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Rockfish (*Sebastes*) that are evolutionarily isolated are also large, morphologically distinctive and vulnerable to overfishing

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ABSTRACT

In an age of triage, we must prioritize species for conservation effort. Species more isolated on the tree of life are candidates for increased attention. The rockfish genus *Sebastes* is speciose (>100 spp.), morphologically and ecologically diverse and many species are heavily fished. We used a complete *Sebastes* phylogeny to calculate a measure of evolutionary isolation for each species and compared this to their morphology and imperilment. We found that evolutionarily isolated species in the northeast Pacific are both larger-bodied and, independent of body size, morphologically more distinctive. We examined extinction risk within rockfish using a compound measure of each species' intrinsic vulnerability to overfishing and categorizing species as commercially fished or not. Evolutionarily isolated species in the northeast Pacific are more likely to be fished, and, due to their larger sizes and to life history traits such as long lifespan and slow maturation rate, they are also intrinsically more vulnerable to overfishing. Finally, the set of northeast Pacific species that are both fished and most intrinsically vulnerable to fishing are among the most evolutionarily distinctive. These findings suggest that, at least for this clade, extra attention should be paid to evolutionary distinctiveness when prioritizing species for conservation.

1. Introduction

As we move into an era of triage in conservation, we require effective methods of prioritizing species for conservation effort (Marris, 2007). One way to efficiently preserve unique genetic information may be to incorporate some measure of an individual species' evolutionary isolation into a prioritization process (Faith, 1992, 2008; Pavoine et al., 2005; Redding and Mooers, 2006; Isaac et al., 2007; see also Wilson, 1992). The concept of using phylogenetic data for conservation prioritization, pioneered by May (1990), Vane-Wright et al. (1991), and Faith (1992), became established through the use of the measure phylogenetic diversity (PD; Faith, 1992). Phylogenetic diversity for a set of species can be measured by simply summing the branch lengths of a phylogeny that subtend all the species in the subset (Faith, 1992). Conservation effort can then be directed towards a subset of species that maximizes PD or that maximizes incremental PD (see, e.g., Forest et al., 2007).

Phylogenetic diversity is primarily used to rank groups of species for conservation effort (Redding et al., 2008); a complementary approach uses measures of evolutionary distinctiveness to prioritize individual species (May, 1990; Vane-Wright et al., 1991; Pavoine et al., 2005; Redding and Mooers, 2006; Isaac et al., 2007; Steel et al., 2007). Under these measures, a species with fewer, more distantly related relatives is given a higher score than a species with many, closely related species. PD and evolutionary isolation measures are intimately related (see Faith, 2008), and using evolutionary isolation measures to prioritize a set of species for conservation preserves more PD than a random sampling of the phylogeny (Redding et al., 2008). Recently, the Zoological Society of London adopted the use of evolutionary isolation measures to prioritize conservation candidates and launched the EDGE (evolutionarily distinct and globally endangered) program, raising not only awareness of conservation issues but also substantial conservation funding (see www.edgeofexistence.org). Under the EDGE program, all species in Class Mammalia and Class Amphibia have been prioritized for conservation effort using an 'EDGE score,' which measures a combination of a species' evolutionary isolation and extinction risk (Redding and Mooers, 2006; Isaac et al., 2007, see Section 2.1).

One published argument made for using evolutionary isolation measures in conservation is that more isolated species are special in other ways (Redding and Mooers, 2006; Isaac et al., 2007;

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Marris, 2007; see also www.edgeofexistence.org). To the extent that evolution is homogeneously divergent and that the amount of evolutionary change is positively correlated with the amount of time elapsed, species with fewer close relatives should be more phenotypically distinctive. To our knowledge, however, the correlation between evolutionary isolation and phenotypic distinctiveness is untested; testing this is one of the goals of the present study.

The genus *Sebastes* is a species-rich (currently 111 named species), ecologically and morphologically diverse group of rockfish. The genus is phylogenetically well-characterized and includes many heavily fished species (Love et al., 2002; Hyde and Vetter, 2007). This makes *Sebastes* a good candidate group to test for a relationship between evolutionary isolation (measured as evolutionary distinctiveness or ED; see below) and both morphological distinctiveness and extinction risk.

The goals of this study are to (1) rank species within a heavily impacted taxonomic group of fish using a new conservation metric (evolutionary isolation); (2) determine whether more evolutionary isolated species are also more morphologically distinctive and more imperilled by fishing; and (3) discuss how rockfish species might be prioritized using a combination of their evolutionary isolation and degree of imperilment.

2. Methods

2.1. Evolutionary distinctiveness

Evolutionary distinctiveness (ED) is a relative measure of genetic non-redundancy of a species. A species' ED score thus can be said to represent that amount of unique evolutionary history captured by that species. Following Isaac et al. (2007); (see also Redding, 2003), we apply the evolutionary distinctiveness metric, and investigate how this score relates to conservation importance. Each branch of a dated phylogenetic tree is assigned a value that is simply its length divided by the number of species subtending the branch (i.e. the size of the group that a particular branch defines). The branch leading to a species is thus unchanged (it is fully non-redundant), while an interior branch leading to a clade of two species would be halved, such that each species represents the unique evolution represented by that branch equally. A particular species' ED score is the sum of these modified branch lengths across all branches that lie on the path from a species to the root of the tree (see Supplementary material for a worked example). This measure apportions the total evolutionary history uniquely among the tips, and is very strongly correlated with other quantitative measures of evolutionary isolation (Redding et al., 2008): species whose lineages contain long branches that are shared with few or no other species will have the highest scores and are considered more evolutionarily distinctive. As ED is also the amount of unique evolution that stands to be lost if that species goes extinct, it is possible to produce an 'expected loss' value, which is simply the ED score (in millions of years of evolution)$^{*}P$ (extinction) over a set time-window (Redding and Mooers, 2006; Isaac et al., 2007), i.e. a species' EDGE score.

Because ED is a measure of redundancy, we are required to use phylogenetic trees that include all living species. Following Hyde and Vetter (2007), who published a near complete phylogeny of the *Sebastes* genus, we use DNA sequence data from eight loci for 99 of 112 species, taxonomic data, and Bayesian analysis to produce a complete phylogeny of the genus including branch lengths representing relative time (Fig. 1; see Supplementary material). In order to accommodate phylogenetic uncertainty, we calculated ED for each species for each tree from the entire set of Bayesian trees ($n = 1502$) that was produced during our analysis. We also calculated ED for the average (consensus) tree from this set. Given that the actual age of the genus is uncertain (C. Brock and M. Alfaro, pers. comm.), we scaled all our *Sebastes* phylogenies to unit depth, making our ED scores relative rather than absolute values. However, by simply multiplying the relative ED scores we report here by one's preferred estimate of the age of the *Sebastes* genus, one can obtain the ED scores in the conventional unit of measurement, millions of years.

2.2. Morphology

One of us (TI) gathered morphological data for 61 of the 75 rockfish species found in the northeast Pacific. Intraspecific sample sizes varied from 1–39 individuals, with a median of five individuals per species. Specimens were obtained from commercial and recreational fisheries and from museum collections and were measured for 18 morphological characteristics: total length, head length, snout length, pre-pectoral length, pre-pelvic length, interopercular width, interorbital width, eye width (horizontal and vertical), upper and lower jaw lengths, gill arch length, gill raker number, longest gill raker length, pectoral fin length and width, pelvic fin length and pelvic spine length. We reduced these data to major axes of variability using a principal component analysis (PCA) on the correlation matrix of species means. All traits except gill raker number were log-transformed to improve normality.

We defined each species' morphological distinctiveness as its multi-dimensional Euclidean distance from the origin in Principal Coordinate space (the center of the distribution of species traits in morphospace). This value was calculated as the square root of the sum of squared principal component scores for a species. A species' morphological distinctiveness score calculated in this way is also equivalent to the square root of the sum of squared differences between the standardized value of this species and the standardized values of all other species, summed over all morphological traits. We first calculated morphological distinctiveness across all 18 principal components. This distinctiveness score is dominated by the first PC axis, which represents overall body size and explains >87% of the variance (see Section 3.2). In order to consider size-independent morphological distinctiveness we also calculated morphological distinctiveness for axes 2–18.

2.3. Conservation status

Very few fish species are listed as at risk by the IUCN (Reynolds et al., 2005), including only two rockfish species, the redfish (*Sebastes fasciatus*) which is found in the North Atlantic and the bocaccio, (*Sebastes paucispinis*; IUCN, 2007). Other rockfish species of conservation concern include the cowcod (*Sebastes levis*) which is listed as a species of special concern under the National Marine Fisheries Service (NMFS, within the National Oceanic and Atmospheric Administration of the United States Department of Commerce; NMFS et al., 2008) as well as the canary rockfish (*Sebastes pinniger*) and the rougheye rockfish (*Sebastes aleutianus*), which have been listed as threatened and of special concern, respectively, under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Environment Canada, 2008). Although it is clear that many rockfish species are imperilled to varying degrees (Musick et al., 2000; Love et al., 2002), their extinction risk cannot be calculated directly as there is insufficient data regarding the rate of adult abundance decline of rockfish species, the most common method used to calculate extinction risk (Dulvy et al., 2004). In fact, there is very little information regarding extinction rates in general in marine populations (Dulvy et al., 2003; Reynolds et al., 2005). We were therefore prevented from directly calculating extinction risk probabilities (as done by, e.g., Redding and Mooers, 2006; Isaac et al., 2007), and instead created a proxy measure.

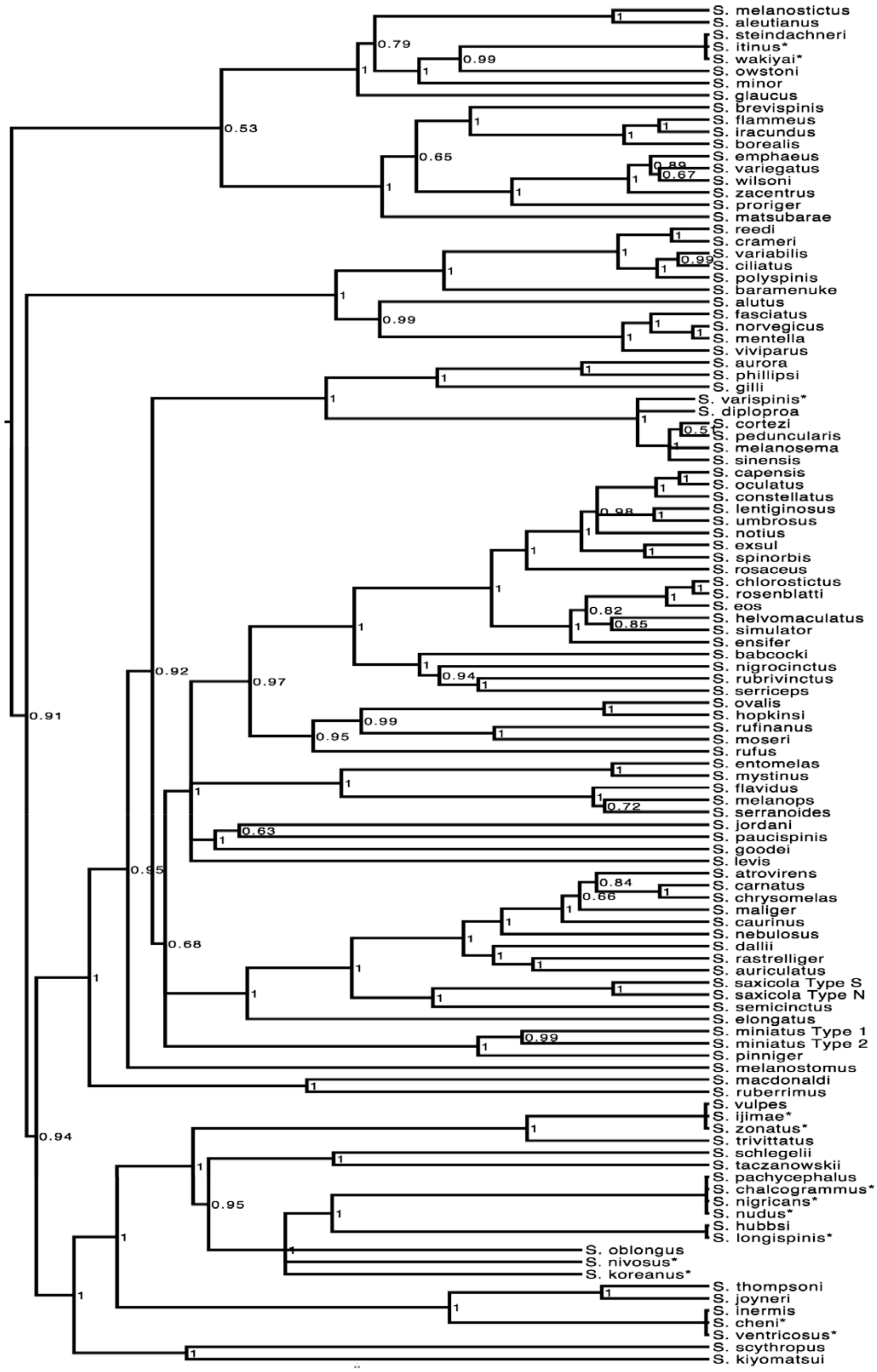

Fig. 1. The consensus tree of the *Sebastes* genus containing 112 species, generated by Bayesian analysis. The posterior probability values are given at each node (species complexes constrained as a monophyletic clade during analysis have posterior prob. = 1). Branches terminating before the present reflect the correction made to account for soft polytomies in ED calculations. Species absent from Hyde and Vetter (2007) and added to the phylogeny using taxonomic data are indicated by an asterisk.

Life history traits and ecological characteristics of marine species are presently used to prioritize fish species for conservation (Musick, 1999; Dulvy et al., 2004; Cheung et al., 2007). Cheung et al. (2005) have developed a fuzzy expert system that estimates a species' intrinsic vulnerability to fishing. This system has been used to demonstrate declines in Indonesian marine resources (Ainsworth et al., 2008) and describe global fishing trends (Cheung et al., 2007). By evaluating a species' life history characteristics, population growth potential and ecology, intrinsic vulnerability to fishing describes the expected population dynamics of a species, thereby also determining the inherent ability of a species to recover from overfishing (Cheung et al., 2005). Intrinsic vulnerability makes use of heuristic rules that are based on the available expert knowledge as well as fuzzy set theory (or "fuzzy logic") to classify each species on a scale from 0 to 100, with 100 being the most intrinsically vulnerable (Cheung et al., 2005). The use of fuzzy logic accommodates uncertainty in the input data and is currently used in, e.g. IUCN Red List designations (Akçakaya et al., 2000) and in identifying translocation sites for wildlife (Paterson et al., 2008). In order to use this measure as a proxy for extinction risk, a species must both be intrinsically vulnerable to, and exposed to, a particular threatening factor. Here, we ask whether or not a species is fished in a commercial fishery. Therefore, a species that is both fished and intrinsically vulnerable to fishing can be said to have a higher risk of extinction. We use this imperilment measure (intrinsic vulnerability + fishing status) as our proxy for extinction risk.

We estimated the intrinsic vulnerabilities for the 69 of the 75 northeast Pacific rockfish species for which data exist using the fuzzy expert system developed by Cheung et al. (2005). We obtained the following nine morphological and life history traits in order to calculate a single intrinsic vulnerability score: maximum total length, maximum age, geographical range, age at first maturity, von Bertalanffy growth parameter *K*, natural morality, fecundity, strength of spatial behaviour and whether aggregating behaviour was related to feeding or spawning (Love et al., 2002; Froese and Pauly, 2008). We followed Cheung et al. (2005) to calculate the vulnerability scores, making only one minor change to the representation of geographical range. We used readily-available latitudinal range data converted to a binary variable based on interquartile ranges (fuzzy set: Highly restricted: <5°; Restricted: 2.5–11°) to make them directly comparable to the measure used in the original paper (a species' known distribution within the Exclusive Economic Zones (EEZs) and Food and Agriculture Organization (FAO) statistical areas; W. Cheung, pers. comm.). We calculated intrinsic vulnerability scores for all but two of the species (*Sebastes melanostictus* and *Sebastes variabilis*) for which we gathered morphological data, as well as for 10 other *Sebastes* species that are found in the northeast Pacific. We did not calculate the intrinsic vulnerability scores for four recently discovered cryptic species, *S. melanostictus, S. variabilis*, *Sebastes miniatus* Type 1 and *Sebastes saxicola* Type N, since their geographic range size is unknown and likely different than their sister species. Finally, for two additional northeast Pacific species, *Sebastes varispinis* and *Sebastes peduncularis*, we could not estimate vulnerability scores due to the lack of data available.

We gathered fishing data for all *Sebastes* species occurring in the northeast Pacific from several sources (Appendix A). In the commercial fishery in Japan, rockfish catch is not identified to the species level in the statistical data (Nakagawa et al., 2007) and therefore we were unable to obtain reliable fishery data for species outside of the northeast Pacific. We considered only commercial fisheries, both because the quality of recreational fishery data is highly variable and because species in our dataset that are not fished commercially also have no substantial recreational fishery (Love et al., 2002). Due to the inconsistencies between Canada and several states in the USA in the way catch data is reported and made publically available, we categorized species simply as fished or not fished. This is a decidedly coarse though likely unbiased measure and finer-scaled data would be preferable.

2.4. Analyses using evolutionary distinctiveness

We tested whether there was a simple parametric correlation between evolutionary distinctiveness and morphological distinctiveness (both total and size-independent distinctiveness). To evaluate the strength of the observed relationship between size-independent morphological distinctiveness and ED (see below), we calculated the expected correlation between ED and a set of traits simulated under random trait evolution, (R package GEIGER; Harmon et al., 2008), treating our PC axes as pseudocharacters. We first estimated the phylogenetic variance-covariance matrix between pseudocharacters (except PC1) under a multivariate Brownian motion model on the consensus phylogenetic tree using GEIGER (following Revell, 2007). We then simulated 999 datasets with the same covariance structure on the consensus rockfish phylogeny, again under a Brownian motion process (following Revell, 2007). The Brownian motion process models random evolution (e.g. under genetic drift or some models of randomly fluctuating natural selection; Felsenstein, 1985) and has traits evolve with variance increasing linearly with time. For each simulated dataset and pseudocharacter, we calculated the distance of each species from that character's across-species mean, a process that mirrors the distance from the origin in PCA space for the original dataset. We then calculated a species's combined pseudocharacter distinctiveness as the square-root(sum of squares) of these new, centered distances. These were then correlated with the ED scores for the species.

To examine how evolutionary distinctiveness and imperilment are related, we first tested whether there was a simple correlation between ED and intrinsic vulnerability. We then examined whether those species that are fished have significantly different intrinsic vulnerability or ED scores than average. To compare ED and imperilment directly, we asked whether the ED scores of species that are relatively imperilled (represented by the 12 species that are both fished and have intrinsic vulnerability to fishing scores within the top 25%) differ from the ED scores of species of lower threat within the northeast Pacific.

Overall, we have ED scores for all 112 species, including the 75 northeast Pacific species, body size data for 92 of the 112 species, vulnerability scores for 69 of the 75 northeast Pacific species, and morphological distinctiveness scores for 61 of the 75 northeast Pacific species (Appendix A).

3. Results

3.1. Evolutionary distinctiveness

The ED scores generated using the trees from the set of Bayesian trees (Appendix A) are normally distributed for each species, with a low coefficient of variation (average CV = 0.11). The correlation between these mean ED scores and the scores that we obtained using the consensus tree is, as expected, very strong ($r = 0.999$, $p < 0.0001$, $n = 112$), indicating that the ED scores from the consensus tree are an accurate representation of evolutionary distinctiveness for each species. We used the mean ED scores for all subsequent analyses unless otherwise noted. As reported for other groups (Redding and Mooers, 2006; Isaac et al., 2007) ED scores for our 112 rockfish species exhibit strong right skew, and were therefore log-transformed prior to all analyses.

Recalling that the tree is scaled to have a depth of 1.0, ED scores ranged from 0.132 ± 0.016 (mean ± standard deviation) for the greenblotched rockfish (*Sebastes rosenblatti*) to 0.831 ± 0.078 for the blackgill rockfish (*Sebastes melanostomus*). The next highest ranked species include sister species ukeguchi-mebaru (*Sebastes scythropus*) and kataboshi-aka-mebaru (*Sebastes kiyomatsui*, ED = 0.824) and the sister species Mexican rockfish (*Sebastes macdonaldi*) and yelloweye rockfish (*Sebastes ruberrimus*, with ED = 0.729). The cowcod, listed as a species of special concern (NMFS et al., 2008), ranked sixth (ED = 0.721) and the bocaccio, a critically endangered species (IUCN, 2007), along with its sister species shortbelly rockfish (*Sebastes jordani*) were ranked eighth and ninth, respectively (ED = 0.698, ED = 0.695). The chilipepper (*Sebastes goodei*, ED = 0.705) and the greenstripe rockfish (*Sebastes elongatus*, ED = 0.673) are also included in the top ten most evolutionarily distinctive species.

3.2. Morphology

PC1 explained 87.4% of the total morphological variation and loaded strongly with all linear measurements, indicating that it describes overall body size (Supplementary Table 1 and Supplementary Fig. 2). PC2 explained 8.2% of variance and loaded mainly with gill raker number and length, while PC3 explained 1.5% of variance and loaded most strongly with eye size. In rockfish these traits are related to aspects of species' niches, for example, PC2 is associated with diet (Ingram and Shurin, 2009). The remaining PC axes combine to explain very small amounts of total morphological variation (<2%) but are included for completeness (Supplementary Fig. 2).

As expected from the large amount of variance explained by PC1, species with extreme body sizes have the highest distinctiveness scores when all 18 PC axes are considered (Appendix A). For example, the most distinctive species is a dwarf species, the Puget Sound rockfish (*Sebastes emphaeus*). If we ignore PC1, thereby obtaining distinctiveness scores that are independent of body size, we found the most morphologically distinctive rockfish in our dataset to be the grass rockfish (*Sebastes rastrelliger*), a species with very short gill rakers.

3.3. Conservation status

Intrinsic vulnerability scores for 69 of the 75 rockfish species that are found in the northeast Pacific (Appendix A) are normally distributed, ranging from 12 (Guadalupe rockfish, *Sebastes notius*) to 80 (shortraker rockfish, *Sebastes borealis*). Other highly vulnerable species include the yelloweye rockfish (intrinsic vulnerability = 78.47), the cowcod (77.97), the bocaccio (70.91) and the canary rockfish (70.07), all of which have been declared overfished in the USA (NMFS et al., 2006), and the rougheye rockfish (77.43), listed as a species of special concern (Environment Canada, 2008). After examining commercial fishing records, we found almost two thirds (48 of 75) of the rockfish species in the northeast Pacific are fished commercially (Appendix A).

3.4. Analyses using evolutionary distinctiveness

There is a weak non-significant correlation between ED and total morphological distinctiveness represented using all 18 PC axes ($r = 0.226$, $p = 0.0797$, $n = 61$). The relationship between ED and size-independent morphological distinctiveness (PC axes 2–18) is, however, significant ($r = 0.312$, $p = 0.015$, $n = 61$, Fig. 2). We found the same relationships across the set of trees produced in the Bayesian analysis (PC axes 1–18: mean $r = 0.221 \pm 0.020$; PC axes 2–18: mean $r = 0.305 \pm 0.061$, $n = 1502$). This suggests that the results above are robust to changes in tree shape found across the set of Bayesian trees.

PC1 (representing size) has a large impact on overall morphological distinctiveness. As expected from the above, there is no relationship between distinctiveness as measured by PC1 alone (i.e. the absolute value of the deviation from the mean of PC1) and ED ($r = 0.202$, $p = 0.119$, $n = 61$). Interestingly, however, ED and raw PC1 are positively correlated ($r = 0.292$, $p = 0.022$), as are ED and total length ($r = 0.344$, $p = 0.0066$, $n = 61$, Fig. 3). When we examine the relationship between ED and body size using maximum total length measurements for a larger proportion of *Sebastes* species (92/112 species, obtained from Froese and Pauly, 2008), we still see a significant and positive relationship ($r = 0.232$, $p = 0.0260$, $n = 92$). Larger species are generally more evolutionarily distinctive.

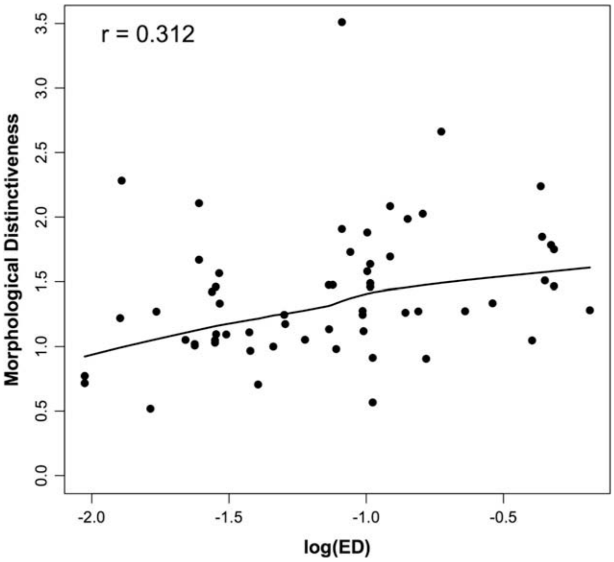

Fig. 2. The relationship between evolutionary distinctiveness (ED) and morphological distinctiveness measured on PC axes 2–18. ($r = 0.312$, $p = 0.015$, $n = 61$). The trend line is a loess smoother (span = 0.75).

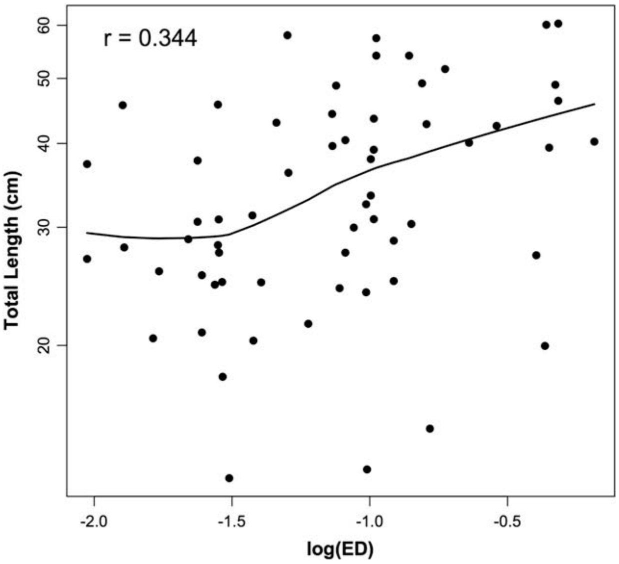

Fig. 3. The relationship between evolutionary distinctiveness (ED) and body size. ($r = 0.344$, $p = 0.0066$, $n = 61$). The trend line is a loess smoother (span = 0.75).

There is only a very weak positive relationship between total ED (using the scores generated from the consensus tree) and our combined pseudocharacter distinctiveness on the consensus tree (mean r across 999 replicates = 0.066, s.d. = 0.17). Sixty-six of the 999 simulated datasets returned a stronger positive correlation between ED and pseudocharacter distinctiveness than that observed ($p = 0.066$), suggesting that the observed correlation between ED and size-independent morphological distinctiveness is even larger than expected under evolution by Brownian motion.

ED and intrinsic vulnerability are positively related ($r = 0.319$, $p = 0.0075$, $n = 69$, Fig. 4), such that intrinsically vulnerable species are more likely to be evolutionarily distinctive. We find that species that are fished in commercial fisheries in the northeast Pacific are significantly more evolutionarily distinctive ($t = 2.64$, $p = 0.010$,

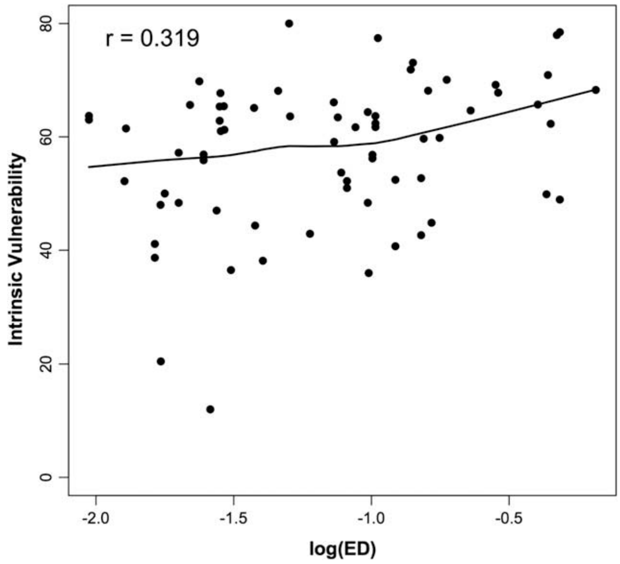

Fig. 4. The relationship between evolutionary distinctiveness (ED) and intrinsic vulnerability to fishing for those *Sebastes* species found in the northeast Pacific. ($r = 0.319$, $p = 0.0075$, $n = 69$). The trend line is a loess smoother (span = 0.75).

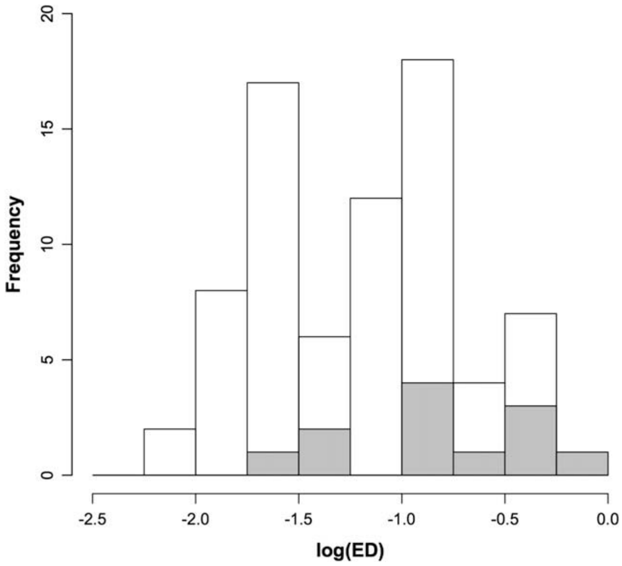

Fig. 5. The frequency distribution of ED scores among all *Sebastes* species found in the northeast Pacific. The shaded portions of the bars indicate species that are relatively imperilled (i.e. these species are commercially fished and their vulnerability scores are within the top 25%). These imperilled species have significantly higher ED scores ($t = 3.100$, $p = 0.0028$, $n = 72$) than those species that are not fished and/or have lower vulnerability scores.

$n = 75$) and more vulnerable ($t = 5.20$, $p < 0.0001$, $n = 69$) than those that are not fished. Indeed, those species that are most imperilled, by being both fished and most intrinsically vulnerable, have significantly higher ED scores than those species that are not fished or, if fished, have lower intrinsic vulnerability scores ($t = 3.10$, $p = 0.0028$, $n = 72$, Fig. 5).

4. Discussion

4.1. Characteristics of evolutionarily distinctive species

We found that for 61 species found in the northeast Pacific, evolutionarily distinctive rockfish species are morphologically distinctive and large-bodied. However, the relationship between morphological distinctiveness and ED is only significant when morphological distinctiveness is considered independently of body size. This indicates that the ED-morphology relationship is complex, such that the processes involved in morphological evolution are not uniform across traits. Our simulation results show that the relationship between size-independent distinctiveness and ED is marginally stronger than expected under evolution by a simple model of neutral change (Brownian motion). There are multiple possible explanations for this phenomenon. Speciation may be non-random with respect to species' traits, such that species in peripheral morphospace have lower diversification rates (Ricklefs, 2005). This might be the expectation under some versions of the niche-filling model, in which new species arise from species nearby in niche space (Price, 1997); species in marginal niche space will thus be less likely to speciate further. Another possibility is that *Sebastes* has experienced non-random extinctions and that evolutionarily distinctive species possess combinations of traits that allow them to persist even though their close relatives have gone extinct. Because we do not know how important extinction has been in shaping the present-day tree, it is hard to evaluate the relative likelihood of these two processes. Patterns of trait evolution vary widely across taxa, and so we make no generalizations about the relationship between ED and morphological distinctiveness based on this one taxon. In addition, our morphological and vulnerability results are based on a subset of the entire genus (from the northeast Pacific). The 61 species for which we obtained morphological data represent the full spread of morphological diversity found in rockfish, and the average ED scores from this subset are also indistinguishable from the entire genus ($t = 0.367$, $p = 0.714$, $n = 112$). It is likely that biogeography and community structure influence the evolution of rockfish morphology, but we have no reason to believe that our sample of rockfish morphologies is biased for the genus.

Our results provide evidence that the relationship between ED and morphological distinctiveness can be a useful way to explore aspects of species diversification. For example, the results may be relevant to the long-standing debate concerning the degree to which phenotypic change along lineages is concentrated at diversification events, though more direct tests of this hypothesis are preferable (Bokma, 2008). The observation that larger species are more likely to be evolutionarily distinctive than smaller species is intriguing, and may point to differences in diversification rates for large and small species in this genus. Although we may expect larger animals to have lower speciation rates because of life history traits such as longer life spans and slower maturation rates, comparative studies in several terrestrial groups have failed to find support for this hypothesis (Gittleman and Purvis, 1998; Orme et al., 2002). Among rockfish, however, preliminary data do suggest that larger species tend to have lower diversification rates (T. Ingram, unpub. data). We suggest that this prediction be tested in other marine fish groups (for freshwater fish see, e.g., Knouft and Page, 2003; Hardman and Hardman, 2008).

While the observation that large rockfish species are more likely to be evolutionarily distinctive is interesting from an evolutionary perspective, body size also has two important influences on the extinction risk of *Sebastes* species. First, larger species have an increased intrinsic vulnerability to fishing (Denney et al., 2002; see also references in Cheung et al., 2005) and second, larger species are also more likely to be fished. Therefore, larger-bodied species are particularly likely to be imperilled and in turn are more likely to have an increased extinction risk: body size mediates the positive relationship between ED and imperilment (Fig. 4). The fact that imperilled species are, on average, more evolutionarily distinctive than the remaining rockfish species (Fig. 5) that are found in the northeast Pacific is therefore not surprising. However, this implies that the species that are most threatened with extinction are precisely those species that represent the largest proportion of genetic and morphological diversity among rockfish species in the northeast Pacific. This is the case: if we constrain ourselves to the total phylogenetic diversity (PD, Faith, 1992) in the tree representing the 75 species in the northeast Pacific (total PD = 27 with root set at 1.0), removing 12 species randomly would yield an average drop of 3.0 units (s.d. = 0.637). If we remove the 12 (top quartile) most imperilled species, we lose 4.9 units, significantly more PD than expected under random species loss ($p < 0.002$, $n = 5000$ simulations).

4.2. Using ED in conservation prioritization

Our results support the implied message of the EDGE conservation program, that species that are globally endangered and have high ED are also "extremely unusual in the way they look, live and behave" and are therefore important species to conserve (see www.edgeofexistence.org). Whether the aesthetic value of conserving strange looking organisms is augmented by links between morphological distinctiveness and functional diversity and ecosystem processes (Tilman et al., 1997; Hulot et al., 2000; Post et al., 2008) remains to be seen.

To prevent such increased losses of biodiversity, we point to two ways to integrate ED into the framework that already exists to prioritize species for conservation. In the first approach one could use imperilment data to categorize species into one of two threat categories (e.g. 'high,' in the top quartile of imperilment, and otherwise 'low') and then use ED as a supplementary measure to rank species according to their conservation priority. Using this method, we found the top 12 species that should receive the most conservation attention (in order from greatest to least) are: blackgill rockfish, yelloweye rockfish, cowcod, bocaccio, canary rockfish, vermillion rockfish (*S. miniatus*), tiger rockfish, silvergray rockfish, rougheye rockfish, shortraker rockfish, quillback rockfish (*Sebastes maliger*) and dusky rockfish (*Sebastes ciliatus*). So, we use ED to isolate which species, among those that have already been identified using imperilment, should be the highest priority.

The second approach to incorporate ED into the prioritization framework would be to use ED as a measure complimentary to imperilment. This can be achieved by examining which species are among *both* the top most evolutionarily distinctive species and the most imperilled species. Of the 69 species for which we have intrinsic vulnerability scores and fishing data, the bocaccio, cowcod, yelloweye and blackgill rockfish species are all among the top 10 most evolutionarily distinctive and most imperilled. All of these species, with the exception of the blackgill rockfish, have been declared overfished by the NMFS, indicating that we have already over-exploited those species that are intrinsically more vulnerable to overfishing. This combined approach is analogous to the EDGE program's approach for combining different prioritization scores (Isaac et al., 2007; Redding and Mooers, 2006), and allows us to identify those species that might not receive conservation attention if only imperilment were considered. For example, the greenstripe rockfish has a relatively low vulnerability score, ranking 17th most vulnerable among the 48 species that are fished along the northeast Pacific coast. However, the greenstripe rockfish has a very high ED score, representing more unique evolutionary heritage than 90% of rockfish species worldwide. Using this approach, it would be identified as a species worth monitoring so that its conservation was assured.

5. Conclusion

We find that evolutionarily distinctive rockfish species are larger, more morphologically distinctive (independent of body size) and significantly more imperilled than those species that have lower ED and that this holds across a distribution of probable phylogenetic trees. The generality of this result depends partly on how body size relates to diversification rates and vulnerability in other taxa. Processes of morphological trait evolution, speciation and extinction will also help to determine attributes of evolutionarily distinctive species in different taxa. Investigation of these processes in additional taxa will allow us to more completely understand the characteristics of high ED species, and to assess how to best incorporate evolutionary distinctiveness into conservation prioritization.

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Appendix A

Mean evolutionary distinctiveness (ED) scores for all *Sebastes* species ($n = 112$), with standard deviations calculated over a probable set of 1502 trees with total tree depth scaled to 1. Of the 75 species found in the northeast Pacific, morphological distinctiveness (MD, calculated using all PCA axes) scores are given for 61 species and intrinsic vulnerability scores (/100) are given for 69 species. Fishing status is given for all *Sebastes* species found in the northeast Pacific. Fishing: 1 = commercially fished, 0 = not commercially fished. The geographical range is given for all species (NEP: northeast Pacific, NWP: northwest Pacific). The species that are among both the top 10 most evolutionarily distinctive and the top 10 most imperilled in the Northeast Pacific (see Section 4.2) are shown in boldface font.

Species	Common name	ED ± s.d.	MD	Vulnerability	Fishing	Fishing references[a]	Range
Sebastes melanostomus	**Blackgill**	**0.831 ± 0.078**	**3.13**	**68.28**	**1**	**9**	**NEP**
Sebastes kiyomatsui	Kataboshi-aka-mebaru	0.824 ± 0.063					NWP
Sebastes scythropus	Ukeguchi-mebaru	0.824 ± 0.063					NWP
Sebastes ruberrimus	**Yelloweye**	**0.729 ± 0.058**	**6.94**	**78.47**	**1**	**4, 5, 6, 8, 9**	**NEP**
Sebastes macdonaldi	Mexican	0.729 ± 0.058	4.32	48.93	0		Southern NEP

(continued on next page)

Appendix A (*continued*)

Species	Common name	ED ± s.d.	MD	Vulnerability	Fishing	Fishing references[a]	Range
Sebastes levis	**Cowcod**	**0.721 ± 0.095**	**4.80**	**77.97**	**1**[b]		**NEP**
Sebastes goodei	Chilipepper	0.705 ± 0.098	1.94	62.31	1	9, 11	NEP
Sebastes paucispinis	**Bocaccio**	**0.698 ± 0.098**	**5.90**	**70.91**	**1**	**9, 11**	**NEP**
Sebastes jordani	Shortbelly	0.695 ± 0.098	6.77	49.87	1	5, 9	NEP
Sebastes elongatus	Greenstripe	0.673 ± 0.079	2.25	65.7	1	9	NEP
Sebastes schlegelii	Kurosoi	0.636 ± 0.071					NWP
Sebastes taczanowskii	Ezo-mebaru	0.636 ± 0.071					NWP
Sebastes rufus	Bank	0.583 ± 0.085	2.85	67.8	1	9	Southern NEP
Sebastes glaucus	Gray	0.578 ± 0.06		69.18	0		N Pacific
Sebastes alutus	Pacific Ocean Perch	0.527 ± 0.044	2.51	64.65	1	6, 7, 8, 9, 11	N Pacific
Sebastes matsubarae	Akodai	0.515 ± 0.057					NWP
Sebastes minor	Akagaya	0.507 ± 0.051					NWP
Sebastes pinniger	Canary	0.483 ± 0.051	5.30	70.07	1	4, 5, 8, 9, 11	NEP
Sebastes gilli	Bronzespotted	0.471 ± 0.052		59.82	1	9	Southern NEP
Sebastes semicinctus	Halfbanded	0.458 ± 0.056	8.75	44.84	0		Southern NEP
Sebastes owstoni	Hatsume	0.458 ± 0.047					NWP
Sebastes miniatus Type 1	Sunset	0.452 ± 0.048			1	Cryptic species of *S. miniatus Type 2*	NEP
Sebastes miniatus Type 2	Vermillion	0.452 ± 0.048	3.67	68.15	1	5, 9	NEP
Sebastes baramenuke	Brickred	0.45 ± 0.041					NWP
Sebastes koreanus		0.447 ± 0.051					NWP
Sebastes nivosus	Gomasoi	0.447 ± 0.051					NWP
Sebastes oblongus	Takenokomebaru	0.447 ± 0.051					NWP
Sebastes babcocki	Redbanded	0.445 ± 0.065	4.25	59.67	1	9	N Pacific
Sebastes moseri	Whitespeckled	0.441 ± 0.065		52.71	0		NEP
Sebastes rufinanus	Dwarf-red	0.441 ± 0.065		42.65	0		Southern NEP
Sebastes nigrocinctus	Tiger	0.428 ± 0.063	2.14	73.09	1	4, 5, 8	NEP
Sebastes brevispinis	Silvergray	0.424 ± 0.039	5.34	71.88	1	4, 8	NEP
Sebastes rubrivinctus	Flag	0.401 ± 0.059	3.23	52.42	1	9	Southern NEP
Sebastes serriceps	Treefish	0.401 ± 0.059	2.74	40.7	1	9	Southern NEP
Sebastes trivittatus	Shimasoi	0.394 ± 0.038					NWP
Sebastes aleutianus	Rougheye	0.377 ± 0.037	5.85	77.43	1	4, 7, 8	N Pacific
Sebastes melanostictus	Blackspotted	0.377 ± 0.037	6.63		1	10	NEP
Sebastes entomelas	Widow	0.373 ± 0.047	2.39	61.72	1	5, 8, 9, 11	NEP
Sebastes mystinus	Blue	0.373 ± 0.047	2.29	62.39	1	5, 9	NEP
Sebastes proriger	Redstripe	0.373 ± 0.039	1.99	63.67	1	8, 9	N Pacific
Sebastes aurora	Aurora	0.369 ± 0.037	1.80	56.19	1	9	NEP
Sebastes phillipsi	Chameleon	0.369 ± 0.037	3.19	56.84	0		Southern NEP
Sebastes dallii	Calico	0.364 ± 0.045	9.76	35.97	0		Southern NEP
Sebastes joyneri	Togotto-mebaru	0.364 ± 0.027					NWP
Sebastes thompsoni	Usu-mebaru	0.364 ± 0.027					NWP
Sebastes hopkinsi	Squarespot	0.363 ± 0.052	4.24	48.37	0		Southern NEP
Sebastes ovalis	Speckled	0.363 ± 0.052	1.41	64.37	1	9	Southern NEP
Sebastes nebulosus	China	0.347 ± 0.043	1.73	61.7	1	4, 8, 9	NEP
Sebastes auriculatus	Brown	0.337 ± 0.042	2.56	50.97	1	9	NEP
Sebastes rastrelliger	Grass	0.337 ± 0.042	4.25	52.2	1	2, 9	NEP
Sebastes saxicola Type N	Stripetail	0.33 ± 0.037		NA[c]	0		NEP
Sebastes saxicola Type S		0.33 ± 0.037	2.96	53.69	0		NEP
Sebastes flavidus	Yellowtail	0.326 ± 0.04	3.98	63.44	1	5, 6, 8, 9, 11	NEP
Sebastes melanops	Black	0.321 ± 0.04	3.09	66.09	1	5, 9, 11	NEP
Sebastes serranoides	Olive	0.321 ± 0.04	1.54	59.12	1	9	Southern NEP
Sebastes hubbsi	Yoroimebaru	0.308 ± 0.033					NWP
Sebastes longispinis	Kôrai -yoroimebaru	0.308 ± 0.033					NWP
Sebastes rosaceus	Rosy	0.294 ± 0.041	3.74	42.9	1	9	NEP
Sebastes caurinus	Copper	0.274 ± 0.034	1.43	63.62	1	4, 8, 9	NEP
Sebastes borealis	Shortraker	0.273 ± 0.028	6.78	80	1	4, 7, 8	N Pacific
Sebastes viviparus	Norway redfish	0.267 ± 0.029					NE Atlantic
Sebastes maliger	Quillback	0.262 ± 0.034	3.44	68.12	1	4, 8	NEP
Sebastes atrovirens	Kelp	0.248 ± 0.032	2.76	38.14	1	9	Southern NEP
Sebastes flammeus	Sankomenuke	0.247 ± 0.022					NWP
Sebastes iracundus	Osaga	0.247 ± 0.022					NWP
Sebastes ensifer	Swordspine	0.241 ± 0.034	4.89	44.35	1	9	Southern NEP

Appendix A (*continued*)

Species	Common name	ED ± s.d.	MD	Vulnerability	Fishing	Fishing references[a]	Range
Sebastes zacentrus	Sharpchin	0.24 ± 0.029	1.11	65.11	1	9	NEP
Sebastes fasciatus	Acadian redfish	0.239 ± 0.019					NW Atlantic
Sebastes inermis	Mebaru	0.229 ± 0.018					NWP
Sebastes ventricosus		0.229 ± 0.018					NWP
Sebastes cheni		0.229 ± 0.017					NWP
Sebastes ijimae	Kôrai-kitsunemebaru	0.224 ± 0.017					NWP
Sebastes vulpes	Kitsunemebaru	0.223 ± 0.016					NWP
Sebastes zonatus	Tanukimebaru	0.223 ± 0.016					NWP
Sebastes emphaeus	Puget Sound	0.221 ± 0.023	10.78	36.49	0		NEP
Sebastes wilsoni	Pygmy	0.216 ± 0.021	6.65	61.25	0		NEP
Sebastes variegatus	Harlequin	0.215 ± 0.021	3.22	65.41	0		NEP
Sebastes helvomaculatus	Rosethorn	0.213 ± 0.031	1.49	67.72	0		NEP
Sebastes polyspinis	Northern	0.213 ± 0.023	2.49	61.02	1	1, 7	N Pacific
Sebastes crameri	Darkblotch	0.212 ± 0.023	1.08	62.84	1	5, 9	NEP
Sebastes reedi	Yellowmouth	0.212 ± 0.023	3.83	65.35	1	6, 8	NEP
Sebastes itinus	Yanagi-mebaru	0.212 ± 0.022					NWP
Sebastes steindachneri	Yanaginomai	0.212 ± 0.021					NWP
Sebastes wakiyai	Gayamodoki	0.212 ± 0.021					NWP
Sebastes simulator	Pinkrose	0.21 ± 0.029	2.63	47	0		Southern NEP
Sebastes mentella	Deepwater redfish	0.208 ± 0.016					N Atlantic
Sebastes norvegicus	Golden Redfish	0.208 ± 0.016					NE Atlantic
Sebastes notius	Guadalupe	0.205 ± 0.03		12	0		Southern NEP
Sebastes carnatus	Gopher	0.2 ± 0.024	4.60	56.89	1	9	Southern NEP
Sebastes chrysomelas	Black and Yellow	0.2 ± 0.024	3.19	55.87	1	9	NEP
Sebastes ciliatus	Dusky	0.197 ± 0.017	1.80	69.8	1	3	N Pacific
Sebastes variabilis		0.197 ± 0.017	1.89		1	3	N Pacific
Sebastes diploproa	Splitnose	0.19 ± 0.016	1.21	65.64	1	9	NEP
Sebastes varispinis	Hidden	0.19 ± 0.016		NA[c]	0		Southern NEP
Sebastes exsul	Buccaneer	0.183 ± 0.024		48.36	0		Gulf of California
Sebastes spinorbis	Spiny-eye	0.183 ± 0.024		57.2	0		Southern NEP
Sebastes nigricans		0.178 ± 0.016					NWP
Sebastes chalcogrammus	Akabuchi-murasoi	0.178 ± 0.015					NWP
Sebastes nudus	Ogon-murasoi	0.178 ± 0.015					NWP
Sebastes pachycephalus	Murasoi	0.178 ± 0.015					NWP
Sebastes sinensis	Blackmouth	0.174 ± 0.013		50	0		Gulf of California
Sebastes cortezi	Cortez	0.171 ± 0.014		48	0		Gulf of California
Sebastes melanosema	Semaphore	0.171 ± 0.013	2.24	20.46	0		Southern NEP
Sebastes lentiginosus	Freckled	0.168 ± 0.023		38.67	0		Southern NEP
Sebastes umbrosus	Honeycomb	0.168 ± 0.023	4.29	41.11	0		E central pacific
Sebastes peduncularis	Gulf	0.168 ± 0.012		NA[c]	0		Gulf of California
Sebastes constellatus	Starry	0.151 ± 0.021	2.71	61.48	1	9	Southern NEP
Sebastes eos	Pink	0.15 ± 0.02	4.18	52.18	0		Southern NEP
Sebastes capensis	False Jacopever	0.135 ± 0.017					SE Atlantic
Sebastes oculatus	Patagonian Redfish	0.135 ± 0.017					SW Pacific, SE Atlantic
Sebastes chlorostictus	Greenspotted	0.132 ± 0.016	1.61	63.02	1	9	NEP
Sebastes rosenblatti	Greenblotched	0.132 ± 0.016	2.07	63.71	1	9	Southern NEP

[a] References: 1. Love et al. (2002), 2. Buonaccorsi et al. (2004), 3. Orr and Blackburn (2004), 4. Fisheries and Oceans Canada (2006), 5. Oregon Department of Fish and Wildlife (2006), 6. Fisheries and Oceans Canada (2007), 7. NMFS et al. (2007), 8. Fisheries and Oceans Canada (2008), 9. Hyde and Vetter (2008) 10. Annual Landing Statistics for 2006; Pers. Comm. NMFS, Fisheries Statistics Division, Silver Spring, MD; see <http://www.st.nmfs.noaa.gov/st1/commercial/index.html>, 11. Orr and Hawkins (2008), 12. Sea Around Us (2008).

[b] Although the cowcod is no longer fished, we have treated this species as fished since its population is severely depleted due to past fishing pressures (Love et al., 2002; NMFS et al., 2006).

[c] Even though we were unable to calculate intrinsic vulnerability scores for these species, we have included them in the ED-imperilment analysis because there is no significant fishery for these species and therefore we are certain they are not among the most imperilled species due to fishing.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.03.020.

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