sampling Site	Morphology	mtDNA	STRUCTURE (q)	NewHybrids
KNA19	HEN	<i>A.inodorus</i>	<i>A.coronus</i>	Admixed (0.21)	b1
KNA70	HEN	<i>A.inodorus</i>	<i>A.coronus</i>	Admixed (0.33)	b1
KNA89	HEN	<i>A.inodorus</i>	<i>A.coronus</i>	Admixed (0.17)	<i>A.coronus</i>
KA270	CUN	<i>A.coronus</i>	<i>A.coronus</i>	Admixed (0.46)	b1
KA278	CUN	<i>A.coronus</i>	<i>A.coronus</i>	Admixed (0.18)	b1
KA33	FLA	<i>A.coronus</i>	<i>A.coronus</i>	Not admixed (0.1)	<i>A.coronus</i> /b1
KN109	HEN	<i>A.inodorus</i>	<i>A.inodorus</i>	<i>A.coronus</i>	<i>A.coronus</i>
KN125	HEN	<i>A.inodorus</i>	<i>A.inodorus</i>	<i>A.coronus</i>	<i>A.coronus</i>

HEN, Hentiesbaai; CUN, Cunene; FLA, Flamingo; b1, backcross with *A. coronus*.

southward distributional shift, which may be attributed to the perennial cold water (11–14 °C) Lüderitz Upwelling Cell situated just south of their primary distribution (Fig. 1). Ultimately, distributional shifts in coastal fishes are more likely to be alongshore due to the narrow habitat range between land and the continental shelf. This is particularly relevant in areas with narrow continental shelves, such as southern Angola and Namibia.

The temperature sensitivity of adult *A. coronus* and the rapid southward distributional shift in this species appear to be correlated with the ocean warming in the ABFZ. Most studies documenting distributional shifts in marine fauna have relied on long-term (>40 years) survey (Perry *et al.*, 2005) or distribution records (Last *et al.*, 2011). The present study shows that rapid distributional shifts are not only possible but likely in areas that are warming rapidly, and particularly in areas where species are near their thermal limits.

Distribution changes in top predator fish species (as in *Argyrosomus*) will have consequences for communities both where they depart and arrive, in a manner recognized in the biological invasion literature (e.g., Parker *et al.*, 1999). The loss of a single species may have significant consequences due to the low functional redundancy in coastal marine assemblages (Micheli & Halpern, 2005), and through changes to ecosystem processes such as a reduction in nutrient cycling associated with local fish extinctions (McIntyre *et al.*, 2007). Similarly, an arriving fish population or species may cause a range of impacts: individual effects such as changes in the behaviour, morphology and life history of fishes; population impacts such as competition and demographic effects; community impacts such as extinctions, changes in community composition and trophic structure; and genetic impacts such as hybridization between related species (Cucherousset & Olden, 2011).

The allozyme analysis conducted on samples of 16 *Argyrosomus coronus* and 13 *A. inodorus* in Namibia showed no evidence for hybridization in 1994. However, the mtDNA and nuclear microsatellite DNA analyses of samples collected in 2009 identified admixed species origins for eight of the 107 kob individuals (67 *A. coronus* and 40 *A. inodorus*) sampled in the same region (Table 1). Although microsatellites may under some circumstances have less power (due to homoplasy in allele arrays present) than allozymes, they are still considered to be powerful genetic markers of hybridisation where differentiated allele arrays exist between species (as in the present study). If they are less powerful, the bias is expected to be in the direction of false negatives rather than false positives. Therefore, the levels of hybridization in the fish collected in 2009 may be higher than reported.

Hybrid zones are areas where genetically distinct individuals interbreed and produce offspring with mixed ancestry (Nielsen *et al.*, 2003). These zones are characteristically flanked by areas that host pure populations of genetically distinct groups (Harrison, 1990). While our detection of hybrid individuals may indicate the presence of a long existing hybrid zone, there are two lines of evidence supporting our hypothesis of a recent hybridization event between the two *Argyrosomus* species. The first is that two individuals with *A. inodorus* phenotype and mtDNA haplotype possessed *A. coronus*-like nuclear microsatellite genotypes. This type of cyto-nuclear discordance is a typical feature in introgressive events (Lu *et al.*, 2001). The second is simply the absence of hybrids in the samples collected in 1994. If the area between Swakopmund and Terrace Bay in Namibia has hosted a historical hybrid zone, based on the proportion of hybrids detected in the second period and the sample sizes analysed during period one we would expect to have seen evidence for at least 2–3 hybrids in the Van Der Bank & Kirchner (1997) study.

Although our sample size was not high, the absence of F1 and F2 individuals in the samples from period 2 was not entirely unexpected: although F1 (and to a certain extent, F2) individuals have been previously described during hybridization events, they are not normally common. This is because the F1 generation is generally the most differentiated from both parental species, and therefore tend to be less fit than pure or backcrossed individuals. Nevertheless, the presence of backcrossed individuals during the second period implies that some F1 individuals, despite their potentially reduced fitness, survived to maturity and were at least partially viable. This finding suggests that continued genetic introgression and the formation of a hybrid swarm between the two species is possible (Rhymer & Simberloff, 1996; Allendorf *et al.*, 2001). With a generation time of approximately 5 and 1.5 years (and potentially earlier breeding ages) for *A. coronus* and *A. inodorus*, respectively, it is likely that a first generation of backcrosses (post F1) could exist in the time period (14 years) between the two sampling periods, particularly if the hybrids retained the generation time of *A. inodorus*.

The recent hybridization combined with the existence of backcrosses to the parental species suggests that the previous isolation of *A. inodorus* and *A. coronus* was maintained through a prezygotic mechanism, such as nonoverlapping breeding grounds or seasons (as *Argyrosomus* species have extensive breeding migrations to distinct spawning sites – Kirchner & Holtzhausen, 2001; Griffiths, 1996). These mechanisms could be breached when the adults of the two species are found together at the same spawning site during the spawning season. Interbreeding of *A. inodorus* and *A. coronus* may have occurred if the documented ocean warming resulted in a southward shift of the spawning grounds of *A. coronus* from southern Angola (Potts *et al.*, 2010) into northern Namibia, which is in the distribution area of adult *A. inodorus*, or if reproductively mature adult *A. coronus* have migrated further south to the spawning grounds of *A. inodorus* at Meob Bay (Kirchner & Holtzhausen, 2001). Hybridization due to secondary contact of previously isolated species has been reported in other marine species (e.g., Albert *et al.*, 2006). However, the present study is the first record of such events occurring in less than two decades under natural conditions (i.e. not due to human-mediated introductions).

In 2009, the hybrids were restricted to samples from the southern distribution of *A. coronus* (central-northern Namibia from Hentiesbaai to the Cunene River mouth), where the two species overlap, and which may now represent an incipient hybrid zone. With the perennial, cold water Lüderitz Upwelling Cell in the south and a warming ABFZ, the already strong thermal gradient in

this region (Baumann & Doherty, 2013) appears to be strengthening. This suggests that the warm temperature sensitive *A. coronus* is likely to shift further southward increasingly forcing the two species together into a smaller area of suitable habitat. If the species distributions are forced together spatially, complete admixture could occur with the loss of one or both pure species (Sato *et al.*, 2010).

Although there are obvious conservation concerns in such hybridization processes (Allendorf *et al.*, 2001; Muhlfeld *et al.*, 2009), hybrid vigour sometimes produces positive outcomes (Barton, 2001; Hoffmann & Sgro, 2011). The mixtures of genotypes arising from hybridization after secondary contact between related species may promote rapid adaptation and facilitate evolution in response to the pressures from new environments (Stemshorn *et al.*, 2011) and climate change (Hoffmann & Sgro, 2011). In the rapidly changing environment of the northern Benguela, hybridization events such as detected here could provide these fish populations with additional genetic variation required for adaptation.

From a fisheries perspective, there is little consensus on the likely life history consequences of hybridization, besides that it may vary depending on the level of introgression (Corsi, 2011). The two *Argyrosomus* species have contrasting life histories, with *A. coronus* exhibiting a larger maximum size (190 cm TL vs. 145 cm TL), a reduced maximum age (13 years vs. 28 years), a faster growth rate ($\omega = 207$ vs. $\omega = 139$) and delayed maturity (4–5 years vs. 1 year) when compared with *A. inodorus* (Potts *et al.*, 2010). While we cannot speculate on the consequences of hybridization on the life history of these *Argyrosomus* it will no doubt, like with other hybridization events around the world, have an impact on the productivity of the resource, on their coastal fisheries and ultimately on the local human populations heavily dependent on this resource.

In summary, in response to changing environments resulting from warming seas rapid transboundary distributional shifts and hybridization events will introduce additional layers of complexity into the management of coastal fisheries. As the present example demonstrates, there will be (human) winners and losers associated with transboundary shifts. The winners may benefit from new fishery resources: Namibian recreational fisheries will benefit from an increase in average size of 'kob' and number of 'trophy' specimens due to the southward distributional shift of *A. coronus*, which are faster growing and attain larger sizes than *A. inodorus*. However, *A. coronus* may face rapid over-exploitation in the intensive coastal Namibian fisheries as present management regulations, which include a size limit set at the size at maturity for *A. inodorus*, were

not developed for its markedly different life history characteristics. Therefore, the benefits of the new resources in a region could quickly diminish if updated management regulations are not implemented. Angolan coastal communities will be the losers in this situation and mitigation measures, such as the promotion of alternative livelihoods, experimental fisheries for tropical species and value added production and marketing will be crucial. Hybridization will also have an impact by changing the life history characteristics and fitness of individuals and populations. The prediction of the extent of the hybridization is further complicated by the difficulty in predicting the impacts of climate change in complex coastal systems. Nevertheless, hybridization events will influence the resilience of fisheries to exploitation and regardless of their positive or negative nature, the response time of fisheries managers to these changes will determine the extent to which coastal communities will benefit or suffer. Ultimately, flexible institutional arrangements that allow rapid responses and international collaboration may dictate the success or failure of coastal fisheries management in a changing climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Catch per unit effort (CPUE) as a function of temperature for juvenile and adult dusky kob (*Argyrosomus coronus*), juvenile and adult leervis (*Lichia amia*) and shad (*Pomatomus saltatrix*). Zero catch rates are open black circles.

Figure S2. Length frequency histograms of *Argyrosomus coronus* (A), *Lichia amia* (B) and *Pomatomus saltatrix* (C) captured in a recreational fishery in southern Angola between 2005 and 2010. Dashed line is the length-at-50% maturity.

Figure S3. Mean catch rate per year for juvenile and adult dusky kob (*Argyrosomus coronus*), juvenile and adult leervis (*Lichia amia*) and shad (*Pomatomus saltatrix*). The black dots are observed catch rate while the red line is the Delta model predicted catch rate including year as a continuous independent variable.

Table S1. The most parsimonious logistic regression (zero model) and log-normal generalized linear models (positive model) for juvenile and adult dusky kob (*Argyrosomus coronus*), juvenile and adult leervis (*Lichia amia*) and shad (*Pomatomus saltatrix*). All reported covariates are statistically significant ($P < 0.05$).