



Key predictors of extinction risk in sea breams and porgies (Family: Sparidae)



Mia T. Comerós-Raynal ^{a,b}, Beth A. Polidoro ^{a,c}, Jennifer Broatch ^c, Bruce Q. Mann ^d, Claire Gorman ^a, Colin D. Buxton ^e, Angela M. Goodpaster ^a, Yukio Iwatsuki ^f, Timothy C. MacDonald ^g, David Pollard ^h, Barry Russell ⁱ, Kent E. Carpenter ^{a,*}

^a IUCN Global Species Programme/Biological Sciences, Old Dominion University, Norfolk, VA, USA

^b American Samoa Environmental Protection Agency, Pago Pago, AS 96799, USA

^c New College of Interdisciplinary Arts and Sciences, Arizona State University, Phoenix, AZ, USA

^d Oceanographic Research Institute, PO Box 10712, Marine Parade, Durban 4056, KwaZulu-Natal, South Africa

^e Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, TAS 7001, Australia

^f Department of Marine Biology & Environmental Sciences, University of Miyazaki, 1-1 Gakuen-kibanadai-nishi, Miyazaki 889-2192, Japan

^g Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL 33701, USA

^h Department of Ichthyology, Australian Museum, Sydney, NSW 2010, Australia

ⁱ Museum & Art Gallery of the Northern Territory, Darwin, NT 0810, Australia

ARTICLE INFO

Article history:

Received 2 February 2016

Received in revised form 17 August 2016

Accepted 22 August 2016

Available online xxxx

Keywords:

Extinction risk modeling

Marine fishes

IUCN Red List of Threatened Species

Marine conservation

Random Forest model

ABSTRACT

Identification, understanding and prediction of the factors that drive species to heightened risk of extinction are important goals for conservation, especially since few areas on the planet remain unaffected by human activities. Global extinction risk assessments of an entire family of ecologically complex marine fishes (family: Sparidae), using the International Union for Conservation of Nature Red List process, showed that 8.6% (13 species) of sparids are threatened. Intense fishing pressure and habitat destruction are the main reasons for the observed population declines. A further 7.9% (12 species) are classified as Near Threatened. The majority of the sparids (69.5%) are assessed as Least Concern, and these tended to have smaller body sizes, more widespread distributions, and shorter life spans. The remaining 21 species (13.9%) are listed as Data Deficient. In addition to presenting the first global assessment of sparid extinction risk, a Random Forest model identified correlates of extinction risk in the Sparidae using 33 biological and threat variables. The model correctly classified up to 90% of Red List category placements and showed complex interactions between intrinsic and extrinsic predictors. Larger body size was the most important predictor of extinction risk.

Sparids with greater maximum sizes, ages, and turnover rates are at higher extinction risk. Conversely, lower area of occupancy and depth limit confer elevated risk. This analysis adds to the growing body of predictive extinction risk models in marine fishes and presents an opportunity to identify and mitigate threats affecting similar groups of highly-valued and ecologically important marine fishes.

© 2016 Published by Elsevier Ltd.

1. Introduction

Current extinction rates are 100 to 1000 times higher than background levels in our planet's record (Pimm et al., 2014; Pimm et al., 1995). Extinctions are drastically altering key ecosystem processes, and increasing evidence suggests that species loss will further accelerate changes in ecosystem functioning, possibly causing detrimental impacts in the persistence and sustainability of Earth's biodiversity (Cardinale et al., 2012; Hooper et al., 2012; MacDougall et al., 2013). There have been few recorded extinctions of marine species in recent history compared to extinctions in the terrestrial realm (Dulvy et al.,

2009; Dulvy et al., 2003; Roberts and Hawkins, 1999). The differences in detection of extinction in the marine realm compared to the terrestrial realm can be partly explained by the differences in rates of taxonomic description and conservation assessment (Dulvy et al., 2003; Webb and Mindel, 2015). Marine extinction is attributed mainly to exploitation, followed by habitat loss and degradation, invasive species, climate change, pollution and disease (Dulvy et al., 2009; Dulvy et al., 2003). Uncertainties about the patterns and trends in extinction rates between the marine and terrestrial realms are still prevalent because marine species are considered to possess extinction resistant traits such as high fecundity, widespread distribution ranges, and high dispersal ability (Reynolds et al., 2005a). High fecundity, however, does not reliably predict recovery from overexploitation (Jennings et al., 1998; Kindsvater et al., 2016; Sadovy, 2001), nor is it a good biological correlate in predicting

* Corresponding author.

E-mail address: kcarpent@odu.edu (K.E. Carpenter).

species' vulnerability and sensitivity to fishing (Juan-Jorda et al., 2013). Widespread ranges and high dispersal ability in marine species may also not confer lower risk as originally thought, as most marine species are rare (Connolly et al., 2014; Pimm et al., 2014; Webb and Mindel, 2015). Furthermore, there is little difference in extinction risk between marine and terrestrial systems once taxonomic knowledge and conservation assessment differences are accounted for, with on average between 20% and 25% of species being threatened with extinction, irrespective of realm (Webb and Mindel, 2015). Improved ability to detect and report extinction could lead to better understanding of extinction patterns in marine species and proactive approaches in the prediction of species' vulnerability (Dulvy et al., 2003; Webb and Mindel, 2015).

One of the important goals of marine conservation is to identify drivers of threat and to quantify the interaction of multiple stressors and how this contributes to extinction risk dynamics (Brook et al., 2008; Darling and Côté, 2008). Vulnerability to extinction risk depends on the interaction between intrinsic attributes such as slow growth, large body size, higher longevity, low natural mortality rates, low production biomass (Harnik et al., 2012; Juan-Jorda et al., 2015; Reynolds et al., 2005a; Roberts and Hawkins, 1999) and exposure to external threats such as overexploitation. These factors determine a species' ability to cope with human-induced and environmental stochastic disturbances, as well as its capacity to bounce back from these external perturbations (Cardillo et al., 2008; Cardillo et al., 2005; Reynolds et al., 2005a). The cumulative effects of extinction drivers can potentially lead to complex interactions among stressors (e.g. synergies, antagonisms and additive effects) that could lead to accelerated biodiversity loss and diminished ecosystem functioning (Brook et al., 2008; Darling and Côté, 2008; Halpern and Kappel, 2012).

In the marine realm, correlates and drivers of extinction risk have been identified for marine mammals (Davidson et al., 2012), sharks and rays (Dulvy et al., 2014) and other marine fishes (Juan-Jorda et al., 2013), though there have been relatively few studies that predict risk (Bender et al., 2013; Cheung et al., 2005; Luiz et al., 2016). There are two types of predictive studies: explanatory (within sample prediction) and predictive modeling (beyond sample prediction). This study makes within sample predictions of extinction risk using life history and threat variables from 130 species of highly-valued marine fishes of the family Sparidae, the sea breams, porgies, and picarels (Sanciangco et al., 2016). The results from the International Union for Conservation of Nature (IUCN) Red List extinction risk assessments provide comprehensive information on intrinsic factors such as distribution range, population status, habitat requirements, body size, longevity, reproductive mode, reproductive schedule, and spawning aggregations, as well as on extrinsic threat factors such as exploitation levels, and the extent and rate of habitat destruction. Using this dataset, we utilize conditional inference trees to identify the most important drivers of extinction risk using 33 intrinsic biological and extrinsic threat variables and develop a Random Forest model to predict risk.

The explanatory model applied in this study differs from predictive models that are able to predict beyond the sample dataset using phylogenetic and geographic proximity in mammals (Jetz and Freckleton, 2015), using 23 life history and ecological and threat variables in mammals (Bland et al., 2014), and in sharks and rays using intrinsic life history and threat variables (Dulvy et al., 2014). The Random Forest model and conditional inference trees used in this study provide a robust and efficient system to identify separate intrinsic and extrinsic traits that correlate to a higher risk of extinction in this important group of marine fishes. It is important to note that Random Forest modeling treats all covariates equally (e.g. all intrinsic and extrinsic threats), and cannot account for the more commonly encountered interactions between intrinsic (or biological) traits and extrinsic traits (such as exposure to threat processes). For example, even once fishing mortality is controlled, large bodied commercially exploited marine fishes have been shown to have higher extinction risk (Jennings et al., 1998; Jennings

et al., 1999). Similarly, Juan-Jorda et al. (2015) showed that the combination of F/Fmsy and life history traits, particularly growth rates, better explain risk status and trends than either fishing mortality or biological traits alone. Other intrinsic and extrinsic combinations that have been correlated to elevated extinction risk for birds (Owens and Bennett, 2000) and for freshwater fishes (Reynolds et al., 2005b), are small body size and small distribution range size combined with habitat loss. In addition to discussion of the Random Forest results, we also hypothesize likely combinations of biological traits (intrinsic traits) and external threats (extrinsic threat processes) that could contribute to elevated extinction risk, based on available Sparidae data and comparison with other taxonomic groups. This and other types of either within sample or beyond sample predictive modeling can provide systematic methods to improve conservation prioritization, and to identify and mitigate threats impacting upon other groups of highly valued and ecologically important marine fishes.

2. Materials and methods

2.1. IUCN Red List assessment process and data collection

The Red List assessment process is highly collaborative and draws upon input from scientific experts from around the world. This process is typically completed in a workshop setting. For the 151 species of sea breams, porgies and picarels (Table A1), Red List Assessment workshops were conducted in Taipei, Taiwan, (2009); Lee Stocking Island, Bahamas (2011); and Doha, Qatar (2013). Prior to the workshops, data were compiled on distribution, population status and trends, fisheries catch, abundance, habitat preference, life history characteristics, threats, and current conservation actions for each species chosen for assessment (Comeros-Raynal et al., 2012). IUCN Red List assessments involved a rigorous review process: each species was evaluated at the workshops against five quantitative measures of extinction risk (criteria A–E) and assigned to one of the six Red List Categories (Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT], Least Concern [LC], and Data Deficient [DD]). Subsequent consultation and follow-up with experts and several IUCN internal consistency checks were conducted prior to publication of these assessments on the IUCN Red List of Threatened Species website (<http://www.iucnredlist.org>) to ensure consistency and comprehensive application of this global categorization system (IUCN, 2014).

Listing in one of the Threatened Categories (CR, EN, or VU) was undertaken if a species qualified or exceeded one of the thresholds specific to the category in one or more of Criteria A–E. The five criteria relate to biological processes contributing to increased extinction risk such as declining and small populations, and restricted ranges (Mace et al., 2008). If a species approached thresholds of a threatened category, it was listed as NT. A category of LC was applied to species that did not come close to meeting any of the threatened category thresholds. The DD category was applied when little was known about the threat processes affecting the species. This category is usually assigned to species with insufficient information to adequately apply the criteria, such as taxonomic uncertainty, lack of key life history information, or the inability to quantify threat impacts on the species.

2.2. Predictor variables

During Red List assessment workshops, biological and ecological data for each species were recorded and coded to a number of classification schemes such as habitat type, threat type, level of use and trade, and generation length; these variables have specific IUCN definitions (IUCN, 2001). These classification schemes were developed to ensure consistency in the interpretation and application of Red List information, and also to facilitate systematic implementation and prioritization of conservation actions (Salafsky et al., 2008). A total of 33 intrinsic and extrinsic variables were recorded (Table 1). Sixteen of these are intrinsic

Table 1

Intrinsic and extrinsic variables used in the Random Forest model to predict extinction risk status in the Sparidae. Variables without units indicate coded designations of presence in each habitat, threat, and resource use classification.

Variables	Units	Variable type
Reproductive mode (e.g., gonochorist, hermaphrodite, or unknown)		Intrinsic trait
Upper depth limit	Meters	Intrinsic trait
Lower depth limit	Meters	Intrinsic trait
Mean depth	Meters	Intrinsic trait
Generation length	Years	Intrinsic trait
Maximum size	Centimeters	Intrinsic trait
Longevity	Years	Intrinsic trait
Area of occupancy (AOO)	Km ²	Intrinsic trait
Coral reef habitats		Intrinsic – habitats
Estuarine habitats		Intrinsic – habitats
Macro-algal habitats		Intrinsic – habitats
Seagrass habitats		Intrinsic – habitats
Loose rock/pebble substratum		Intrinsic – habitats
Muddy substratum		Intrinsic – habitats
Rock and rocky reef habitats		Intrinsic – habitats
Sandy substratum		Intrinsic – habitats
Commercial and subsistence importance		Extrinsic – use and trade
Recreational fishing		Extrinsic – use and trade
Habitat degradation from agricultural & forestry effluents		Extrinsic – threats
Habitat modification from industry		Extrinsic – threats
Habitat modification from water abstraction		Extrinsic – threats
Habitat degradation from waste water pollution		Extrinsic – threats
Climate change events – drought		Extrinsic – threats
Direct and indirect harvesting		Extrinsic – threats
Habitat degradation from solid waste		Extrinsic – threats
Climate change events – habitat shifts		Extrinsic – threats
Habitat modification from urbanization		Extrinsic – threats
Habitat degradation from industrial & military effluents		Extrinsic – threats
Habitat modification and degradation from ecosystem alterations		Extrinsic – threats
Habitat modification and degradation from recreational activities		Extrinsic – threats
Climate change events – severe weather		Extrinsic – threats
Climate change events – temperature extremes		Extrinsic – threats
Habitat modification and degradation from tourism		Extrinsic – threats

variables or biological attributes that pertain to life history and ecological traits, and 17 are extrinsic variables or external processes that stem from anthropogenic influence and impacts.

2.3. Species range maps

Species distribution maps were generated using ArcGIS 10.1 (ESRI 2012) by drawing a minimum convex polygon connecting all known and inferred points of occurrence for each species based on primary literature, published reports, and online museum records. To better visualize the distribution patterns of nearshore species, a standardized

basemap cut to a maximum depth of 200 m with a 100 km buffer from the shoreline was used. This standardized species distribution basemap appropriately represents the maximum limit of continental and island shelves of 200 m isobaths (Sanciangco et al., 2013) and the generally shallow, coastal habitats of most of the sparids. The basemap was derived from bathymetric data from the National Geophysical Data Center's (NGDC) ETOPO1 one arc-minute global relief model (Amante and Eakins, 2009). This approach was well suited for global biodiversity analyses of near-shore fishes and improved the accuracy and representation of the occupancy of these species. In addition, this standardized spatial approach refined the known occurrence of these species by excluding unsuitable habitat (e.g. waters deeper than 200 m), which the species are known to inhabit during only a limited portion of their early life history stage (e.g. only as pelagic larvae).

2.4. Spatial analyses

2.4.1. Richness patterns

To understand spatial patterns associated with the conservation status of the sparids, species richness patterns were determined using a geoprocessing script (Carpenter and Springer, 2005; Sanciangco et al., 2013) developed in ArcGIS. This script estimated richness by adding species distributions that overlap in a 10 km by 10 km raster grid. This script assigned a value for each cell that corresponded to the number of overlapping species distributions at the cell location, indicating species concentrations in each cell.

2.5. Statistical analyses of predictors of heightened extinction

Intrinsic and extrinsic variables systematically coded from textual documentation in each species' IUCN Red List account were used to predict the Red List category for the sparids, with the exclusion of Data Deficient (DD) ($n = 21$) species. For the analyses, species listed as CR, EN, and VU were combined as *threatened* (thr , $n = 13$); *Near Threatened* (NT, $n = 12$), and *Least Concern* (LC, $n = 105$) remained the same for a total of 130 species included in the analyses. Note that the methods used in this paper do not require a binomial outcome. The methodologies allow the prediction of multiple categories. The *threatened* category was created because the sparids lack sufficient numbers in those categories. Subsequent applications of the methodology need not reduce the categories. A subset of 90 species (70%) were randomly selected as the initial training dataset to identify the most important intrinsic and extrinsic variables to predict extinction risk category placement. The accuracy in which these variables predicted the risk category (thr , NT, LC) was tested on the remaining 40 species (30%). Random Forest modeling was used to estimate the probability that a species was categorized as threatened (CR, EN, VU), Near Threatened (NT), or Least Concern (LC).

Random Forest is a powerful machine learning tool well suited for analyzing ecological datasets (Cutler et al., 2007), and has been successfully applied to modeling extinction risk in mammals (Bland et al., 2014; Davidson et al., 2009), marine mammals (Davidson et al., 2012), and amphibians (Murray et al., 2011). Random Forests are an ensemble of decision trees (classification or regression trees) generated through recursive partitioning, and used for prediction (Breiman, 2001; Cutler et al., 2007; Strobl et al., 2009b). Random Forest exhibits a number of characteristics that make it suitable for extinction risk prediction, including few assumptions on data distribution, and an ability to impute values for missing variables and to handle different types and large amounts of data (Cutler et al., 2007; Strobl et al., 2009b). Prior to this analysis, we imputed missing data values of the predictor variables using the proximity of the Random Forest (see rfimpute, Liaw and Wiener, 2002).

We used conditional inference trees, a non-parametric class of regression trees to identify the most important variables that drive extinction risk, or in the case of sparids, resilience to threats as the majority are listed as Least Concern. Conditional inference trees are preferred over a Random Forest model for the identification of important variables. The

conditional inference tree method for variable importance is more robust to mixed-type variables inherent in the dataset including continuous and categorical variables. A Random Forest model will arbitrarily put too much importance on a continuous variable over a categorical variable (Strobl et al., 2009a,b); thus, random forests will only be used for prediction in this analysis. The intrinsic and extrinsic explanatory variables found to make the highest contribution to predicting a Red List Category in the training dataset model using the conditional inference trees (see Table 1 for variables and explanatory contribution) were then used in the Random Forest model on the remaining validation dataset. The performance of the final Random Forest model in the test validation dataset (40 species) was measured in terms of the overall proportion of correctly classified species, proportion of correctly classified for each category (true positives-sensitivity), proportion of incorrectly classified species for each category (true negatives-specificity), proportion of threatened species incorrectly classified as Least Concern (false negatives), and proportion of LC and NT species incorrectly classified as threatened (false positive) (Di Marco et al., 2015). We used the *Random Forest* (Liaw and Wiener, 2002) and *party* (Hothorn et al., 2006) packages in R (R Core Team, 2014) for this analysis. To overcome overestimation of the importance of correlated predictor variables, conditional variable importance measure in the *party* package was used to identify the important variables in driving extinction risk. This measure reflects the true impact of each predictor variable through the use of a conditioning grid that was automatically provided by the fitted model (Strobl et al., 2008; Strobl et al., 2009a).

To further investigate and clarify the differences across extinction risk categories, a one-way Analysis of Variance (ANOVA) of the entire dataset (i.e. with the exception of DD species) using four continuous variables identified as important to the training dataset in the Random Forest analysis was conducted in SPSS 22 (IBM Corp., 2013). The Red List categories were the independent variables and the major predictors of extinction risk, including generation length, longevity, AOO, and maximum size, were used as the dependent variables. Maximum size and longevity were log-transformed to meet assumptions of normality and homogeneity of variance. This analysis was conducted to determine significant differences ($p < 0.05$) among Red List categories and within the categories across the four predictors of extinction risk in the Sparidae.

3. Results

Of the 151 globally recognized members of the family Sparidae (Table 2), 8.6% (13 species) were listed in threatened categories, while an additional 12 species (7.9%) were listed as NT. The species in the threatened (CR, EN, VU) and NT categories are characterized by having more restricted geographic range sizes (average AOO of 192, 915 km²), larger body sizes (average 90 cm total length), and are longer-lived (average 28 years) compared to LC species with average AOO of 670, 206 km², average maximum sizes of 48 cm total length, average longevity of 19 years, and median depths of 50 m. The mean depths of threatened species is 62 m while LC species occur in average depths of 75 m.

Two sparids were listed at the highest level of extinction risk (CR) under Criterion A, namely *Chrysoblephus cristiceps* (Dageraad) and *Polysteganus undulosus* (seventy-four Seabream). These South African endemics have experienced population declines in excess of 90% over

three generation lengths (>30 years). Four species were listed as EN under either Criterion A: *Chrysoblephus gibbiceps* (Red Stumpnose Seabream), *Evygnis cardinalis* (Threadfin Porgy), and *Petrus rupestris* (Red Steenbras), or a combination of both Criteria A and B: *Lithognathus lithognathus* (White Steenbras). There were seven species listed as VU: *Acanthopagrus sivicolus*, *A. vagus*, *Cheimerius matsubarae*, *Cymatoceps nasutus*, *Dentex dentex*, *Polysteganus praeorbitalis* and *Rhabdosargus globiceps*. The majority of the species (69.5%) were LC, while the remainder of the species, were categorized as DD (13.9%) because they were either: 1) known only from type specimens, 2) recently described, 3) pending taxonomic revision or validation, or 4) endemic to regions with limited information available. Species-specific documentation of the Sparidae assessments is freely available on the IUCN Red List of Threatened Species database (<http://www.iucnredlist.org>).

3.1. Spatial patterns of species richness and extinction risk

Two centers of sparid species richness occur in temperate regions at the opposite ends of the African continent: off northwestern Africa and in the Mediterranean Sea, and off eastern South Africa (Fig. 1). The region of southern Africa encompassing Namibia, South Africa and Mozambique comprises the highest concentration of threatened (CR, EN, VU) species, with up to eight species per 10 km² grid occurring in the region (Fig. 2). Additionally, 69% (9 species) of those at high extinction risk, were known to only occur in southern Africa (Table A2).

3.2. Major drivers of extinction risk

There were nine key explanatory variables of extinction risk identified by the conditional inference trees used in the final Random Forest model (in decreasing order of importance): maximum size, generation length, longevity, rock and rocky reef habitat, recreational fishing, severe weather events possibly exacerbated in frequency and intensity by climate change, direct and indirect harvesting, area of occupancy, and lower depth limit (Fig. 3). The combination of these variables were used in a Random Forest model to predict the risk category using the validation set. The Random Forest model correctly classified the Red List categories of the sparids with 90% accuracy (overall percent species correctly classified) (Table 3). The model performed well correctly in classifying all of the Least Concern species. However, the model correctly identified the Near Threatened species only 25% of the time, misclassifying them as Least Concern 75% of the time. Similarly, the one threatened species was incorrectly identified as non-threatened. In other words, the Random Forest model was very good at identifying species that were at low risk of extinction, because the majority of species were listed as Least Concern and, with only 130 species included in the analyses, the dataset did not contain enough threatened species to make statistically significant predictions for species to be placed in threatened categories. Due to the lack of threatened species in the sparids, the model was not extended to predict the risk category of the Data Deficient species based on important factors for fear it would inaccurately misclassify threatened species. However, the methodology can be extended to a more diverse species for accurate predictions. For example, species with average maximum sizes of <48 cm total length are likely to be placed in lower risk of extinction categories compared to those with average sizes of >60 cm total length (Fig. 4). Conversely, examination of the traits identified as important in the Random Forest model can be used as an exploratory tool to discover traits which may correlate with a higher risk of extinction, and to identify typical threshold values of low risk (LC), NT, and high risk threatened (VU, EN, CR) categories. For example, the 13 threatened (CR, EN, VU) and 12 NT species possess traits that predispose them to higher vulnerability to extinction, including late maturity, relatively large size, hermaphroditic reproduction, limited distributional ranges, and specialized habitat requirements. The sparid species listed in one of the threatened or NT categories have longer generation lengths (average of 12 years), larger

Table 2
IUCN Red List Categories for all known sparid species.

Critically endangered	2
Endangered	4
Vulnerable	7
Near Threatened	12
Least concern	105
Data deficient	21
Total	151

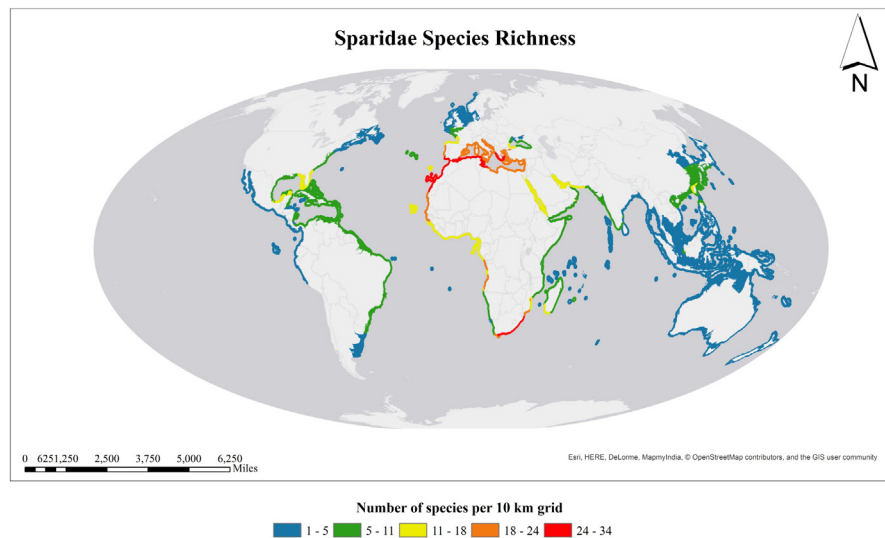


Fig. 1. Patterns of Sparidae species richness per 10 km² grid.

maximum sizes (average 90 cm), are longer-lived (average 28 years), and are found in more restricted geographic range sizes (average AOO of 192,915 km²) compared to Least Concern species that have an average generation length of 10 years, an average maximum size of 48 cm, an average longevity of 19 years, and an average AOO of 670,206 km². It should be noted that the Random Forest methodology for classification is more complex than establishing simple threshold values. The iterative process utilizes thousands of thresholds to yield more accurate predictions than a single process such as discriminant analysis (Liau and Wiener, 2002).

Comparisons of the means of important predictors such as maximum size, generation length, longevity and AOO showed significant differences in two drivers of extinction risk: longevity ($F = 4.9$; $df = 4$; $p = 0.05$) and maximum size ($F = 5.8$; $df = 5$; $p = 0.001$). The results show that there were significant differences in longevity and maximum sizes across the different levels of extinction risk, and within the Red List categories ($p = 0.01$ and $p = 0.001$), respectively. Identification of these threshold values, in combination with threat information, may allow for

classifying Data Deficient species in the absence of any other available data.

4. Discussion

The Sparidae are primarily coastal species inhabiting temperate to tropical waters around the world (Carpenter, 2001). Most sparid species have limited distributional ranges and are endemic or allopatric in warmer temperate regions (Mann, 2013). The pattern of relative richness observed in the Eastern Central Atlantic is unique in that this region is not generally regarded as a diversity hotspot for most other percoid families (Hanel and Tsigenopoulos, 2011). Conversely, the Western Central Pacific, which is considered a diversity hotspot for many other percoid families (Carpenter and Springer, 2005; Gaither and Rocha, 2013), is not a region of major importance in terms of sparid diversity (Hanel and Tsigenopoulos, 2011; Orrell et al., 2002).

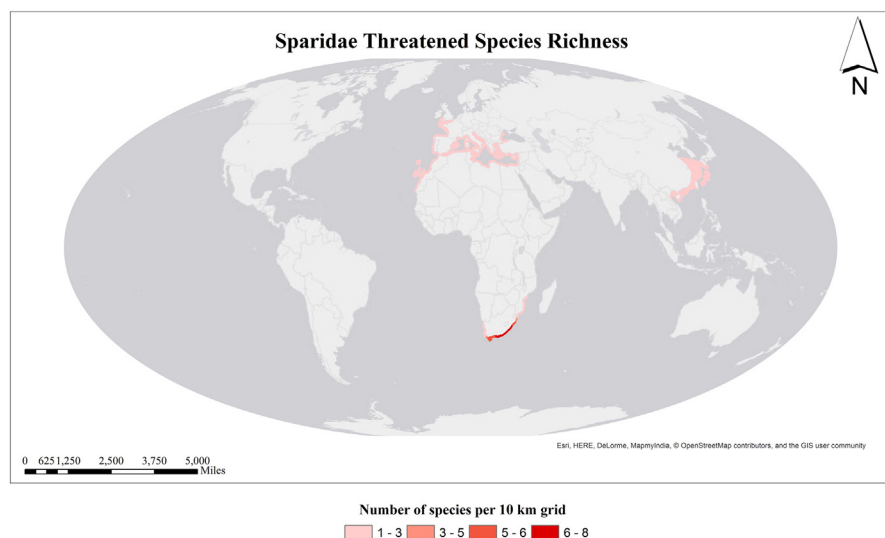


Fig. 2. Concentration of species in elevated extinction risk categories (CR, EN, VU).

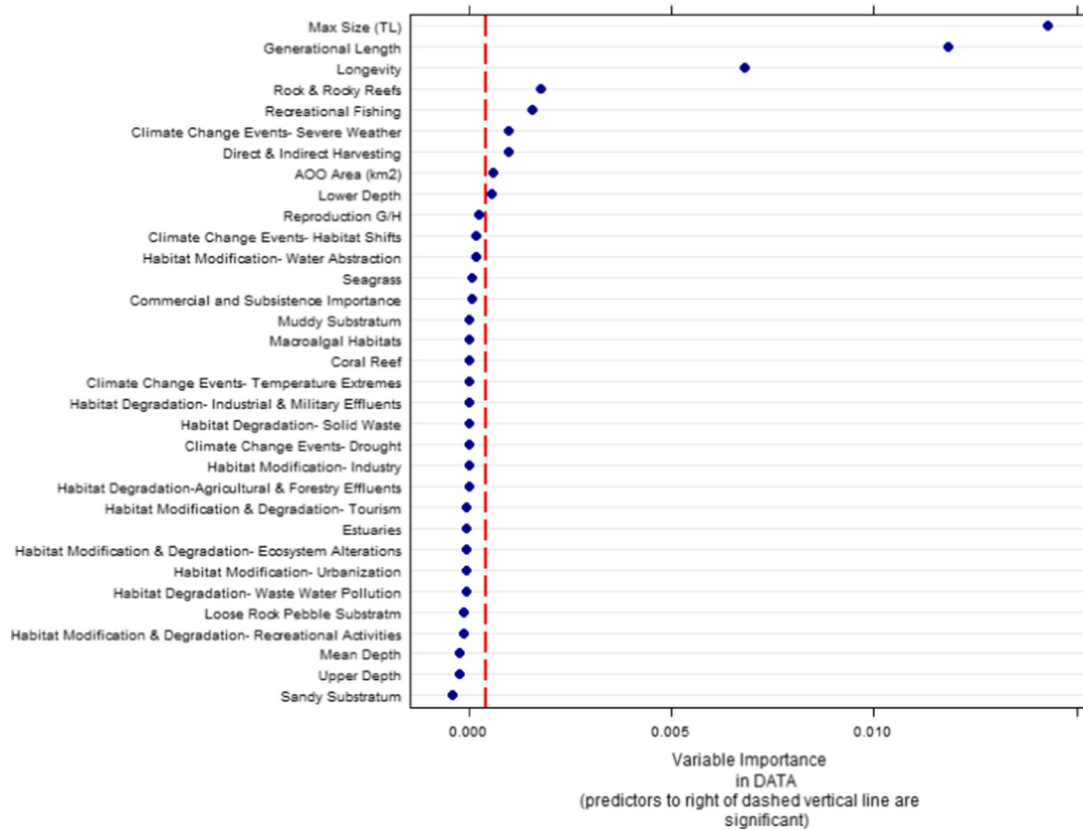


Fig. 3. Relative importance of each predictor variable in the model for predicting extinction risk status in the Sparidae. Variable importance values above the absolute value of the lowest negative-scoring variable are considered important.

4.1. Area of concern: southern Africa

The threatened species endemic to Namibia, South Africa and Mozambique have been heavily impacted by commercial and recreational fishing and have shown strong population declines (Mann, 2013). Two species, *Acanthopagrus vagus* (Riverbream) (VU) and *Lithognathus lithognathus* (White Steenbras) (EN) rely on estuarine habitat as juveniles and adults, and are further negatively affected by reduction of the area and quality of this essential habitat (Bennett, 2012; James, 2001; Mann et al., 2002). These endemic species possess intrinsically sensitive traits such as greater generation lengths, maximum sizes, extended longevity, and hermaphroditic reproductive mode which in combination with exploitation can lead to higher risk of extinction. Four species (44.4%) of these southern African endemics are either protandrous (i.e. *A. vagus*) or protogynous hermaphrodites (i.e. *C. cristiceps*, *C. nasutus*, *P. praeorbitalis*) (Buxton and Garratt, 1990). Exploitation of species with these reproductive strategies can lead to skewed sex ratios and compromised reproductive outputs (Bender et al., 2013; Buxton, 1993; Donaldson and Sadovy, 2001; Hawkins and Roberts, 2004; Sadovy, 2001; Sadovy et al., 2003), effects that can increase the probability of extinction in overexploited stocks. The South

African endemic *C. cristiceps* (CR) is a relatively large, protogynous hermaphrodite that exemplifies this problem. Its stock has collapsed, with approximately 5% spawning biomass per recruit being recorded in the Eastern Cape region (Buxton, 1993). The catch-per-unit effort has also declined significantly throughout its range except in the Tsitsikamma National Park, a large no-take MPA on the Eastern Cape coast (Buxton, 1993; Crawford and Crous, 1982; Griffiths, 2000; Hecht and Tilney, 1989). Commercial linefish catches indicated declines in excess of 50% from 1984 to 2007 (National Marine Linefish System unpublished data), and additional modeling of the probability of capture showed a 95% decline from 1985 to 2010 across its range (Winker et al., 2014). There is also strong evidence of overfishing in exploited areas as fish are recruited into the fishery before reaching maturity (Buxton, 1993; Hecht and Tilney, 1989). Heavy exploitation has also led to skewed sex ratios towards females and lowered mean sizes (Buxton, 1993). Despite the importance of reproductive mode and other life history characteristics as correlates of extinction risk in exploited fishes (Harnik et al., 2012; Juan-Jorda et al., 2015; Reynolds et al., 2005a; Roberts and Hawkins, 1999), reproductive mode was not identified by the model as an important driver for sparids. This is attributed to the small sparid dataset with the majority of species listed as LC. Of these LC species, the majority have unknown reproductive modes. The model did not distinguish between the three reproductive modes: unknown, gonochorist or hermaphroditic in the prediction of extinction risk.

4.2. Intrinsic and extrinsic predictors of extinction risk in the Sparidae

The dual use of the conditional inference trees and Random Forest model provides a novel approach to identifying species traits that are important in determining extinction risk placement. The nine significant drivers identified in this study include maximum size, generation length, longevity, rock and rocky reef habitats, area of occupancy, and

Table 3
Performance measures of the Random Forest model.

Percent correctly classified	Least concern 35/35 = 100%	Near Threatened 1/4 = 25%	Threatened 0/1 = 0%
Least concern	35	0	0
Near Threatened	3	1	0
Threatened	1	0	0
Overall Percent Correctly Classified 36/40 = 90%			

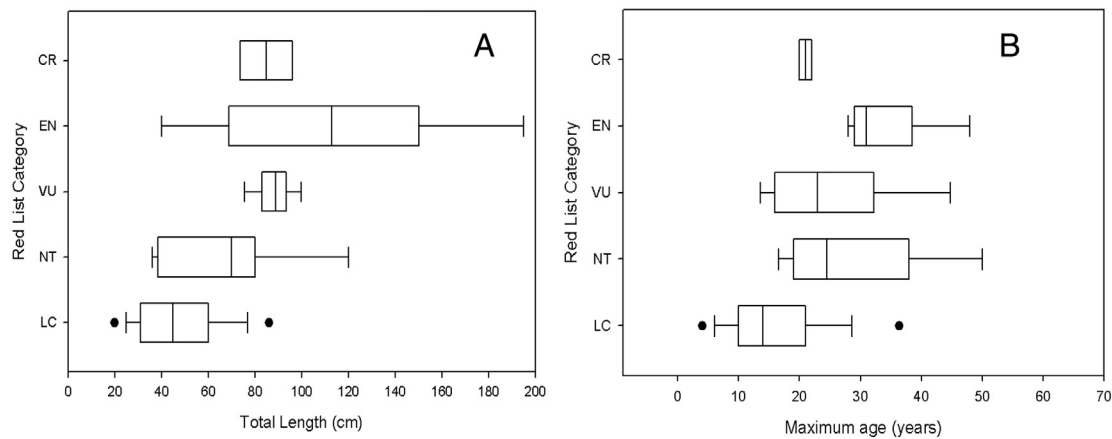


Fig. 4. Differences in A) maximum size and B) longevity across the five Red List categories of extinction risk. Center lines = median values, box boundaries = 25th and 75th percentiles, whiskers = 10th and 90th percentiles, dots = outliers.

lower depth range, recreational fishing, severe weather events, and direct and indirect harvesting. These traits are correlated with different types of population vulnerability (low or declining abundance and small or declining size) that are differentially impacted by different forms of threat whether by direct mortality from overexploitation or by direct effect on distribution range sizes from habitat loss and modification (Reynolds, 2003). The model also gives insight on the different combinations of the sparids' intrinsic sensitivity and exposure to extrinsic threatening events that lead to these species' vulnerability. The combination of significant intrinsic and extrinsic traits that are likely acting in tandem in the Random Forest model include large maximum size, slow population turnover (generation length), and longevity that are directly negatively impacted by overexploitation. Species occurring in rocky reef habitat, having shallow depth ranges and narrow distribution ranges are also directly affected by both commercial and recreational fishing pressure, while small range sizes and lower depth ranges are directly impacted by severe weather events. The distinction between the different types and causes of vulnerability are particularly important in understanding the biological correlates of extinction and in the a priori determination of how species respond to different types of threats (Jennings et al., 1998). This is particularly relevant for prioritizing conservation efforts for marine fishes where the majority of species are considered to be data limited.

Large body size has often been attributed to steeper population declines and higher risk of extinction in exploited species (Hutchings et al., 2012) because it is highly correlated with other extinction-prone life history traits such as low intrinsic rate of population increase, late maturity, lower average population density and higher trophic level (Reynolds et al., 2005a). Species that have large body sizes are also disproportionately valued and targeted for human consumption, especially in recreational fisheries where larger fish are often sought after as trophy species (Cardillo et al., 2005; Collette et al., 2011). The largest-bodied sparid, *Petrus rupestris*, attains sizes of up to 200 cm (TL) and a weight of over 50 kg and is assessed as Endangered. This South African endemic is threatened by severe stock reduction that has led to range contraction over the last 30 years (Winker et al., 2014). Large body size in combination with a small and declining range size and pressures from fishing and habitat destruction have led to this species' listing in the second highest level of extinction risk (Mann et al., 2014b).

Although maximum size has been widely used as a correlate of species' vulnerability to population decline (Jennings et al., 1998), growth rates have been shown to better predict population declines in other commercially important groups such as tunas (Juan-Jorda et al., 2015). As high-quality life history data become more available and accessible, predictive models using global datasets such as that available for the sparids can be improved through testing whether time-related traits

such as growth rates and age at maturity are better determinants in predicting species' vulnerability to fishing pressure. Additionally, for small datasets such as that for the family Sparidae which lack equally represented Red List categories, the conditional inference trees can be used to identify the intrinsic and extrinsic traits that predispose listing of species to a lower risk of extinction and a Random Forest model can be tested for accuracy in risk category predictions.

Restricted geographic range, narrow habitat breadth or specialized habitat requirements have been shown to increase risk of extinction across a suite of terrestrial (Cardillo et al., 2008) and marine species (Reynolds et al., 2005a). For example, in the Ryukyu Islands endemic *Acanthopagrus sivicolus* is facing higher extinction risk because of degradation of its restricted estuarine habitats (Iwatsuki and Carpenter, 2014). The Random Forest model also identified rocky reefs and lower depth as significant in the placement of extinction risk. Threatened sparids are mostly found over rocky reefs, loose rock and pebble substrata and/or in estuaries. The presence of sparids in rocky reef habitats is not necessarily a trait that increases extinction risk per se, however, considering that most line fishermen actively target reef areas using echo-sounders and global positioning systems, this habitat preference puts them at greater risk. The finding of rocky reefs as a significant predictor variable is a little surprising given the emphasis on habitat vulnerability of primary habitat-forming groups such as coral reefs (Carpenter et al. 2008), mangroves (Polidoro et al. 2010), and seagrasses (Short et al. 2011). Our model shows that the diversity of habitats that a species is found and narrow geographical distribution could contribute to the observed variation in risk by habitats in the sparids. This is shown in the six threatened sparids that occur in rocky reefs that are limited to 2–3 habitat types: rocky reefs, loose rock/pebble substratum, and macroalgal habitats. Of these six at risk species, five are endemic to the region of southern Africa. These species are not only rare from declining abundance from fishing pressure, but are also directly impacted by small or declining range size from habitat modification and climate change impacts.

Climate change is known to impact biological phenomena (phenology) and distributions of species (Gattuso et al., 2015; Pinsky et al., 2013; Sunday et al., 2015), and to increase these species' risk of extinction (Foden et al., 2013; Urban, 2015). For example, the Galapagos endemics *Archosargus pourtalesii* and *Calamus taurinus* are at higher risk because their shallow water habitats are directly impacted by oceanographic environmental changes, such as those associated with El Niño Southern Oscillation events (Carpenter et al., 2014; Pollard et al., 2014). South African endemics with small latitudinal ranges that are already experiencing population declines from fishing pressure and habitat loss are also limited in their ability to adapt to a warming ocean (Sunday et al., 2015). The Endangered *Lithognathus lithognathus* is a

large, slow-growing, late maturing, and estuarine-dependent species endemic to South Africa. The estimated area of occupancy of this species calculated from available estuarine habitat for juveniles is ~146 km²; its specialized habitat and extremely limited geographic range, coupled with intense fishing pressure, have led to drastic population declines across its distributional range (Mann et al., 2014a). There is variability in how species respond to climate change both on land and in the ocean, with some species rapidly extending their ranges while others move in the opposite direction to that predicted (Parmesan and Yohe, 2003; Pinsky et al., 2013). Biological differences, species traits, and climate change velocity – i.e. the rate and direction of climate shifts across the landscape – can be used to explain the observed responses of some species (Pinsky et al., 2013; Sunday et al., 2015). Endemic species and those with narrow latitudinal ranges are less able to track thermal preferences (Sunday et al., 2015) and are also intrinsically at higher risk of extinction from stochastic events and changes in metapopulation dynamics (Purvis et al., 2000; Roberts and Hawkins, 1999).

Large-bodied endemic sparids are at a considerably higher risk of extinction and are thus in “triple” jeopardy from overfishing, habitat degradation, and climate change impacts, deserving utmost priority in setting appropriate conservation goals and actions. Recreational and commercial line-fishing is the biggest contributor to population declines of South African endemics. In addition to direct harvesting, indirect harvesting (e.g. bycatch of the inshore trawl fishery) also impacts these species and has been identified as another significant predictor of risk in the model. However, the combination of occurrence over rocky reefs, recreational and commercial fishing, average minimum depths of 8 m, climate change events, and small distributional ranges all act in concert to increase risk of extinction. Thus, the five most threatened South African endemics, *Chrysoblephus cristiceps* (CR), *Polysteganus undulosus* (CR), *Chrysoblephus gibbiceps* (EN), *Lithognathus lithognathus* (EN), and *Petrus rupestris* (EN), are at greatest risk of extinction among the Sparidae. While the direct impacts of the increasing frequency and intensity of severe weather events due to climate change on these species are not known, important habitats such as estuaries in South Africa are predicted to be impacted by climate change through shifts in precipitation patterns affecting the quality, rate, magnitude, and timing of freshwater delivery to these estuaries. For example, climate change events in the St. Lucia estuarine system may have contributed to the local demise of sawfishes in addition to overfishing (Everett et al., 2015). Severe weather events will lead to changes in species composition and ecological functioning of fish communities and will have implications for the management of fisheries resources (James et al., 2013). The threat of extreme weather events is particularly relevant to *Lithognathus lithognathus*, which is an obligatory estuarine inhabitant for up to three years as juveniles (Bennett, 2012; Bennett et al., 2011).

4.3. Conservation actions and solutions

4.3.1. South Africa

Conservation and management of threatened sparids in South Africa is focused on spatial habitat protection (i.e. no-take marine protected areas [MPAs]) and conventional fisheries management approaches (i.e. temporal closures, size limits, bag limits, fishing effort limitations, etc.). No-take MPAs have shown considerable success in protecting a number of sparid species with higher abundances and biomass of fish recorded inside these MPAs (inter alia Buxton 1992; 1993; Buxton and Smale 1989; Cowley et al. 2002; Garratt 1993; Gotz et al. 2011; Kerwath et al. 2009; Maggs et al. 2013). South Africa has recently undertaken a bold initiative to increase its network of MPAs (Sink 2016) and the increased protection of suitable shelf habitat bodes well for improved conservation of South Africa's threatened endemic sparid species. The reduction in commercial line-fishing effort implemented by the South African government between 2003 and 2006 has also resulted in the improvement of the stock status of a number of sparid species including *Argyrozona argyrozona*, *Chrysoblephus puniceus* and

Pachymetopon blochii (Winker et al. 2012). Species-specific limitations such as the moratorium implemented on the capture of *Polysteganus undulosus* in 1998 (Mann 2007), the de-commercialization of certain species such as *Lithognathus lithognathus* and the implementation of closed fishing seasons during the spawning period for species such as *Petrus rupestris* are also beginning to show positive results (Mann, 2013). However, more effective enforcement and improved monitoring is urgently needed to ensure continued protection of these endemic fish populations.

4.3.2. Mediterranean Region

The primary conservation and management action for sparids in this region has been the creation of MPAs, especially in northern Mediterranean coastal areas (Francour et al. 2001; Abdulla et al., 2008). Many of these MPAs, however, are primarily zoned for multiple use, and very few contain substantial no-take sanctuary areas. There are few other effective protection measures currently in place, either for species or ecosystems, in the Mediterranean region (Bianchi and Morri 2000). Improved fisheries and conservation management measures such as species-specific catch limitations and reduction in commercial spearfishing effort are needed. For the single threatened sparid species, *Dentex dentex* (Common Dentex) occurring in the Mediterranean, recovery recommendations include establishment of a minimum catch size and a restriction on spear fishing in critical habitat areas (Abdul Malak et al., 2011).

Conservation and management actions for the family should focus on expanding no-take marine reserves covering critical habitat areas (e.g. estuaries and shelf areas). Additionally, species-specific fisheries management such as that undertaken in South Africa, need to be expanded to other regions where the level of threatening processes is high (e.g. overexploitation and habitat degradation and modification) such as in the Mediterranean, and also the South China Sea. Furthermore, in recognition of the differential combinations of inherent traits and external risks, continued monitoring of threatened populations and those that possess, and are exposed to, the significant drivers of risk identified by this model are needed. Expansion of the sparid model to include high-resolution life history data such as growth rates that are geographically matched to regional or local population status can provide information on the best life history determinants of risk to fishing (Juan-Jorda et al., 2015). Additionally, incorporation of threat datasets such as global human impacts, could improve our understanding of specific traits and combinations that predispose sparids to higher risk. The use of external threat datasets which have the ability to detect both spatial and temporal changes in impacts could potentially lead to close monitoring and updating of species' conservation status over time.

4.3.3. Detecting risk in data deficient, least concern and Near Threatened sparids

The uncertainty of threat status of DD species can potentially lead to underestimation of true extinction risk and missed opportunity to provide appropriate conservation measures to protect these species (Davidson et al., 2012; Bland et al., 2014; Dulvy et al., 2014). A relatively low proportion (13.9%) of sparids are listed as DD. Species information limited to museum specimens and taxonomic validation account for listing of 15 out of 21 DD sparids. These species occur in shallow depths and have limited distributional ranges. For example, *Acanthopagrus akazakii* is known only from New Caledonia (Iwatsuki et al. 2016), *A. omanensis* is endemic to southern Oman (Iwatsuki and Heemstra 2010), *A. taiwanensis* is found only in southwestern Taiwan (Iwatsuki and Carpenter 2006), and *A. randalli* is known only from the Persian Gulf (Iwatsuki and Carpenter 2009). These DD species likely have small population sizes and specialized niches that may predispose them to a higher risk of extinction. Furthermore, fishing pressure from recreational fishing and direct and indirect harvesting are the major threats impacting these species, with some experiencing negative effects from habitat modification and climate change events. Although

the Random Forest model was not able to make predictions beyond the sample dataset, the major drivers of extinction risk and the different combinations shown to increase risk can be applied for future re-assessments of these species and to pro-actively monitor populations of potential “at-risk” species that possess these traits and are exposed to these differing threat combinations. For example, taxonomy of the Yellowfin Seabream (*Acanthopagrus latus*) was recently reviewed and validated as an endemic to the east Asian shelf (Iwatsuki 2013). This species is an important component of commercial and recreational fisheries throughout its range. It is a relatively large species (up to 50 cm TL) and can reach maximum ages of up to 24 years (Russell and Pollard 2014). This species is also a protandrous hermaphrodite. It has experienced localized declines in parts of its range and there is limited information for species-specific conservation efforts. Data Deficient sparids such as *A. latus*, that meet threshold values of the traits identified by the model as significant in determining placement of threatened and NT sparids can therefore be prioritized for species re-assessments and conservation management.

For LC and NT species that comprise the majority of the sparids listed (i.e., non-threatened), pro-active measures such as those identified for DD species could also be applied. Species that possess a combination of traits such as exceeding maximum sizes of 48 cm total length, are reaching maximum ages of > 19 years, are heavily fished, have limited ranges and are not subject to any management action may be identified as priority species for re-assessments particularly if they also occur in regions where cumulative human impacts are high. In addition to these measures, integrating threat datasets with species conservation status can help managers identify species that are predisposed to a higher level of extinction risk, provide insights on urgent conservation actions, and help to prioritize areas where conservation intervention is urgently needed to reduce negative impacts (Joppa et al. 2016). Such pro-active measures are needed for effective and repeatable approaches for monitoring the conservation status of species over time.

5. Conclusion

Fishes of the family Sparidae are relatively unique compared to many other coastal, commercial species in having limited distributional patterns in the primarily temperate regions which they inhabit. Pro-active measures such as identification of traits that predispose species to higher risk of extinction and areas of geographic conservation concern can be used to inform broad-scale conservation assessment and monitoring for other data-limited marine fishes. As a group, the majority (69.5%) of the world's 151 Sparidae species are at low risk of global extinction, based on the assessment methodology of the IUCN Red List of Threatened Species. Some species in southern Africa, however, are of particular concern, as 69% (9 species) of all sparids listed in one of the three threatened categories occur there. In this region, these species are undergoing severe declines due to intensive commercial and recreational fishing, restricted range and loss of critical estuarine habitat, and also a relatively low reproductive turnover coupled with these species' complex life histories. Additionally, these South African endemic species generally exhibit narrow latitudinal ranges that may negatively impact their ability to adapt to a warming ocean and extreme weather events resulting from climate change (Sunday et al., 2015).

The conditional inference trees and Random Forest model, applied for the first time in a family of ecologically and economically important marine fishes, was able to predict the most important intrinsic and extrinsic characteristics and the combinations of these traits that drive extinction risk. For datasets typical of marine species, which lack equally represented Red List categories and are often data-limited, this modeling approach is robust in identifying traits that are most important in driving extinction risk. Additionally, the use of the Random Forest model on a standardized, global dataset may provide guidance on measures to protect threatened species, threshold values for estimating risks or impacts on species listed as DD, and in guiding future research, stock

assessments and Red List re-assessments. Our results suggest that detection of traits that drive extinction risk in species can provide a targeted set of metrics to efficiently identify the species that are at highest risk of endangerment and guide allocation of resources for the protection and continued monitoring of these species' populations.

Acknowledgements

We thank Tom Haas and the New Hampshire Charitable Foundation for generous support of IUCN Red List Assessments and the Global Marine Species Assessment. We thank Roger McManus and Jean-Christophe Vié for their continued advice and support for IUCN's Marine Biodiversity Unit. The Moore Family Foundation and the Qatar National Research Foundation provided support for workshops in the Bahamas and Qatar, respectively. We extend our thanks to the following workshop co-organizers: Kwang-Tsao Shao, Min Liu, and Vera Shiwei (Taiwan), Heather Harwell and Cristiane Elfes (Bahamas), Friedhelm Krupp, Abdulrahman Al-Muftah, and Jack Buchanan (Qatar). We would also like to thank the IUCN Snappers, Seabreams, and Grunts Specialist Group and the Sparidae assessors and reviewers for their support in the Red Listing process. We also thank Rosemary Raynal for editing; Michael Lane and Colin Attwood for statistical and technical support and assistance; Gina Ralph for facilitating at the Qatar workshop; and Emilie Stump for graphic design support.

References

- Abdul Malak, D., Livingstone, S.R., Pollard, D., Polidoro, B.A., Cuttelod, A., Bariche, M., Bilecenoglu, M., Carpenter, K.E., Collette, B.B., Francour, P., Goren, M., Kara, M.H., Massuti, E., Papaconstantinou, C., Tunesi, L., 2011. Overview of the Conservation Status of the Marine Fishes of the Mediterranean Sea. IUCN, Gland, Switzerland and Malaga, Spain (61 pp).
- Abdulla, A., Gomei, M., Maison, E., Pianté, C., 2008. Status of Marine Protected Areas in the Mediterranean Sea. IUCN, Malaga, Spain and WWF, France (152 pp).
- Amante, C., Eakins, B.W., 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources, and Analyses, in NOAA Technical Memorandum NESDIS NGDC-24. Colorado, National Geophysical Data Center Boulder, p. 19.
- Bender, M.G., Floeter, S.R., Mayer, F.P., Vila-Nova, D.A., Longo, G.O., Hanazaki, N., Carvalho-Filho, A., Ferreira, C.E.L., 2013. Biological attributes and major threats as predictors of the vulnerability of species: a case study of Brazilian reef fishes. *Oryx* 47, 259–265.
- Bennett, R.H., 2012. Movement Patterns, Stock, Delineation and Conservation of an Exploited Fishery Species *Lithognathus lithognathus* (Pisces: Sparidae). Rhodes University, South Africa.
- Bennett, R.H., Childs, A.R., Cowley, P.D., Næsje, T.F., Thorstad, E.B., Økland, F., 2011. First assessment of estuarine space use and home range of juvenile white steenbras, *Lithognathus lithognathus*. *Afr. Zool.* 46, 32–38.
- Bland, L.M., Collen, B., Orme, C.D.L., Bielby, J., 2014. Predicting the conservation status of data-deficient species. *Conserv. Biol.* <http://dx.doi.org/10.1111/cobi.12372>.
- Breiman, L., 2001. Random Forests. *Mach. Learn.* 45, 5–32.
- Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460.
- Buxton, C.D., 1993. Life history changes in exploited reef fishes on the east coast of South Africa. *Environ. Biol. Fish.* 36, 47–63.
- Buxton, C.D., Garratt, P.A., 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Environ. Biol. Fish.* 28, 113–124.
- Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* 275, 1441–1448.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W.E.S., Orme, C.D.L., Purvis, A., 2005. Multiple Causes of High Extinction Risk in Large Mammal Species Science. 309 pp. 1239–1241.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., et al., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–68.
- Carpenter, K.E., 2001. Sparidae. Porgies (seabreams). In: Carpenter, K.E., Niem, V.H. (Eds.), The living marine resources of the Western Central Pacific. Bony fishes part 3 (Menidae to Pomacentridae). Food and Agriculture Organization, Rome, pp. 2990–3003.
- Carpenter, K.E., Springer, V.G., 2005. The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environ. Biol. Fish.* 72, 467–480.
- Carpenter, K.E., Pollard, D., Russell, B., Buxton, C.D., 2014. In: IUCN (Ed.), *Calamus taurinus*, in the IUCN Red List of Threatened Species.
- Cheung, W.W.L., Pitcher, T.J., Pauly, D., 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biol. Conserv.* 124, 97–111.
- Collette, B.B., Carpenter, K.E., Polidoro, B.A., Juan-Jorda, M.J., Boustany, A., Die, D.J., et al., 2011. High value and long life - double jeopardy for tunas and billfishes. *Science* 333, 291–292.

- Comeros-Raynal, M.T., Choat, J.H., Polidoro, B., Clements, K.D., Abesamis, R.A., et al., 2012. The likelihood of extinction of iconic and dominant herbivores and detritivores of coral reefs: the parrotfishes and surgeonfishes. *PLoS One* 7.
- Connolly, S.R., MacNeil, M.A., Caley, M.J., Knowlton, N., Cripps, E., Hisano, M., Thibaut, L.M., Bhattacharya, B.D., Benedetti-Cecchi, L., Brainard, R.E., et al., 2014. Commonness and rarity in the marine biosphere. *Proc. Natl. Acad. Sci.* 111, 8524–8529.
- Crawford, R.J.M., Crous, H.B., 1982. Trends in commercial handline catches of redfishes along the southern Cape coast, Republic of South Africa. *Koedoe* 25.
- Cutler, D.R., Edwards Jr., T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. *Ecology* 88, 11.
- Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. *Ecol. Lett.* 11, 1278–1286.
- Davidson, A.D., Boyer, A.G., Kim, H., Pompa-Mansilla, S., Hamilton, M.J., Costa, D.P., Ceballos, G., Brown, J.H., 2012. Drivers and hotspots of extinction risk in marine mammals. *Proc. Natl. Acad. Sci.* 109, 3395–3400.
- Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H., Ceballos, G., 2009. Multiple ecological pathways to extinction in mammals. *Proc. Natl. Acad. Sci.* 106, 10702–10705.
- Di Marco, M., Collen, B., Rondinini, C., Mace, G.M., 2015. Historical drivers of extinction risk: using past evidence to direct future monitoring. *Proc. R. Soc. B* 282 (20150928).
- Donaldson, T.J., Sadovy, Y., 2001. Threatened fishes of the world: *Cheilinus undulatus* (Ruppell, 1835 (Labridae)). *Environ. Biol. Fish.* 62, 428.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S., White, W.T., Baldwin, I.T., 2014. Extinction risk and conservation of the world's sharks and rays. *eLife* 3.
- Dulvy, N.K., Pinnegar, J.K., Reynolds, J.D., 2009. Holocene extinctions in the sea. In: Turvey, S.T. (Ed.), *Holocene Extinctions*. Oxford University Press, Oxford, pp. 129–150.
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64.
- Everett, B.J., Cliff, G., Dudley, S.F.J., van der Elst, R.P., 2015. Do sawfish *Pristis* spp. represent South Africa's first local extirpation of marine elasmobranchs in the modern era? *Afr. J. Mar. Sci.* 37, 275–284.
- Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vie, J.-C., Akcakaya, R., Angulo, A., et al., 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* 8, e65427.
- Gaither, M.R., Rocha, L.A., 2013. Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: evidence for the centre of overlap hypothesis. *J. Biogeogr.* 40, 1638–1648.
- Gattuso, J.P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F., Allemand, D., Bopp, L., Cooley, S.R., Eakin, C.M., Hoegh-Guldberg, O., Kelly, R.P., Pörtner, H.O., Rogers, A.D., Baxter, J.M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., Sumaila, U.R., Treyer, S., Turley, C., 2015. Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science* 349.
- Griffiths, M.H., 2000. Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *S. Afr. J. Mar. Sci.* 22, 81–110.
- Halpern, B.S., Kappel, C.V., 2012. Extinction Risk in a Changing Ocean. In: Hannan, L. (Ed.), *Saving a Million Species: Extinction Risk from Climate Change*. Island Press, Washington, D.C., pp. 285–307.
- Hanel, R., Tsigonopoulos, C.S., 2011. Phylogeny, evolution and taxonomy of sparids with some notes on their ecology and biology. In: Pavlidis, M.A., Mylonas, C.C. (Eds.), *Sparidae. Biology and Aquaculture of Gilthead Sea Bream and Other Species*. Wiley-Blackwell, Malaysia, pp. 51–69.
- Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z.V., Finnegan, S., Lindberg, D.R., Liow, L.H., et al., 2012. Extinctions in ancient and modern seas. *Trends Ecol. Evol.* 27, 608–617.
- Hawkins, J.P., Roberts, C.M., 2004. Catastrophes, phase shifts, and largescale degradation of a Caribbean coral reef. *Conserv. Biol.* 18, 215–226.
- Hecht, T., Tilney, R.L., 1989. The Port Alfred fishery: a description and preliminary evaluation of a commercial linefishery on the South African East Coast. *S. Afr. J. Mar. Sci.* 8.
- Hooper, D.U., Adair, E.C., Carinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., et al., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–109.
- Hothorn, T., Buehlmann, P., Dudoit, S., Molinaro, A., Van Der Laan, M., 2006. Survival ensembles. *Biostatistics* 7, 355–373.
- Hutchings, J.A., Myers, R.F., Garcia, V.B., Lucifora, L.O., Kuparinen, A., 2012. Life-history correlates of extinction risk and recovery potential. *Ecol. Appl.* 22, 1061–1067.
- IBM Corp., 2013. IBM SPSS Statistics for Windows Version 22.0. IBM Corp., Armonk, NY.
- IUCN, 2001. IUCN Red List Categories and Criteria Version 3.1.
- IUCN, Standards and Petitions Subcommittee, 2014. Guidelines for Using the IUCN Red List Categories and Criteria. p. 87.
- Iwatsuki, Y., Carpenter, K.E., 2014. In: IUCN (Ed.), *Acanthopagrus siviculus*, in the IUCN Red List of Threatened Species.
- James, N.C., 2001. The Status of the Riverbream, *Acanthopagrus berda* (Sparidae) in the Estuarine Systems of the Northern KwaZulu-Natal. University of Natal, South Africa.
- James, N.C., van Niekerk, L., Whitfield, A.K., Potts, W.M., GÄtz, A., Paterson, A.W., 2013. Effects of climate change on South African estuaries and associated fish species. *Clim. Res.* 57, 233–248.
- Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. *Proc. R. Soc. B* 265, 333–339.
- Jennings, S., Reynolds, J.D., Polunin, N.V.C., 1999. Predicting the vulnerability of tropical reef fishes to exploitation using phylogenies and life histories. *Conserv. Biol.* 13, 1466–1475.
- Jetz, W., Freckleton, R.P., 2015. Towards a general framework for predicting status of data-deficient species from phylogenetic, spatial and environmental information. *Philosophical Transactions of the Royal Society Biological Sciences* 370, 20140016.
- Juan-Jorda, M.J., Mosqueira, I., Freire, J., Dulvy, N.K., 2013. Life history correlates of marine fisheries vulnerability: a review and a test with tunas and mackerel species. In: Briand, F. (Ed.), *Marine Extinctions - Patterns and Processes*, pp. 113–128 (Monaco).
- Juan-Jorda, M.J., Mosqueira, I., Freire, J., Dulvy, N.K., 2015. Population declines of tuna and relatives depend on their speed of life. *Proc. R. Soc. B* 282 (20150322).
- Kindsvater, H.K., Mangel, M., Reynolds, J.D., Dulvy, N.K., 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution* 6, 2125–2138.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2, 18–22.
- Luiz, O.J., Woods, R.M., Madin, E.M.P., Madin, J.S., 2016. Predicting IUCN Extinction Risk Categories for the World's Data Deficient Groupers (Teleostei: Epinephelidae) Conservation Letters.
- MacDougall, A.S., McCann, K.S., Gellner, G., Turkington, R., 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494, 86–90.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akcakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22, 1424–1442.
- Mann, B.Q., 2013. Southern African Marine Linefish Species Profiles. South African Association for Marine Biological Research Durban, South Africa.
- Mann, B.Q., Buxton, C.D., Pollard, D., Carpenter, K.E., Iwatsuki, Y., 2014a. *Lithognathus lithognathus*. IUCN Red List of Threatened Species. IUCN.
- Mann, B.Q., Buxton, C.D., Pollard, D., Carpenter, K.E., Winker, H., 2014b. *Petrus rupestris*. The IUCN Red List of Threatened Species 2014. IUCN.
- Mann, B.Q., James, N.C., Beckley, L.E., 2002. An assessment of the recreational fishery in the St. Lucia estuarine system, KwaZulu-Natal, South Africa. *S. Afr. J. Mar. Sci.* 24, 263–279.
- Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proc. R. Soc. B* 278, 1515–1523.
- Orrell, T.M., Carpenter, K.E., Musick, J.A., Graves, J.E., 2002. Phylogenetic and Biogeographic Analysis of the Sparidae (Perciformes: Percoidae) from Cytochrome *b* Sequences. *Copeia* 3, pp. 618–631.
- Owens, I.P., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci.* 97, 12144–12148.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344. <http://dx.doi.org/10.1126/science.1246752>.
- Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. *Science* 269.
- Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., Levin, S.A., 2013. Marine taxa track local climate velocities. *Science* 341, 1239–1242.
- Pollard, D., Buxton, C.D., Carpenter, K.E., 2014. *Archosargus pourtalesii*, in the IUCN Red List of Threatened Species. IUCN.
- Purvis, A., Gittleman, J.L., Mace, G.M., 2000. Predicting extinction risk in declining species. *Proc. R. Soc. B* 267, 1947–1952.
- R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reynolds, J.D., 2003. Life histories and extinction risk. In: Blackburn, T.M., Gaston, K.J. (Eds.), *Macroecology*. Blackwell Publishing, Oxford, pp. 195–217.
- Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005a. Biology of extinction risk in marine fishes. *Proc. R. Soc. B* 272, 2337–2344.
- Reynolds, J.D., Webb, T.J., Hawkins, L.A., 2005b. Life history and ecological correlates of extinction risk in European freshwater fishes. *Can. J. Fish. Aquat. Sci.* 62, 854–862.
- Roberts, C.M., Hawkins, J.P., 1999. Extinction risk in the sea. *Trends Ecol. Evol.* 14, 241–246.
- Sadovy, Y., 2001. The threat of fishing to highly fecund fishes. *J. Fish Biol.* 59, 90–108.
- Sadovy, Y., Kulbicki, M., Labrosse, P., Letourneur, Y., Lokani, P., Donaldson, T.J., 2003. The humphead wrasse, *Cheilinus undulatus*: synopsis of a threatened and poorly known giant coral reef fish. *Rev. Fish Biol. Fish.* 13, 327–364.
- Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H.M., Collen, B., Cox, N.A., Master, L.L., O'Connor, S., Wilkie, D., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv. Biol.* 22, 897–911.
- Sanciangco, M.D., Carpenter, K.E., Betancur-R, R., 2016. Phylogenetic placement of enigmatic percormorph families (Teleostei:Percomorphaceae). *Mol. Phylogenet. Evol.* 94, 565–576.
- Sanciangco, J.C., Carpenter, K.E., Etnoyer, P.J., Moretzsohn, F., 2013. Habitat availability and heterogeneity and the Indo-Pacific warm pool as predictors of marine species richness in the tropical Indo-Pacific. *PLoS One* 8, e56245.
- Strobl, C., Hothorn, T., Zeileis, A., 2009a. Party on! A new, conditional variable importance measure for Random Forests available in the party package. Technical Report Number 050. Department of Statistics, p. 15.
- Strobl, C., Malley, J., Tutz, G., 2009b. An introduction to recursive partitioning: rationale, application and characteristics of classification and regression trees, bagging and random forests. *Psychol. Methods* 14, 323–348.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., Zeileis, A., 2008. Conditional variable importance for random forests. *BMC Bioinformatics* 9, 1–11.
- Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Slawinski,

- D., Feng, M., Radford, B.T., Thompson, P.A., Bates, A.E., 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* 18, 944–953.
- Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348, 571–573.
- Webb, T.J., Mindel, B.L., 2015. Global Patterns of Extinction Risk in Marine and Non-Marine Systems *Current Biology*. 25 pp. 1–6.
- Winker, H., Parker, D., Attwood, C.G., 2014. Severe declines in standardized abundance indices of dageraad (*Chrysoblephus cristiceps*) and red steenbras (*Petrus rupestris*) over the period 1985 to 2011. LSWG 2011/7 No. 6. Linefish Scientific Working Group Document of Department of Agriculture, Forestry and Fisheries.