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Assessment of the likely sensitivity to climate change for the key marine species in the southern Benguela system

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Climate change is altering many environmental parameters of coastal waters and open oceans, leading to substantial present-day and projected changes in the distribution, abundance and phenology of marine species. Attempts to assess how each species might respond to climate change can be data-, resource- and time-intensive. Moreover, in many regions of the world, including South Africa, species may be of vital socioeconomic or ecological importance though critical gaps may exist in our basic biological or ecological knowledge of the species. Here, we adapt and apply a trait-based sensitivity assessment for the key marine species in the southern Benguela system to estimate their potential relative sensitivity to the impacts of climate change. For our analysis, 40 priority species were selected based on their socioeconomic, ecological and/or recreational importance in the system. An extensive literature review and consultation with experts was undertaken concerning each species to gather information on their life history, habitat use and potential stressors. Fourteen attributes were used to estimate the selected species' sensitivity and capacity to respond to climate change. A score ranging from low to high sensitivity was given for each attribute, based on the available information. Similarly, a score was assigned to the type and quality of information used to score each particular attribute, allowing an assessment of data-quality inputs for each species. The analysis identified the white steenbras *Lithognathus lithognathus*, soupfin shark *Galeorhinus galeus*, St Joseph *Callorhynchus capensis* and abalone *Haliotis midae* as potentially the most sensitive species to climate-change impacts in the southern Benguela system. There were data gaps for larval dispersal and settlement and metamorphosis cues for most of the evaluated species. Our results can be used by resource managers to determine the type of monitoring, intervention and planning that may be required to best respond to climate change, given the limited resources and significant knowledge gaps in many cases.

Keywords: data-poor assessment, eastern boundary upwelling system, ecological assessment, macroecology, marine fisheries, phenology, species traits, South Africa

Online supplementary information: Species assessment profiles of the 40 selected species from the southern Benguela system, including detailed information and literature references for the abundance, distribution and phenology attributes, are available at <https://doi.org/10.2989/1814232X.2018.1512526>

Introduction

Climate change is a complicated and multi-faceted driver of anthropogenic change affecting marine ecosystems. Its effects interact with other stressors such as fishing and pollution (Halpern et al. 2015) and affect the capacity of a species to respond to these other pressures (e.g. Ling et al. 2009; Perry et al. 2010; Poloczanska et al. 2016). The effects of climate change are already evident in marine ecosystems, and include increases in ocean temperatures and changes in wind speed and direction, ocean chemistry, and direction and strength of currents (Pörtner et al. 2014). For instance, mean sea surface temperatures

have increased at an average decadal rate of more than 0.1 °C over the last 40 years (Hansen et al. 2006; Pörtner et al. 2014). A wide range of effects on marine organisms, including changes in structure and phenology of planktonic communities (Edwards and Richardson 2004; Sommer and Lengfellner 2008; Morán et al. 2010), and in reproductive cycles, distribution, movement and migration of marine animals and plants (Poloczanska et al. 2013; Burrows et al. 2014; Poloczanska et al. 2016) have been recorded as a result of warming sea temperatures. Local or regional declines in biomass as species

undertake climate-driven spatial shifts in distribution are already having consequences for economic development, food security and livelihoods (Barange et al. 2011, 2014; Pecl et al. 2017). An understanding of the likely current and predicted effects of climate change are thus necessary to afford the best opportunity to adapt to these future changes, to maximise any opportunities and minimise any negative consequences (Hobday et al. 2016). However, studies evaluating species' vulnerability to climate change are usually costly, being data- and resource-intensive, and thus are still lacking in many regions of the world. Rapid assessments that allow us to determine what species are likely to be most sensitive will help data-limited but resource-dependent communities and industries to adapt, as well as to identify priority species for research.

The likely response of marine species to climate change can be predicted to some extent based on their behaviour, habitat usage and life-history traits (e.g. Pecl et al. 2014; Potts et al. 2014; Pacifici et al. 2015; Sunday et al. 2015). Several approaches have been used to estimate the vulnerability of species to climate change, including correlative, mechanistic, trait-based and combined approaches (Pacifici et al. 2015). Correlative and mechanistic approaches require detailed species-specific information on distribution and behaviour of individuals, which is derived from laboratory and field studies (Pacifici et al. 2015). These approaches are data-intensive and may require considerable modelling expertise, which in many cases makes them more difficult to implement. In contrast, trait-based approaches can be undertaken for many species concurrently and are more rapid to implement than other approaches because they use existing information on species' biology as well as expert opinion to predict vulnerability to climate change (e.g. Hobday et al. 2011; Pecl et al. 2014).

In South Africa, the implementation of assessments such as trait-based approaches provides a means to estimate the sensitivity of important species to climate change, which could provide valuable information for adaptation plans for action. This is important because species-specific information on optimal thermal and pH ranges is lacking for most marine species, yet changes in environmental drivers have been observed in recent decades and are forecast to continue. For instance, a warming trend on the east coast of South Africa and cooling trends on the west and south coasts have been recorded in the last 20–30 years (Rouault et al. 2010). Changes in upwelling intensity have also been observed—specifically, a significant increase in upwelling on the Agulhas Bank (Lamont et al. 2017). Rainfall patterns in South Africa are also predicted to be affected by climate change (Lumsden et al. 2009; du Plessis and Schloms 2017), altering the frequency, magnitude and timing of freshwater delivery to estuaries (James et al. 2013). Like many regions of the world (e.g. Sundby and Nakken 2008; Bates et al. 2013; Poloczanska et al. 2016; Pecl et al. 2017), these changes in environmental drivers have resulted in distributional shifts for many species. In South Africa, this has included seaweeds (e.g. *Ecklonia maxima*), west coast rock lobster *Jasus lalandii*, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* over the last two to three decades (Cockcroft et al. 2008; Crawford et al. 2008; Bolton et al. 2012), with strong ecological and

economic repercussions for the associated industry sectors.

This study estimates the likely sensitivity to climate change of important species in the southern Benguela system using a trait-based approach accounting for abundance, distribution and phenology attributes. The overall relative sensitivity of a species was estimated using two different methods of integrating the data, as well as a leave-one-out sensitivity analysis to address the influence of any one attribute on the sensitivity score. This study aimed to: (i) identify species that are likely to have a higher sensitivity to climate change; (ii) identify critical knowledge gaps for key species in the southern Benguela system; and (iii) highlight research priorities.

Materials and methods

The southern Benguela upwelling system constitutes the southern portion of the Benguela upwelling system, one of the four major eastern boundary upwelling systems in the world. The southern Benguela upwelling system is bounded to the east by the Agulhas Bank, which is characterised by tropical and oligotrophic waters. For the purpose of this study, the southern Benguela ecosystem extends from the political border with Namibia at the Orange River Mouth (29° S) in the northwest, to the city of East London (28° E), South Africa, in the southeast (Shannon et al. 2003), thus including the west coast of South Africa, which is influenced by the southern Benguela upwelling system, and the Agulhas Bank off the south coast.

Sensitivity assessment

A three-step method was used in this study, following the rapid sensitivity assessment methodology developed by Pecl et al. (2014), to evaluate the likely relative sensitivity of key marine species of the southern Benguela system to potential climate change impacts. The steps are described in order in the sections below.

Initial ranking of species

First, species from the southern Benguela were selected based on their economic (fisheries targets), ecological (e.g. endemic and threatened species), and recreational importance through a consultative process. A list of potential species was circulated to local experts to ask for their feedback in prioritising species to be included in our assessment following the above-mentioned criteria. Based on the opinion of local experts and three of the authors of this manuscript, 40 species were selected for our analysis.

Species profiles

Extensive literature reviews were conducted to collate relevant information for all 40 selected species. The reviews focused on the description of life stages, information on distribution and abundance, the influence of environmental variables on spawning and growth, and the habitat use of each species. Literature reviews also identified potential stressors (e.g. overfishing, pollution, and reductions in freshwater inflow to estuaries) for all selected species. The data collected from the literature review, combined with expert opinion, were used to construct profiles for each species (see template in Table 1).

Ecological assessment

The ecological sensitivity of a species was assessed based on their life-history traits. The sensitivity assessment consisted of 14 attributes accounting for characteristics that influence a species' abundance, distribution and phenology, following Pecl et al. (2014) (Table 1). Six attributes were included in the abundance category by considering information on fecundity, recruitment, average age at maturity, stock status, additional stressors, and whether the species is a generalist or a specialist in terms of food or habitat.

All these attributes in combination enabled the estimation of how resilient a species would likely be to climate-driven changes. For instance, species with high fecundity are, in general, expected to be more resilient because their greater number of offspring increases the likelihood of sufficient survival and recruitment to enable the population to withstand changes in the environment (e.g. Denney et al. 2002; Dulvy et al. 2003). In contrast, a species with sporadic recruitment, high age at maturity and an overexploited population is expected to have a lower capacity to

Table 1: Species assessment profile template, including abundance, distribution and phenology categories, as well as their attributes and criteria

Attribute category and description	Sensitivity category			
	Low sensitivity (score 1); high capacity to respond	Medium sensitivity (score 2)	High sensitivity (score 3); low capacity to respond	
Abundance	Fecundity: egg production	>20 000 eggs per year	100–20 000 eggs per year	<100 eggs per year
	Recruitment period: successful recruitment event that sustains the abundance of the resource	Consistent recruitment events every 1–2 years	Occasional and variable recruitment period	Highly episodic recruitment event
	Average age at maturity	≤2 years	2–10 years	>10 years
	Status of spawner biomass or stock	Robust	Uncertain or vulnerable	Threatened or depleted
	Additional stressors	Stock is experiencing no known stress other than fishing, or only one other known minor stressor	Stock is experiencing moderate stress other than fishing; stock is experiencing no more than three known stressors	Stock is experiencing high stress other than fishing; stock is experiencing four or more known stressors
	Generalist vs specialist: food and habitat	Reliance on neither habitat nor prey	Reliance on either habitat or prey	Reliance on both habitat and prey
Distribution	Capacity for larval dispersal or larval duration: hatching to settlement (benthic species); hatching to yolk-sac re-adsorption (pelagic species)	>2 months	2–8 weeks	<2 weeks or no larval stage
	Capacity for adult/juvenile movements: lifetime range post-larval stage	>1 000 km	10–1 000 km	<10 km
	Physiological tolerance: latitudinal coverage of adult species as a proxy for environmental tolerance	>20° latitude	10–20° latitude	<10° latitude
	Spatial availability of unoccupied habitat for most-critical life stage: ability to shift distributional range	Substantial unoccupied habitat; >6° latitude or longitude	Limited unoccupied habitat; 2–6° latitude or longitude	No unoccupied habitat; 0–2° latitude or longitude
Phenology	Environmental variable as a phenological cue for spawning or breeding: cues include salinity, temperature, currents and freshwater flows	No apparent correlation of spawning with environmental variable	Weak correlation of spawning with environmental variable	Strong correlation of spawning with environmental variable
	Environmental variable as a phenological cue for settlement or metamorphosis	No apparent correlation with environmental variable	Weak correlation with environmental variable	Strong correlation with environmental variable
	Temporal mismatches of life-cycle events: duration of spawning, breeding or moulting season	Continuous duration; >4 months	Wide duration; 2–4 months	Brief duration; <2 months
	Migration (seasonal or spawning)	No migration	Migration is common for some of the population	Migration is common for the whole population

respond to the effects of climate change since its resilience will be affected by the stress it is already experiencing, combined with a low growth rate and population fecundity (Dulvy et al. 2003; Perry et al. 2010).

Four attributes were used to estimate a species' sensitivity to possible changes in distribution driven by climate change. Information on adult/juvenile movements and the potential 'room' for a species to shift further poleward or eastward (i.e. currently unoccupied habitat within a species' potential distribution) were used as a proxy to determine whether a species could likely distributionally shift given its suggested environmental tolerance, which is inferred from a species' latitudinal coverage. For example, if a species has a wide latitudinal coverage (e.g. more than 20°), then it can be assumed that it has a broader physiological tolerance and will be better able to withstand greater environmental variability than a species with a narrow latitudinal coverage (e.g. less than 10°).

The sensitivity of species to changes in phenology, the seasonal life-cycle events, and the influence of environmental variability on the timing of these events was assessed using four attributes. Specifically, the influence of environmental variables as a cue for spawning and settlement, and the temporal duration of spawning or breeding, were used as proxies to infer how strong the influence of environmental variables is on the spawning, settlement or breeding of a species. It is expected that the stronger the relationship between environmental variables and a species' phenology, the higher the sensitivity of a species to climate-driven changes. A species with a longer spawning duration (e.g. more than four months in one year) yet with no apparent correlation between spawning and environmental variables will likely be less sensitive to environmental changes.

To estimate the sensitivity of a species to climate change, each attribute for each species was given a score of 1 (low sensitivity) to 3 (high sensitivity) based on the available information (Table 1). Each attribute was scored according to the information obtained from the literature review (i.e. peer-reviewed publications, unpublished reports and theses) and expert opinion. Detailed information and the references used to score the attributes for the 40 species are listed in the online Supplementary Information. Eleven experts participated in this assessment: three experts for linefishes and estuarine species, one for demersal fishes, two for pelagic fishes, one for sharks, and four for invertebrate species. For taxa such as the seaweeds *Ecklonia maxima*, *Laminaria pallida* and others, brown mussel *Perna perna*, and two tuna species, two of the authors reviewed the information gathered on these species to ensure consistency in the assessment. The scoring system used here is particularly useful when information is limited, as is the case for several species in the southern Benguela, because the method is easily understood and can be readily applied by a wide variety of experts (Pecl et al. 2014).

Species sensitivity

Overall species sensitivity was determined using the two methods described in Pecl et al. (2014) and Hare et al. (2016). Relative overall sensitivity was determined using the individual scores from the 14 attributes for each species. Using these scores, species were allocated to one of four

levels of relative sensitivity to the likely effects of climate change (low, medium-low, medium-high and high). First, using the 'sum of averages' method (Pecl et al. 2014), scores of the attributes in each category of abundance, distribution and phenology were averaged, yielding a range of 1 to 3. Next, the average scores for each category were added to yield an overall sensitivity score with a possible range of 3 to 9. This process was repeated for all the selected species. If a species had a score of ≥ 4.5 , then it was assigned to a medium-low sensitivity level, whereas if it scored ≥ 6 and < 7.5 it was considered to have a medium-high sensitivity (Table 2).

The second method used a set of 'logic rules' (modified from Hare et al. 2016) to estimate the overall sensitivity of a species based on the total number of attributes that were scored as low, medium or high sensitivity for each species. For instance, if a species had 5 or more attributes that scored at a high sensitivity, then the overall relative sensitivity of this species was considered high (Table 2).

Finally, the results of these sensitivity analyses were compared to determine how consistent the estimation of overall relative sensitivity was between the two methods. To understand the influence of individual attributes on the estimation of species sensitivity, a leave-one-out sensitivity analysis was conducted for both methods (sum of the averages and logic rule). Individual attributes were systematically excluded one at a time from the sensitivity calculations to determine whether the sensitivity of a species changed when excluding a specific attribute. Sensitivity scores are presented as the mean \pm SD; these values were calculated from the set of results obtained from the leave-one-out sensitivity analysis and therefore provide a measure of the uncertainty in the estimates. The confidence of the data used to determine sensitivity was scored using a data-quality scoring system ranging from 0 to 3, with a score of 0 indicating that no data were available to determine an attribute, and a score of 3 indicating that the data used were optimal (i.e. that recent data were available for the particular species under consideration and from the specific regions where the assessment took place) (Table 3).

Results

A total of 40 species were selected by experts as priority species to be included in this study (Table 4), and included a range of trophic levels, from planktivores to predators. Several species included in our assessment are endemic to southern Africa (e.g. white steenbras *Lithognathus lithognathus*, black *Cymatoceps nasutus* and white musselcracker *Sparodon durbanensis*), while others have a wider distributional range (e.g. Cape horse mackerel *Trachurus capensis*, and anchovy). Some of the species found to be most sensitive to climate change are also important fisheries targets.

Rank sensitivity of species

Abundance

Species sensitivity regarding abundance ranged from low to medium for all species. The majority (34) of the species had an abundance score less than 2, suggesting that their sensitivity to climate change in this regard was relatively low

Table 2: Logic rules and average scores used to allocate species to an overall sensitivity designation, based on the sensitivity scores of each of the 14 attributes

Overall sensitivity	Logic rule	Average scores
High	5 or more attributes score 'high'	≥7.5 to ≤9.0
Medium-high	4 attributes score 'high,' and 3 or more score 'medium'	≥6.0 to <7.5
Medium-low	2 or 3 attributes score 'high,' and 3 or more score 'medium'	≥4.5 to <6.0
Low	4 or less attributes score 'medium' or 'high'	≥3.0 to <4.5

Table 3: Guidelines for data-quality scoring of each species for each attribute under the three attribute categories. Adapted from Hare et al. (2016)

Data-quality score	Description
3	Adequate Data – The score is based on data that have been observed, modeled or empirically measured for the species in question and come from a reputable source. The parameter (e.g. age at maturity or biomass) is unlikely to have changed since the assessment.
2	Limited Data – The score is based on data that have a higher degree of uncertainty. The data used to score the attribute may be based on related or similar species or come from outside the study area, or the reliability of the source may be limited. The parameter may have changed since assessment.
1	Expert Judgment – The attribute score reflects the expert judgment of the reviewer and is based on their general knowledge of the species, or other related species, and the species' relative role in the ecosystem.
0	No Data – No information on which to base an attribute score. Very little is known about the species or related species and there is no basis for forming an expert opinion.

(Figure 1a). Only six species had a sensitivity score of ≥2 (medium sensitivity), with the highest score for abundance being 2.17. In terms of abundance, Cape horse mackerel, anchovy, chub mackerel *Scomber japonicus*, gurnard *Chelidonichthys capensis*, the hakes *Merluccius paradoxus* and *M. capensis*, seaweeds, and squid *Loligo reynaudii* were classified as the least-sensitive species, whereas soupfin shark *Galeorhinus galeus*, spotted gully shark *Triakis megalopterus*, white stumpnose *Rhabdosargus globiceps* and white steenbras were the most sensitive. Fishing was the main stressor experienced by most species (31); however, species such as abalone *Haliotis midae*, west coast rock lobster, and estuarine breeding species experienced stressors additional to fishing, such as habitat loss, illegal fishing and pollution.

The average data-quality score for the abundance attributes ranged from 1.8 to 3, indicating that the data used to determine the abundance scores were mostly derived from studies on similar species or from actual information for a given species in our general region of interest (Figure 2). Brown mussel *Perna perna* and snoek *Thyrsites atun* had the lowest data-quality scores for the abundance category because of the lack of data for some attributes.

Distribution

Sensitivity in terms of the distribution category ranged from medium to high. The distribution scores of 30 species were ≥2, with the highest distribution score of 3 occurring for abalone, suggesting that the distributions of most species in the southern Benguela have potentially medium to high relative sensitivity to climate change (Figure 1b). Shallow-water hake *Merluccius capensis*, smoothhound *Mustelus mustelus* and soupfin shark were ranked as less-sensitive species, whereas distribution scores for red roman

Chrysoblephus laticeps, the sole *Austroglossus pectoralis* and abalone were high, indicating that their distributions are more likely to be negatively affected as a result of climate change as compared with the lower-ranking species.

The average data-quality score for the distribution attributes ranged from 2.3 to 3 (Figure 2), again suggesting high confidence in the sources used to determine these scores. One gap in information among the distribution attributes was a species' capacity for larval dispersal, with information available for only 30 species.

Phenology

Sensitivity scores ranged from low to high, indicating a broad range of potential sensitivity among the selected species in this category. Phenology scores for 26 species were ≥2, with a maximum score of 2.67, indicating a medium-to-high relative sensitivity to climate change for most species (Figure 1c). Panga *Pterogymnus laniarius* had the lowest sensitivity among species, whereas west coast rock lobster, white steenbras and soupfin shark were ranked as the most-sensitive species in terms of phenology. This suggests that the timing of these species' life cycles is likely to be affected in response to climate change.

Data-quality scores ranged from 1.8 to 3, with sole having the lowest data-quality score (Figure 2). Information on environmental variables as phenological cues for settlement or metamorphosis was available for only 13 species; overall, this was the attribute with the least available information for all species.

Overall sensitivity

Using the sum of the averages for each category, overall sensitivity scores for the 40 species ranged from 4.67 to 7.5 (Figures 1 and 3), indicating that most species are

Table 4: The 40 species included in the southern Benguela sensitivity assessment

Group	Common name	Scientific name
Benthic invertebrate	Abalone	<i>Haliotis midae</i>
Pelagic fish	Albacore	<i>Thunnus alalunga</i>
Pelagic fish	Anchovy	<i>Engraulis encrasicolus</i>
Linefish	Black musselcracker	<i>Cymatoceps nasutus</i>
Benthic invertebrate	Brown mussel	<i>Perna perna</i>
Demersal fish	Cape horse mackerel	<i>Trachurus capensis</i>
Linefish	Cape stumpnose	<i>Rhabdosargus holubi</i>
Linefish	Carpenter	<i>Argyrozona argyrozona</i>
Pelagic fish	Chub mackerel	<i>Scomber japonicus</i>
Demersal fish	Deep-water hake	<i>Merluccius paradoxus</i>
Estuarine-dependent fish	Dusky kob	<i>Argyrosomus japonicus</i>
Linefish	Galjoen	<i>Dichistius capensis</i>
Linefish	Geelbek	<i>Atractoscion aequidens</i>
Demersal fish	Gurnard	<i>Chelidonichthys capensis</i>
Estuarine fish	Harder	<i>Liza richardsonii</i>
Demersal fish	Kingklip	<i>Genypterus capensis</i>
Demersal fish	Monkfish	<i>Lophius vomerinus</i>
Demersal fish	Panga	<i>Pterogymnus lanarius</i>
Linefish	Red roman	<i>Chrysoblephus laticeps</i>
Linefish	Red stumpnose	<i>Chrysoblephus gibbiceps</i>
Pelagic fish	Sardine	<i>Sardinops sagax</i>
Plants/algae	Seaweeds	<i>Ecklonia maxima</i> , <i>Laminaria pallida</i> , others
Demersal fish	Shallow-water hake	<i>Merluccius capensis</i>
Linefish	Silver kob/kabeljou	<i>Argyrosomus inodorus</i>
Sharks and rays	Smoothhound shark	<i>Mustelus mustelus</i>
Linefish	Snoek	<i>Thyrsites atun</i>
Demersal fish	Sole	<i>Austroglossus pectoralis</i>
Sharks and rays	Soupin shark	<i>Galeorhinus galeus</i>
Mobile invertebrate	South coast rock lobster	<i>Palinurus gilchristii</i>
Estuarine-dependent fish	Spotted grunter	<i>Pomadasys commersonnii</i>
Sharks and rays	Spotted gully shark	<i>Triakis megalopterus</i>
Mobile invertebrate	Squid/chokka	<i>Loligo reynaudii</i>
Sharks and rays	St Joseph	<i>Callorhynchus capensis</i>
Mobile invertebrate	West coast rock lobster	<i>Jasus lalandii</i>
Linefish	West coast steenbras	<i>Lithognathus aureti</i>
Linefish	White musselcracker	<i>Sparodon durbanensis</i>
Estuarine-dependent fish	White steenbras	<i>Lithognathus lithognathus</i>
Linefish	White stumpnose	<i>Rhabdosargus globiceps</i>
Linefish	Yellowtail	<i>Seriola lalandi</i>
Pelagic fish	Yellowfin tuna	<i>Thunnus albacares</i>

likely to have medium relative sensitivity to the effects of climate change. Cape horse mackerel, shallow-water hake and sardine scored as having lower sensitivity to climate change than the other species; the latter two species also scored a low sensitivity in the abundance and distribution categories. White steenbras had the highest relative sensitivity score among all species and it was among the most-sensitive species in all three categories. Fourteen species were assigned to a medium-high sensitivity level (scores of ≥ 6.0 and < 7.5); in order of sensitivity these were: black musselcracker, west coast steenbras *Lithognathus aureti*, galjoen *Dichistius capensis*, kingklip *Genypterus capensis*, dusky kob *Argyrosomus japonicus*, spotted gully shark, white musselcracker, red roman, spotted grunter *Pomadasys commersonnii*, west coast rock lobster, white stumpnose, soupin shark, abalone and St Joseph *Callorhynchus capensis*. Most species scoring a medium-high or high sensitivity to climate change also have a threatened or depleted stock status. Similarly, several of these

species (e.g. black musselcracker, red roman, west coast steenbras, white musselcracker and white stumpnose) are endemic to southern Africa. Our results suggest that these species likely have a low capacity to respond to effects of climate change.

When using a logic rule to determine allocation to a sensitivity category, the results were mostly consistent with those when using the sum of averages in the final sensitivity designation (Figure 4). The sensitivity of Cape horse mackerel and sardine to the effects of climate change was also estimated as low, while a relatively higher sensitivity to climate change was estimated for abalone, soupin shark and white steenbras. Black musselcracker, brown mussel, St Joseph and west coast rock lobster were assigned to the medium-high sensitivity level; these species showed characteristics such as a threatened stock status, low fecundity, high age at maturity or a strong correlation with an environmental variable. All other species scored a medium-low sensitivity.

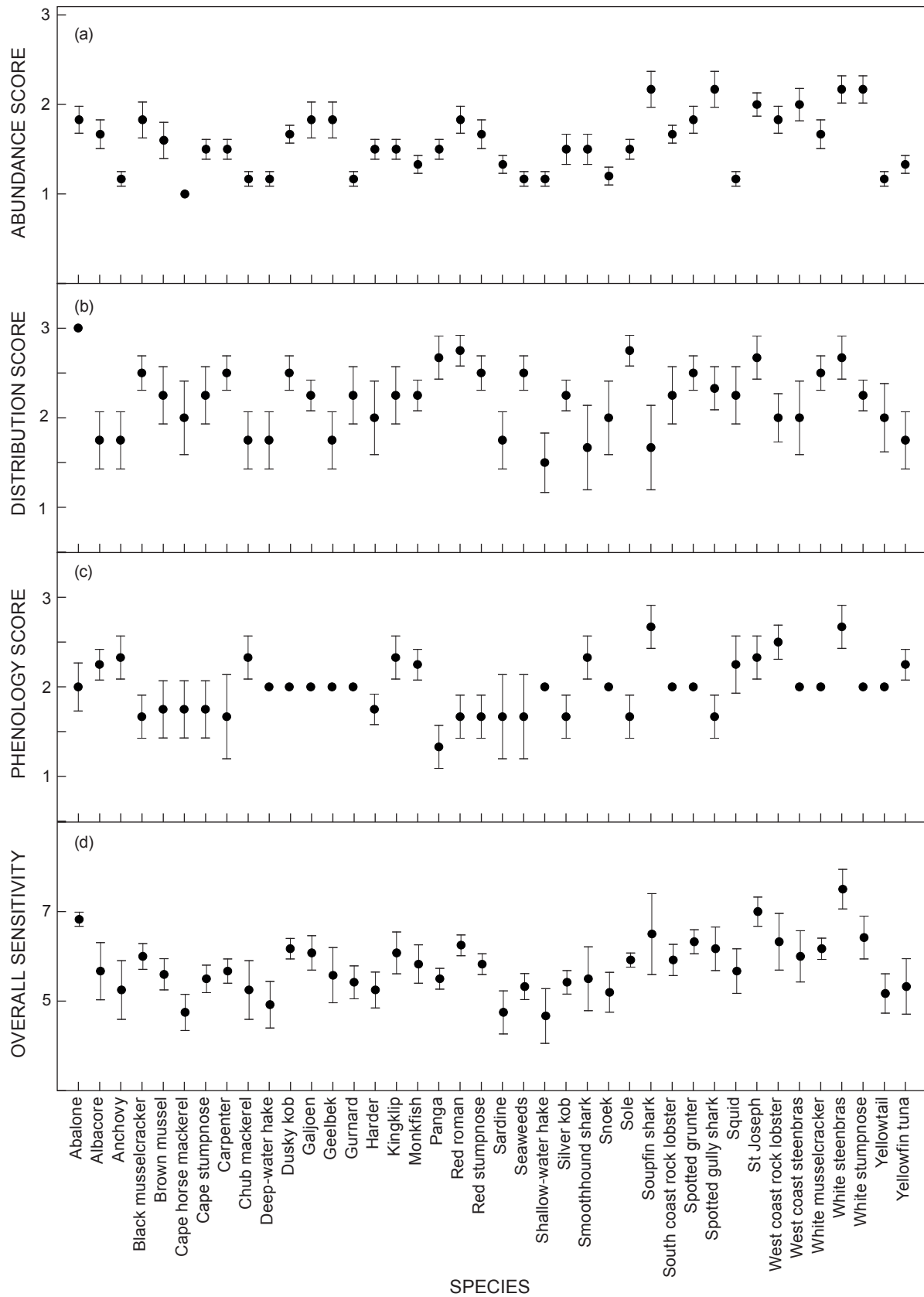


Figure 1: Scores (mean ± SD) of (a) abundance, (b) distribution, and (c) phenology attributes, as well as (d) overall sensitivity for the 40 analysed species from the southern Benguela system. The mean and SD were calculated from the set of results obtained from the leave-one-out sensitivity assessment

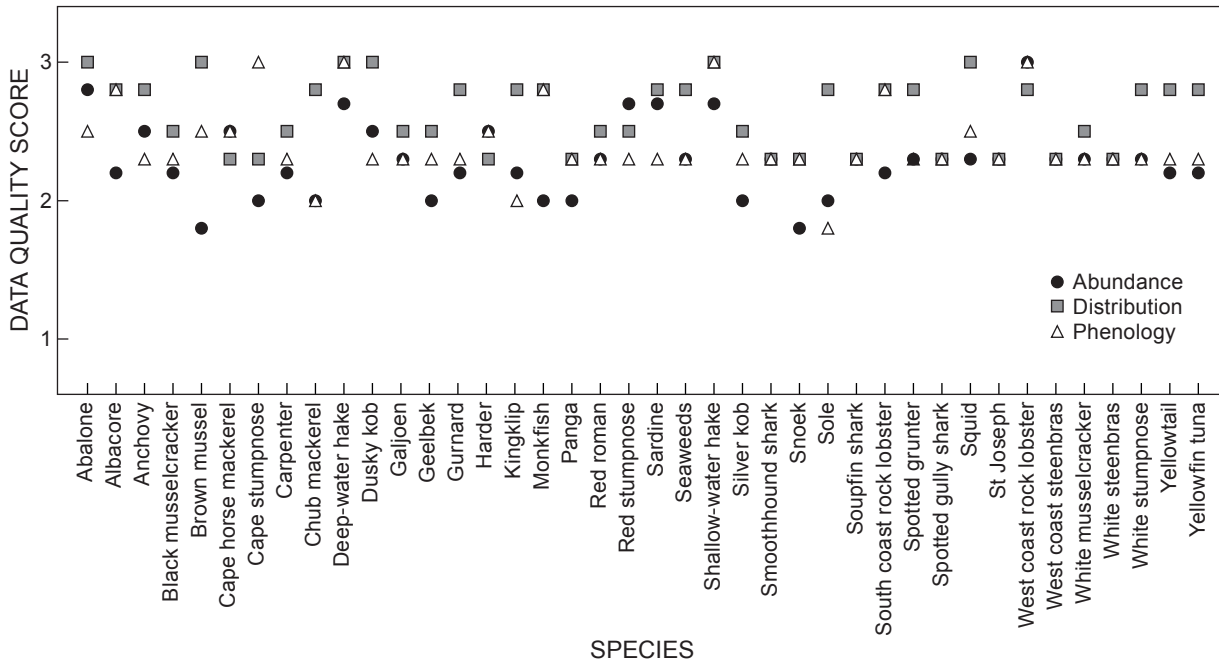


Figure 2: Data-quality scores for the abundance, distribution and phenology categories for the 40 analysed species from the southern Benguela system

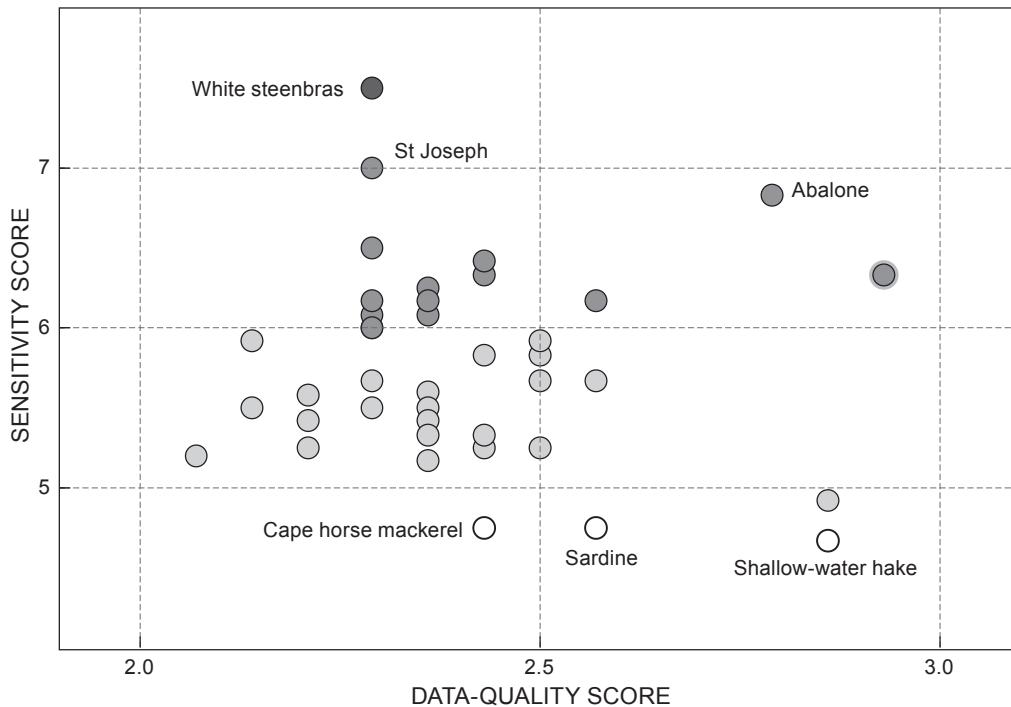


Figure 3: Overall sensitivity and data-quality scores for 40 species from the southern Benguela system, using the sum of averages method of data integration. The species with the lowest and highest sensitivity are named

Sensitivity analysis

The leave-one-out sensitivity analysis indicated that removal of abundance attributes (such as fecundity) and additional stressors resulted in an increase in the total

number of species with a medium sensitivity, to 11 and 10 species, respectively, as compared with a total of 6 species when considering the full set of attributes. Abalone, black musselcracker, galjoen, geelbek *Atractoscion aequidens*,

SENSITIVITY SCORE	High	Abalone White steenbras	Soupin shark	
	Medium-high	Black musselcracker Brown mussel	St Joseph West coast rock lobster	
	Medium-low	Snoek Panga Sole Chub mackerel Geelbek Silver kob Yellowfin tuna Carpenter Kingklip Smoothhound shark Spotted gully shark West coast steenbras	Cape stumpnose Galjoen Gurnard Red roman White musselcracker Yellowtail Spotted grunter White stumpnose Harder Monkfish Seaweeds	Albacore Anchovy Red stumpnose South coast rock lobster Dusky kob Squid Deep-water hake Shallow-water hake
	Low		Cape horse mackerel	Sardine
		Low	Medium	High
		DATA-QUALITY SCORE		

Figure 4: Overall sensitivity and data-quality designation using a logic rule for the 40 key species in the southern Benguela system. Bold font indicates species endemic to South Africa

red roman, spotted grunter and west coast rock lobster were among those recorded as having a medium sensitivity with the leave-one-out sensitivity analysis.

Marked changes in the average score for distribution were observed with the removal of particular distribution attributes in the sensitivity analysis. Removal of the attributes for capacity for adult/juvenile movement and physiological tolerance changed the scores of 9 and 8 species, respectively, towards higher sensitivity values, while the opposite was evident when removing the spatial availability of unoccupied habitat attribute, where 6 species changed scores towards lower sensitivity values. Anchovy, chub mackerel, geelbek, sardine, smoothhound shark and soupfin shark were some of the species that increased their sensitivity from low to medium with the leave-one-out sensitivity analysis. In terms of phenology attributes, removal of the attributes temporal mismatches of life-cycle events and migration led to changes in the sensitivity scores of 9 and 8 species, respectively (e.g. brown mussel, Cape stumpnose *Rhabdosargus holubi*, carpenter *Argyrozona argyrozona* and seaweeds) towards higher sensitivity values.

The removal of individual attributes in the sensitivity analysis did not result in marked changes in the estimation of overall sensitivity designation. The average data-quality score for the 40 species ranged from 2.07 to 2.93 (Figure 3), suggesting that overall there is relatively high confidence in the data sources used to determine sensitivity.

Discussion

Our study found that few species were assigned to the low-sensitivity and high-sensitivity categories, with most species scoring a medium-low or medium-high sensitivity. Previous studies conducted elsewhere on climate sensitivity or vulnerability (e.g. Pecl et al. 2014; Hare et al. 2016) identified several species in each analysis as highly

sensitive, unlike our study where only a few species were identified as among the most sensitive to climate-change effects. It had been of concern that a greater number of species might be ranked as highly sensitive, given the large environmental changes recorded in the southern Benguela system in recent years (Rouault et al. 2010; Mead et al. 2013; Lamont et al. 2017), but this did not appear to be the case. Both methods of integrating the individual attributes to assign an overall relative sensitivity for each species identified white steenbras as most sensitive to the likely effects of climate change. Abalone and soupfin shark were also ranked among the most-sensitive species, using the logic-rule method. All these species have a depleted stock status, highlighting that if the impacts of species sensitivity to climate change are to be minimised, it is necessary to reduce additional stressors that can be controlled, such as fishing effort.

Our study identified that most species scoring a medium-high and high sensitivity to climate change are endemic to southern Africa and/or have a threatened or depleted stock status. Southern Africa has a high level of endemism in coastal fishes as compared with other regions of the world; Turpie et al. (2000) identified a total of 227 coastal fish species endemic to southern Africa, of which 101 are endemic to South African waters. Although marine species generally face fewer constraints to their movements than terrestrial species, climate change may pose a greater threat to species when their dispersal capabilities are limited or suitable habitat is unavailable (Perry et al. 2005). This is especially so for endemic or range-restricted species. Overfishing may also accelerate the decline of species at their distributional edges. Hsieh et al. (2008) found that the distributions of exploited fish populations show a stronger change in response to climatic variations. This may be a consequence of reduced spatial heterogeneity of these

populations caused by fishery-induced age truncation or constriction of their spatial distribution. As such, Rijnsdorp et al. (2009) hypothesise that species with restricted-habitat requirements and those under intense fishing pressure are prone to loss of genetic diversity and may be more vulnerable to climate change than other species.

White steenbras was identified as the species most sensitive to the likely effects of climate change. This species is endemic to southern Africa and is an important component in the catches of recreational and subsistence anglers in the coastal and estuarine waters of the southern and southeastern coastal regions of South Africa (Bennett 1993b; Pradervand and Baird 2002). Long-term catch data indicate major declines in this species—with, for example, the catch rate by recreational shore anglers declining by 90% since the mid-1970s—and the stock has been classified as collapsed (Bennett and Lamberth 2013). A number of aspects of the biology of white steenbras make it vulnerable to population declines. These include estuarine dependence (this species is entirely dependent on estuaries as nursery areas), confinement of juveniles and subadults to the surf zone, large size at maturation, predictable aggregation of mature individuals, distinct spawning seasonality, short recruitment period and inability to access temporarily open/closed estuaries during overwash events (Bennett 1993a; James et al. 2007; Bennett et al. 2012). These population traits make the species particularly vulnerable to estuarine degradation and overfishing, and its reduced abundance, limited distribution and distinct spawning phenology make this species very sensitive to climate change.

Abalone also scored a high sensitivity to the likely effects of climate change. Abalone is a slow-growing species, reaching 50% sexual maturity at a shell width of 35 mm or approximately 30 months of age (Visser-Roux 2011). Its abundance is mostly concentrated in waters of less than 5 m depth. As with white steenbras, abalone is also endemic to South Africa and has a depleted to heavily depleted stock status (DAFF 2016). Heavy illegal fishing combined with a change in habitat associated with the eastward shift of west coast rock lobster (Blamey et al. 2010) resulted in temporary closure of the fishery in 2008, with the increase in abalone poaching mainly associated with a substantial increase in the abalone price during the 1990s (Raemaekers et al. 2011). Data on confiscations and inspection effort, as well as an analysis of international trade data, suggest that poaching has increased substantially since the fishery was reopened in 2010 (De Greef and Raemaekers 2014; DAFF 2016). The decline in abundance, depleted stock status, changes in habitat and limited distribution likely all contribute to a high sensitivity of abalone to climate change.

Southern shark and St Joseph were also found to be highly sensitive to climate change. Southern sharks are known to mature at about 6 years and attain a maximum age in South Africa of at least 33 years (McCord 2005), although this may be an underestimate when compared with Australian records of 77 years (Walker 1997), making them vulnerable to overexploitation, as indicated by a stock collapse off Gansbaai in the 1960s (Davies 1964). St Joseph are directly targeted by the net fishery (da Silva et al. 2015;

DAFF 2016) and are a bycatch of inshore trawlers; the status of the stock is unknown, making predictions of impacts difficult, although they are likely to be vulnerable as trawlers catch juveniles and egg cases, and also disturb the substrate where they feed (Freer and Griffiths 1993). Changes in the inshore region may impact the nursery areas and inshore pupping sites of southern sharks and other cartilaginous fishes, such as the St Joseph, which uses inshore coasts and bays for mating and egg laying (Freer and Griffiths 1993). Specifically, changes in temperature and the frequency of storm events as a result of climate change could affect their populations due to loss of eggs through stranding.

West coast rock lobster and black musselcracker consistently scored a medium-high sensitivity to climate change using both methods to allocate relative sensitivity. West coast rock lobster is a cold-temperate spiny lobster species occurring from Walvis Bay in Namibia to East London in South Africa. This species is heavily depleted (DAFF 2016), and it is both a keystone predator influencing benthic community structure in subtidal reef habitats and the target for a valuable (more than US\$40 million per annum) commercial fishery that provides employment for over 4 200 people in communities along the west coast of South Africa (Cockcroft et al. 2008). Juvenile and adult west coast rock lobster are physiologically well adapted to the highly dynamic nature of an upwelling system and are therefore expected to be resilient to many aspects of predicted climate-change scenarios (Augustyn et al. 2017). However, several life-history traits of this species, such as its long larval phase, make it particularly vulnerable to climate variability and hence climate-change impacts.

The black musselcracker is a large, protogynous spard endemic to South Africa between Cape Agulhas (in the Western Cape Province) and Cape Vidal (in northern KwaZulu-Natal Province). It is slow-growing (Buxton and Clarke 1989), late-maturing (females at approximately 10 years, with sex change to males occurring at approximately 18 years) and long-lived, with a maximum recorded age of 45 years. Juveniles and young adults are considered to be highly resident (Murray 2012) with many of the larger adults returning to waters of the Transkei region (eastern part of the Eastern Cape Province) (Dunlop and Mann 2011; Murray 2012). The resident nature of the species enables it to receive protection within carefully selected closed areas or marine protected areas (MPAs). Black musselcrackers are targeted and caught by rock-and-surf anglers, deep-sea anglers (recreational and commercial) and spearfishers, although the levels of exploitation of the species by the commercial sector declined after it became unprofitable due to stock declines in the late 1980s (Hecht and Buxton 1993). It has been estimated that the stock was at 20% of pristine levels in 2002 (Griffiths and Lamberth 2002). Trends in CPUE, mean size and percentage of catch composition have all declined in areas outside of MPAs, where fishing effort for the species is considerable (Penney et al. 1999; Murray 2012). The life-history characteristics of the species combined with high levels of fishing effort make it extremely vulnerable to overfishing and climate change.

Sardine and Cape horse mackerel were consistently identified as the species least sensitive to climate change

using both data-integration methods. Sardine is one of the main targets of the fishery for small pelagic species, the most important fishery in the country in terms of landings (DAFF 2016). Although sardine was identified among the less-sensitive species to climate change, it experienced an eastward shift in its distribution in South Africa from 2001 (Coetzee et al. 2008). This distributional shift had major consequences for the industry, which was forced to shift its main fishing grounds from the west coast (where the processing factories are located) to the south coast of South Africa (Coetzee et al. 2008). Simulations of future impacts of climate change on the southern Benguela system using an end-to-end model suggested that small pelagic species will be negatively affected by warming sea temperatures (Ortega-Cisneros et al. 2018). Moreover, low biomass of sardine has been recorded for the last few years, with negative implications for the stakeholders of this fishery and likely negative impacts on predators such as seabirds and some fish species.

Cape horse mackerel is a semi-pelagic schooling fish that occurs on the continental shelf off southern Africa, from southern Angola to the east coast of South Africa. The fishery faces many management challenges because of the highly migratory nature of this species and its uncertain stock status. In South Africa, adult Cape horse mackerel are most abundant on the south coast. They are caught in the directed midwater trawl fishery on the south coast and as an incidental bycatch by the deep-sea trawl fishery. Juvenile Cape horse mackerel is also an incidental bycatch of the small-pelagic fishery on the west coast of South Africa (DAFF 2016). Cape horse mackerel is considered a low-cost high-protein food source, which makes it a good candidate for food security, especially for countries in the developing world. The fish is generally frozen whole and exported to many African countries, where it is an affordable source of high-quality protein; there is also a local market for horse mackerel across South Africa, particularly in rural areas.

Shallow-water hake was also ranked among the least-sensitive species. One of two hake species found off South Africa, its distribution ranges from southern Angola to northern KwaZulu-Natal, and from 30 to 500 m depth; by contrast, distribution of the deep-water hake *Merluccius paradoxus* extends to 800 m depth. The distribution of the shallow-water hake favours the south coast of South Africa as the species prefers habitats with a wide shelf. The shallow-water hake undertakes a diel vertical migration, being demersal by day and nektonic by night (Durholtz et al. 2015). The South African deep-sea trawl industry catches both species of hake. Shallow-water hake makes up about 20% of the catch on the west coast, and 70% on the south coast. It is an MSC-certified seafood, and 70% of the catch is exported (to Europe, Australia and the United States), with annual sales exceeding US\$350 million. In fact, the industry's approach of meeting demand on both the domestic and international markets has resulted in impressive product development and market expansion, enabling it to remain lucrative (Durholtz et al. 2015).

The handline jig fishery for squid (also called chokka squid) is fairly small by international standards (6 000–13 000 tonnes caught annually), yet it is the third-most-valuable fishery in South Africa, generating in the

region of US\$30 million annually (Cochrane et al. 2014). It is concentrated off the Eastern Cape coast, providing employment for some 3 000 fishers (DAFF 2012), and is a valuable source of income for this region. Although not recorded as highly sensitive to climate change, this short-lived species fluctuates greatly in biomass and unusually low catches were recorded between 2013 and 2015, which was a concern for both fishers and managers (DAFF 2016). Environmental variability plays a key role in ensuring successful recruitment, with key life-history stages vulnerable to changing conditions (Downey et al. 2010). It is important that the reasons for unusually low catches of squid during the past are fully investigated, and, if changing environmental conditions are found to be at least partly responsible, and are likely to occur more frequently, mitigation measures should be put in place. Being able to predict years when low catches may occur will provide an important early warning to fishers and managers, and allow adaptable measures to be introduced, such as longer closed-fishing seasons to protect spawning squid, and financial subsidies for fishers whose annual income is likely to be substantially less than the norm.

Studies evaluating the sensitivity of marine species to climate change, whether conducted by means of experiments or fieldwork, are mostly lacking in South Africa (cf. Duncan et al. 2017). Thus, comparisons of our findings with empirical studies are limited by data availability. Our results are, however, in agreement with a global analysis of species' sensitivity to climate change which identified endemic species as being among the most vulnerable to climate change (Jones and Cheung 2018). Our results are also in line with a vulnerability assessment of South African fisheries, which reported that linefish fisheries were the most vulnerable to climate change owing to large numbers of people involved in the fisheries as well fishers' poor ability to adjust to climate-change-induced conditions (Hampton et al. 2017). However, that same study also identified small pelagic fishes as among the most-vulnerable species to climate change, whereas in our study sardine ranked among the least-sensitive species. This difference is partially attributed to methodological differences; for example, our study did not take into account the economic value of a fishery or the number of people involved in a fishery in the allocation of a sensitivity score. Important fisheries targets, in particular sardine and squid, scored a low or medium-low sensitivity to climate change in our study, whereas high variabilities in their biomass and catches have been recorded in recent years. In this regard, it might be worth including an attribute accounting for recent observed changes in a species' biomass or distribution when estimating its relative sensitivity to climate change.

The impacts of climate change on marine species and fisheries in South Africa are still largely difficult to detect (Jarre et al. 2015), but significant changes are being observed that are likely related to climate change. In addition to the shifts in distribution mentioned above, small-scale fishers in South Africa report that in recent decades they have experienced rougher sea conditions and changes in prevailing wind directions and strength and in local currents (Sowman and Raemaekers 2018). Using the RCP 8.5 scenario of the Intergovernmental Panel on

Climate Change (IPCC) for predictions, sea surface temperatures in the southern Benguela ecosystem could increase by 3 °C by the year 2099 as compared with the observed temperatures in 1999 (Popova et al. 2016). Similarly, first signs of surface- and bottom-water undersaturation are expected by the end of the century off the west coast of South Africa (Popova et al. 2016). This means that impacts are likely to be more strongly felt in the future and should be taken into account in fisheries management to minimise potential undesirable consequences. Our study found that most of the species assessed that had a medium-high or high sensitivity to climate change were already considered to be threatened or depleted, and therefore would be particularly susceptible to any additional stresses. A priority adaptation for conservation and sustainable use of South Africa's marine species must be to enable those populations that are below desirable limits to recover to more resilient and productive levels. This will require effective implementation of ecosystem-based approaches to all human impacts on the ocean, including effective implementation of an ecosystem approach to fisheries (Cochrane et al. 2004; Paterson and Petersen 2010). Control of illegal, unregulated and unreported (IUU) fishing is a particularly urgent need concerning inshore species, including abalone, west coast rock lobster and a number of linefish species, for which IUU fishing plays an important role in the poor stock status (e.g. Branch and Clark 2006; Brill and Raemaekers 2013; DAFF 2016). For more-resident and less-mobile species, ensuring that the current system of MPAs is functioning effectively within the broader management framework will be important (DAFF 2016). If marked changes in distribution are observed, it may be necessary to adapt the design and placement of reserves to respond to these changes (McLeod et al. 2009).



The trait-based approach used here is a relatively rapid, repeatable and transparent assessment method for estimating the sensitivity of multiple species to climate change. The assessment integrates, synthesises and summarises known information, and highlights data and knowledge gaps, providing a sound basis for prioritisation of further research, or potentially, management interest. However, there are caveats associated with trait-based approaches, including that the vulnerability thresholds associated with each trait are often unknown, the traits are weighted equally (which might not be appropriate), and there is uncertainty associated with the choice of traits. Moreover, as with any analysis combining different scores, the method of data-integration employed can affect the results obtained. To test the robustness of our final sensitivity rankings, we used two different methods of integrating the attribute scores and found a high degree of consistency between the method based on average scores and the method based on the number of high-sensitivity traits.

Our study identified the capacity for larval dispersal and phenological cues for settlement or metamorphosis as the main information gaps for species in the southern Benguela system; this was the case even for species of commercial importance. Information on fecundity was also lacking for many species, and hence the associated scores were mostly assigned based on expert opinion. These information gaps can be considered a research priority and our results should

help focus future attention on species or species groups that are estimated to be most sensitive. Despite the information gaps and uncertainty in the allocation of relative sensitivity, our overall assessment suggests that several species in the southern Benguela system are likely to be affected by climate change. Several of these species are important fisheries targets in South Africa, suggesting that the likely impacts of climate change will also affect the country's economy. Fisheries management authorities in South Africa need to consider these probable future impacts and implement strategies that ensure the long-term sustainability of fisheries resources and ecosystems.

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