

VULNERABILITY OF SEAMOUNT FISH TO FISHING: FUZZY ANALYSIS OF LIFE-HISTORY ATTRIBUTES

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ABSTRACT

Based on life history and ecological characteristics, several authors have placed seamount fishes at the extreme end of the vulnerability spectrum. However, it was still unclear if there is justification for the generalization that seamount fishes overall possess specific life-history characteristics that render them more vulnerable to fishing than other species. In this contribution, we test the hypothesis that seamount fishes generally have a high vulnerability to fishing, and that this is correlated with their life-history characteristics. Despite rather broad definitions, our global analysis shows that seamount fishes, particularly seamount-aggregating fishes, have higher intrinsic vulnerability than other groups of marine fishes. The pattern is similar when we considered only commercially exploited species. Biological characteristics leading to greater vulnerability of seamount fishes include a long lifespan, late sexual maturation, slow growth and low natural mortality. In light of our research, this experience supports that seamount fishes, especially those that aggregate on seamounts, are highly vulnerable to exploitation and that fishing on seamount will tend to be unsustainable, given current levels of exploitation and current fishing methods. A number of seamount populations have already been depleted. More will be depleted and some will go extinct if fishing on seamounts continues at current, or even more moderate levels.

INTRODUCTION

Seamounts are biologically distinctive habitats of the open ocean exhibiting a number of unique features (Rogers, 1994). Seamounts have received much attention mainly because of the presence of substantial aggregations of fishes in mid- and deep-water (Boehlert and Sasaki, 1988; Koslow, 1996; 1997; Koslow et al., 2000), which became the prime target of a highly technological fishery. Based on life history and ecological characteristics, several authors have placed seamount fishes at the extreme end of the vulnerability spectrum (Koslow, 1997; Branch, 2001; Boyer et al., 2001; Clark, 2001). However, with the exception of work by Koslow (1996) and Froese and Sampang (this vol.), few attempts have been made to review, summarize and compare the life-history of seamount species. Therefore, the generalization that seamount fishes overall possess specific life-history characteristics that render them more vulnerable than other species is still uncertain.

Responses of a fish species to exploitation may be partly determined by life history and ecological characteristics (Adams, 1980; Roff, 1984; Stokes et al., 1993; Kirkwood et al., 1994). Fish that mature late and have low growth and low mortality rates, likely have higher vulnerability to fishing (Jennings et al., 1998; 1999; Russ and Alcala, 1998; Musick, 1999; Denney et al., 2002; Froese and Sampang, this vol.). In addition, species that display social aggregation behaviours such as shoaling, schooling (Pitcher and Parrish, 1993) or shoal spawning may have higher vulnerability because of increased catchability (Sadovy and Domeier, in press), leading to hyperstability of catch rates (Pitcher, 1995; 1997; Hilborn and Walters, 1992; Walters, 2003), and the possible disruption of group spawning behaviour by fishing (Johannes, 1998; Sala et al., 2001; Sadovy and Domeier, in press).

Even though the designation of 'seamount' species has been widely employed (e.g. Koslow, 1996; Probert et al., 1997; Probert, 1999; Koslow et al., 2000; Fock et al., 2002; Tracey et al., 2004), rigorous criteria used in identifying these taxa have not been clearly defined (see Froese and Sampang, this vol., and Watson and Morato, this vol.). Koslow (1996) categorized species that aggregate in association with seamounts and other topographic features as 'seamount-associated' fishes. Some of the most well known representatives of this group include the deep-water fishes: Orange roughy (*Hoplostethus atlanticus*), Alfosinos (*Beryx splendens* and *B. decadactylus*), Patagonian toothfish (*Dissostichus eleginoides*), Oreos (e.g. *Alloctytus niger*, *Pseudocyttus maculatus*), Pelagic armorhead (*Pseudopentaceros wheeleri*), several species of Rockfishes (*Sebastes* spp.) (Koslow 1996; Koslow et al., 2000) and probably Roundnose grenadier (*Coryphaenoides rupestris*) (Vinnichenko, 2002a). Vulnerability of 'seamount-associated' fishes is of particular concern from a management point of view because they are the prime targets of seamount fisheries.

Many other fish species, however, occur on seamounts or congregate over their summits to feed on the rich booty. This may be the case for some sharks (Klimley et al., 1988; Hazin et al., 1998), tunas (Holland et al., 1999; Itano and Holland, 2000; Sibert et al., 2000) and other large pelagic predators (Ward et al., 2000; Sedberry and Loefer, 2001). Some other fish species aggregate around shallow seamounts mainly for spawning, for instance, reef-associated fish such as groupers (*Mycteroperca rosacea*, *Paranthias colonus*) and jacks (*Caranx sexfasciatus*, *Seriola lalandi*) (Sala et al., 2003). Recently, Tsukamoto et al. (2003) found that the spawning site of the Japanese eel (*Anguilla japonica*) in the western North Pacific, appears to be near three seamounts, 2000-3000 km away from their freshwater adult feeding habitats. In this study 'seamount fishes' were considered as all fish species that have been reported for seamounts, and 'seamount-aggregating fishes' were those that fall into the category defined by Koslow (1996).

In this paper we attempt to test the hypothesis that seamount fishes generally have a high vulnerability to exploitation and that this is correlated with their life history characteristics. We build on previous studies that have found that vulnerability of fishes to exploitation is correlated with their life history characteristics (Froese and Sampang, this vol.; Cheung et al. this vol.). We estimate vulnerability quantitatively by analysis of life-history characteristics using a fuzzy-logic algorithm.

METHODS

Compilation of species list

Seamount fishes are defined as fish that have been reported as occurring on seamounts. In order to include some of the most important seamount fishes, a list of fish species occurring for seamounts worldwide (Froese and Sampang, this vol.) was augmented from additional sources (Appendix 1): Menezes (2003) and Melo and Menezes (2002) for fish species occurring on the Azorean seamounts; OASIS (2004) for species collected on Seine and Sedlo Seamounts (North-eastern Atlantic); Moore et al. (2001; 2002) for species from Bear seamount (North-western Atlantic); Kukuev (2002) for species at Mid Atlantic Ridge seamounts; Canessa et al. (2003) for Bowie seamount (North-eastern Pacific); Hughes (1981) for some Alaskan seamounts (North-eastern Pacific); and Tracey et al. (2004) for species occurring on New Zealand seamounts (South-western Pacific). A total of 794 species of marine fishes were classified as occurring on seamounts (even if rare). Additionally, we compiled a list (Table 1) of 23 seamount-aggregating fishes as defined by Koslow (1996). We acknowledge that this list (Table 1) is preliminary and its accuracy will improve as we gain more knowledge about the ecology of seamount and deepwater fish species.

Comparisons of biological characteristics and vulnerabilities

Using Fishbase (Froese and Pauly, 2003) and other sources, we compiled 6 life history attributes for over 14,000 marine fish species (Table 2: longevity, T_{Max} ; age at maturity, T_m ; asymptotic length, L_{∞} ; fecundity, Fec ; von-Bertalanffy growth parameter, K ; and natural mortality rate, M) together with information on preferred habitat (pelagic, demersal, reef-associated, benthopelagic, bathypelagic and bathydemersal). We used only those parameters directly estimated from empirical studies, while excluding those that were calculated from empirical relationships between life history parameters. If more than one estimate was available for a particular life history parameter of a particular species, we used the arithmetic mean.

The intrinsic vulnerability (Vul) was estimated for over 14,000 species of marine fishes based on their life history and ecological characteristics using a fuzzy¹ expert system (Cheung et al., this vol.). Cheung et al. (this vol.) defined two categories of extinction risk: (1) Intrinsic vulnerability, i.e., vulnerability to exploitation inherent to a species, as determined by its life history and ecology, and independent of external factors such as fishing intensity and environment; and (2) Total vulnerability, i.e., the risk of extinction resulting from both intrinsic and external factors. Only 1600 vulnerability estimates (Table 2) were included in comparative analyses because those species for which total length was the only available parameter were excluded from further analyses.

¹ Fuzzy logic was originally developed to represent gradation of truth, instead of classifying objects as either 'true' or 'false', thus allowing vagueness, while based on rigorous mathematic. The explicit use of vagueness in fuzzy logic is very useful for handling the uncertainty inherent to extinction vulnerability (see Cheung et al., this vol.).

Table 1. List of species considered as seamount-associated fishes (*sensu* Koslow, 1996).

Species	Aggregation	Reference
<i>Alepocephalus bairdii</i>	Maybe	6, 11
<i>Allocyttus niger</i> ^c	True	3, 4
<i>Allocyttus verrucosus</i> ^a	Maybe	12
<i>Aphanopus carbo</i> ^b	True	10
<i>Beryx decadactylus</i>	True	4, 9
<i>Beryx splendens</i>	True	3, 4, 7, 9
<i>Coryphaenoides rupestris</i>	True	8, 5
<i>Dissostichus eleginoides</i>	True	4
<i>Epigonus telescopus</i> [*]	True	10, 5
<i>Hoplostethus atlanticus</i>	True	3, 4, 8, 5
<i>Hoplostethus mediterraneus</i>	Maybe	6
<i>Lepidion eques</i> [*]	Maybe	6
<i>Mora moro</i>	Maybe	6
<i>Neocyttus rhomboidalis</i> ^{*, a}	Maybe	11
<i>Pseudocyttus maculatus</i> ^a	True	3, 4
<i>Pseudopentaceros richardsoni</i>	True	9
<i>Pseudopentaceros wheeleri</i> [*]	True	2, 3, 4
<i>Sebastes entomelas</i> ^{*, c}	Maybe	1
<i>Sebastes helvomaculatus</i> ^{*, c}	Maybe	1
<i>Sebastes marinus</i>	True	5
<i>Sebastes mentella</i>	True	8
<i>Sebastes paucispinis</i> ^c	Maybe	1
<i>Sebastes ruberrimus</i> ^c	Maybe	1

* intrinsic vulnerability index not estimated due to insufficient parameters; a) forming large shoals over rough ground near pinnacles and canyons; b) not a typical seamount-associated fishes (*sensu* Koslow, 1996); c) juveniles form large schools. References: 1) Parker and Tunnicliffe, 1994; 2) Rogers, 1994; 3) Koslow, 1996; 4) Koslow et al., 2000; 5) Hareide and Garnes, 2001; 6) Piñeiro et al., 2001; 7) Ramos et al., 2001; 8) Shibanov et al., 2002; 9) Vinnichenko, 2002a; 10) Vinnichenko, 2002b.; 11) Allain et al., 2003; 12) Fishbase: Froese and Pauly (2003).

We compared biological characteristics and the estimated fuzzy intrinsic vulnerabilities between non-seamount fishes, seamount fishes and seamount-aggregating fishes. Intrinsic vulnerability was also estimated for those species reported in the Food and Agriculture Organization (FAO) official landing statistics, to test if commercially targeted seamount fish species were also more vulnerable than other fish species. To explore what fish groups may be responsible for differences in vulnerabilities between seamount and non-seamount fishes, we estimate vulnerabilities for different fish groups occurring and non-occurring on seamounts. Additionally, we addressed the question whether seamount fishes are more vulnerable than deep-sea fishes in general by comparing intrinsic vulnerability of bathydemersal fishes not occurring on seamounts (our 'deep-sea' control fish group) with seamount fishes and seamount-aggregating fishes. Differences between the biological characteristics and intrinsic vulnerability estimates of the two groups were tested with Mann-Whitney (U) non-parametric statistics (see Zar, 1999).

Responses to fishing

We evaluated the relationship between vulnerability estimates and biomass change over time caused by fishing using a simulation model. We used a mass-balanced ecosystem model (Ecopath with Ecosim, see Christensen and Walters, 2004 for details) developed for a theoretical, isolated North Atlantic seamount (Morato and Pitcher, 2002). This model included 37 functional groups, of which twenty were fish groups assembled according to environment preference (i.e., depth and habitat: e.g. benthic, pelagic or benthopelagic), body size, energetics and life-history characteristics (see Morato and Pitcher, 2002 for a complete description of the model). The seamount fisheries were loosely based on those operating at the Azores / Mid Atlantic Ridge, and thus divided in 6 fleets (see Morato and Pitcher, 2002). We simulated biomass changes over 20 years by assuming a fishing mortality rate of 0.3 for one fish group at a time.

Table 2. Occurrence of fish species on seamounts, and number of species for which specific parameters are available. Data for those species that form aggregations on seamounts is also shown”.

Species group	Number of spp	T_{max}	T_m	M	K	L_{∞}	Fec	Vul^*
Non-Seamounts	14927	432	462	177	1089	11903	483	1409
Seamounts	795	90	83	37	148	723	76	191
Seamount-aggregating	23	19	16	10	18	22	11	18

*Here T_{max} is the longevity; T_m the mean age at first maturity; M is the natural mortality, K is a parameter of the von-Bertalanffy Growth Function (VBGF) of dimension 1/time; L_{∞} is another VBGF parameter, closely related to maximum observed length (L_{max}); Fec is total fecundity, and Vul is the intrinsic vulnerability. Even though vulnerability was estimated for almost all fish species (n= 14148), this table only shows the number of species included in further analysis, i.e. excluding those species for which only L_{∞} was available.

Additionally, we compared the relative extinction risk between each seamount fish group in the simulation model using a quantitative index. The index takes into account the fuzzy intrinsic vulnerabilities of the composite species of each functional group, and the simulated changes in biomass of the group (Cheung et al., this vol.). Essentially, a functional group with a higher index (scaled between 1 to 100) implies a higher risk of extinction for the species it contains.

RESULTS

We found significant differences in longevity and age at maturity among seamount, non-seamount and seamount-aggregating fishes (Figure 1). The longevity (Figure 1a) of seamount fishes was significantly higher than non-seamount fishes (median = 25 years and 12 years respectively; U ; $p < 0.001$). Seamount-aggregating fishes have the highest longevity among the three categories (median T_{Max} = 52 years), although the difference is significant only the comparison is with non-seamount fishes (U ; $p < 0.001$). Non-outliers' ranges of longevity of seamount-aggregating fishes (11.6-149 years) are also larger than both the seamount fishes (1-118 years) and non-seamount fishes (0.5-48 years). Accordingly, the age at maturity (Figure 1b) of both seamount and seamount-aggregation fishes were significantly higher (median T_m = 4.3 years and 9.9 years respectively) than the non-seamount fishes (median T_m = 3.0 y) (all U ; $p < 0.001$). Seamount-aggregating fishes also have a significantly higher age at maturity than seamounts fishes (U ; $p < 0.001$).

Comparisons of natural mortality rate (Figure 1c) and the von Bertalanffy growth parameter K (Figure 1d) among the three categories of fishes show similar, but reciprocal, trends as longevity and age at maturity. Seamount-aggregating fishes have the lowest natural mortality and lowest K values (median M = 0.16 and median K = 0.09), while non-seamount fishes have the highest values among the three fish categories (median M = 0.60 and median K = 0.34). All paired comparisons were significantly different at the 1% confidence level (U ; $p < 0.001$), with the exception of the comparison of natural mortality for seamount fishes and seamount-aggregating fishes, which was significant different at the 5% confidence level (U ; $p = 0.037$).

We observed a significant difference between the estimated intrinsic vulnerabilities of seamount, non-seamount and seamount-aggregating fishes. Median intrinsic vulnerabilities (Figure 2a) for non-seamount fishes, seamount and seamount-aggregating fishes were estimated to be 45.0, 51.8 and 68.2 respectively. The differences in intrinsic vulnerabilities are significant both comparing non-seamount and seamounts fishes (U ; $p < 0.001$) and comparing seamount fishes and seamount-aggregating fishes (U ; $p < 0.007$).

Vulnerabilities of fish reported as catches in the FAO landings statistics were also higher for seamount fishes, and significantly different from the median for non-seamount fishes (U ; $p < 0.001$). However, there were no significant differences between the vulnerabilities of seamount fishes and seamount-aggregating species (U ; $p < 0.111$), even though the median was higher for the later. Additionally, we estimated the mean of vulnerability weighted by the logarithm of the catch (Table 3). Similarly, vulnerability was higher for seamount-aggregation species and lower for non-seamount fishes.

Table 3. Intrinsic vulnerability weighted by log(catch) for seamount and seamount-aggregating species reported explicitly in FAO catches.

	Non-seamounts	Seamounts	Seamount-aggregating
Number of Species	508	102	13
Vulnerability	39.9	47.9	64.5

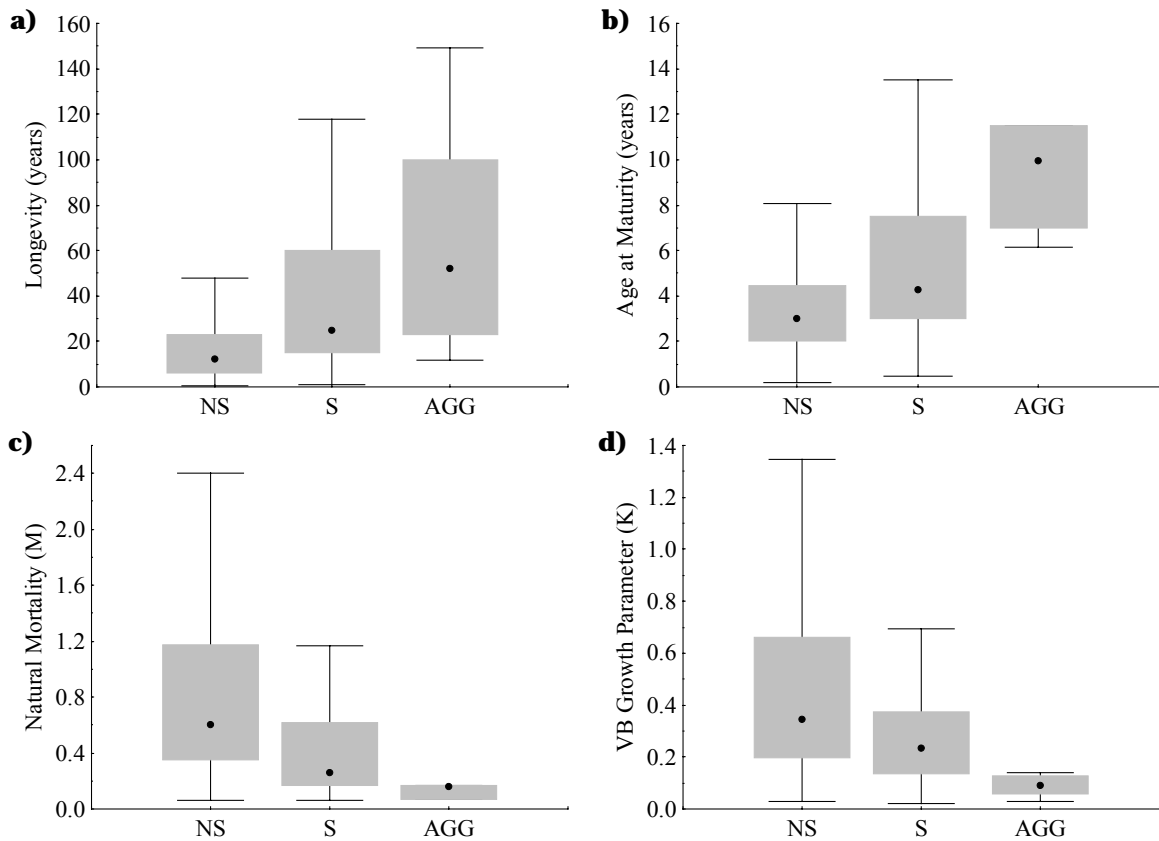


Figure 1. Comparison of some life-history characteristics of non-seamount fish species (NS), fish occurring on seamounts (S), and seamount-aggregating species (AGG); a) longevity (T_{Max}); b) age at maturity (T_m); c) natural mortality (M); d) von Bertalanffy growth parameter (K). In the graphs, the middle point is the median, the box represents the 25%-75% percentiles, and the whisker the range, excluding outliers.

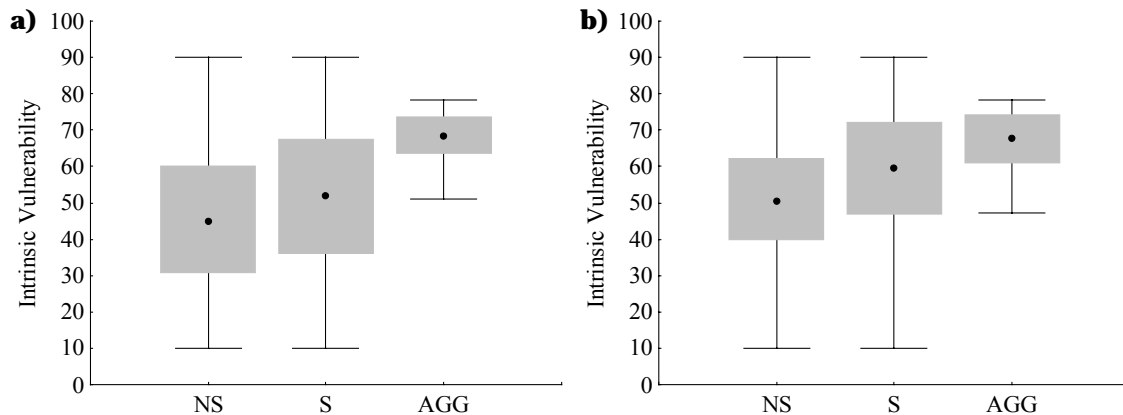


Figure 2. Intrinsic vulnerability index for fish species no-occurring on seamounts (NS), occurring on seamounts (S), and seamount-aggregating species (AGG); a) including all fish species; b) for species reported in FAO official landing statistics. In the graphs the middle point is the median, while the box represents the 25%-75% percentiles, and the whisker the range, excluding outliers.

The differences in vulnerability between seamount and non-seamount fishes were mainly due to benthopelagic and demersal fishes (Figure 3), which were found to have significant different medians of intrinsic vulnerability (U ; Demersal $p= 0.003$; Benthopelagic $p= 0.001$). For all other fish groups, the paired comparisons of medians were not significantly different. We also found that the bathydemersal fishes, benthopelagic and demersal fishes were among the most vulnerable fish groups, with seamount-aggregating fishes having the highest intrinsic vulnerability.

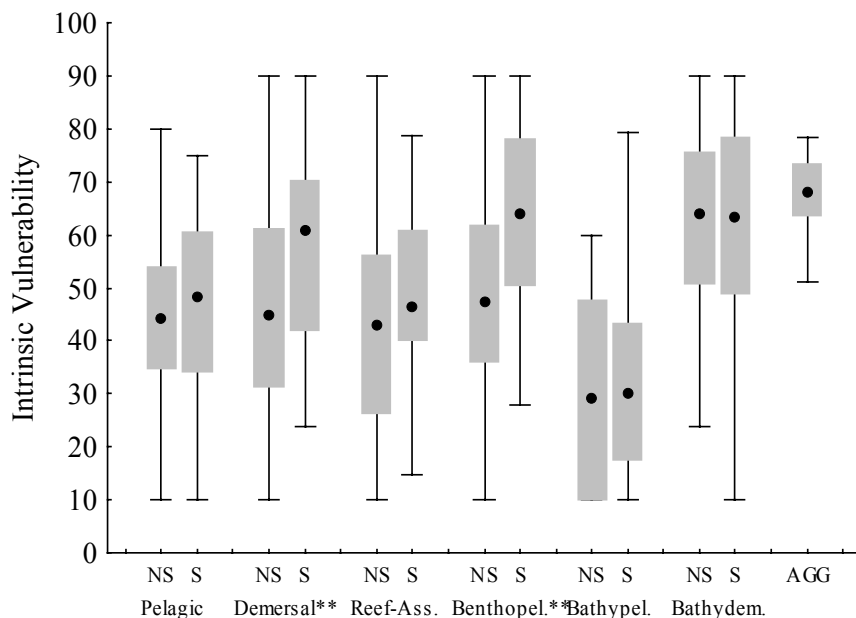


Figure 3. Intrinsic vulnerability index for fish species of different habitats: not-occurring on seamounts (NS), occurring on seamounts (S). The vulnerability for seamount-aggregating species (AGG) is also presented. In the graphs the middle point is the median, the box the 25%-75% percentiles, and the whisker is the range. ** indicates significant differences between medians (Mann-Whitney test; Pelagic: $p= 0.471$; Demersal: $p= 0.003$; Reef-Associated: $p= 0.076$; Benthopelagic: $p= 0.001$; Bathypelagic: $p= 0.806$; Bathydemersal: $p= 0.833$).

Vulnerabilities of the ‘deep-sea fish’ group (bathydemersal fishes not occurring on seamounts) (median $Vul= 64.0$) were not significantly different from seamount demersal fishes (median $Vul= 61.0$; $U, p= 0.194$), seamount benthopelagic fishes (median $Vul= 64.0$; $U, p= 0.819$) and seamount bathydemersal fishes (median $Vul= 63.5$; $U, p= 0.833$). Seamount-aggregating fishes (median $Vul= 68.2$) were the only group having higher vulnerability estimates than the ‘deep-sea fish’ group, but this difference were not significant ($U, p= 0.335$).

We found that vulnerabilities estimates for bathydemersal fishes non-occurring on seamounts, the ‘deep-sea fish’ group, (median $Vul= 64.0$) were similar and not significantly different from the vulnerabilities estimated for seamount demersal fishes (median $Vul= 61.0$; $U, p= 0.194$), seamount benthopelagic fishes (median $Vul= 64.0$; $U, p= 0.819$) and seamount bathydemersal fishes (median $Vul= 63.5$; $U, p= 0.833$). Seamount-aggregating fishes (median $Vul= 68.2$) was the only group having higher vulnerability estimates than the ‘deep-sea fish’ group, but this difference were not significant ($U, p= 0.335$).

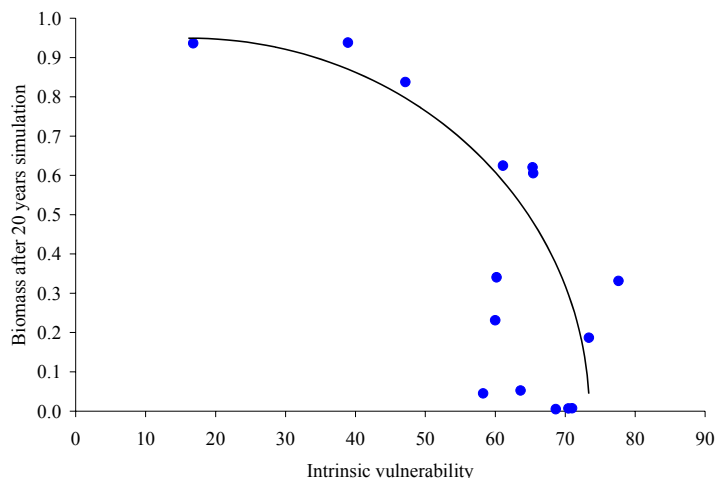


Figure 4. Biomass decline over time for fish groups with different intrinsic vulnerabilities. Biomass change was estimated by a generic seamount ecosystem model (Morato and Pitcher, 2002) and simulating the effect of a 0.3 fishing mortality rate for each group over a 20 years period.

We found that the intrinsic vulnerabilities estimated from the fuzzy system were significantly related ($R^2= 0.645, p= 0.007$) to the simulated population declines of marine fish groups (Figure 4) caused by fishing. Groups of species with higher vulnerabilities had larger biomass declines than species with lower vulnerabilities. Moreover, our simulation showed that even at modest levels of fishing, seamount species were depleted, not sustained.

Our estimates of relative risk of extinction (Figure 5) showed that seamount fishes (Orange roughy, Alfonsinos and seamount-aggregating fish) have the highest indices, followed by deepwater bottom fish (bathydemersal and bathybenthic) and elasmobranchs (rays, skates and sharks).

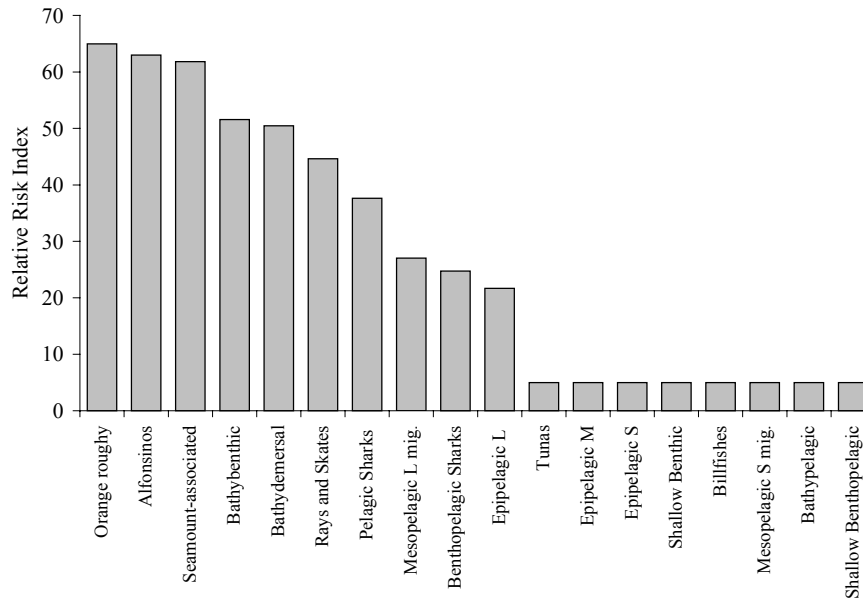


Figure 5. Relative risk of extinction for fish groups used in a generic seamounts ecosystem model (Morato and Pitcher, 2002).

DISCUSSION

Despite our rather broad definitions, our global analysis of over 14,000 species shows that seamount fishes, particularly seamount-aggregating fishes, have higher intrinsic vulnerability than other groups of fishes. The pattern is similar when we considered commercially-exploited species only. Biological characteristics leading to greater vulnerability include a longer lifespan, later sexual maturation, slower growth and lower natural mortality. These findings are in agreement with the life-history features of seamount fishes proposed by Koslow (1996; 1997), although very few complete case studies are available.

The high vulnerability raises serious conservation concerns about the exploitation of seamount fishes. Our simulation model confirmed that the biomass of fish with higher vulnerabilities declined more rapidly under exploitation. Although data limitations prevents us from validating the modelling results using empirical data, evidence from other species assemblages suggests a significant positive correlation between vulnerability and population decline (Cheung et al., this vol.). Considering that seamount fishes are increasingly being targeted by fishing (Watson and Morato, this vol.), highly vulnerable seamount species such as Orange roughly, Alfonsinos and other seamount-aggregating fishes may be under considerable risk of local extinction under only moderate fishing intensity ($F=0.3 \text{ year}^{-1}$ in our simulation model).

In the light of this analysis, we may ask whether seamount fisheries may be sustainable in the long term (Clark, 2001); our simulations suggest that exploitation rates of more than 5% are not sustainable. Examples from all over the world have shown the 'boom and bust' characteristic of seamount trawling fisheries, with rapid stock reduction and serial depletion of successively exploited new seamounts. The case of the Orange roughly, a seamount-aggregating fish, is well known. In Namibian waters, Orange roughly has been fished down to 10% of its pre-exploitation biomass in six years (Branch, 2001), while in Australia, biomass levels dropped to 7-13% in about 15 years (Lack, 2003). The Orange roughly stock in New Zealand was fished down to 15-20% of pre-exploitation level in less than 15 years (Clark, 2001), while annual sustainable levels of fishing have been estimated to be less than 2% of pre-exploitation level (Francis et al., 1995), which may not be economically viable. Another example is Russian fishing on seamounts at the Mid Atlantic Ridge. Vinnichenko (2002a) showed that the total catch (mainly of Alfonsino, *Beryx splendens* and Scabbardfish *Lepidopus caudatus*) at nine seamounts in the South Azores area and in three seamounts at the Corner Rising area declined, in each area, from 12,000 t to below 2,000 t in just two years. In a larger area of the ridge that included 34 seamounts, catches declined from 30,000 t to below 2,000 t in about 15 years (mainly Roundnose grenadier, *Coryphaenoides rupestris*, and Orange roughly).

Deep-water species have also been considered sensitive to exploitation owing to their biological parameters (Merrett and Haedrich, 1997; Roberts, 2002). Our analysis supports this theory by showing that bathydemersal fishes were far more vulnerable than any other non-seamount group of fish; only seamount aggregating fish had higher vulnerabilities.

The high vulnerability of seamount fishes should be a strong reason for more precaution in managing seamount resources. Collapse of seamount fisheries have often been attributed to lack of management. However, even in places where detailed research programmes were implemented at the same time that trawl fisheries exploitation started, and where scientific recommendation for management were followed and fisheries controlled, catches have declined unexpectedly fast and stocks have been depressed well below the biomass generating maximum sustainable yield (Boyer et al., 2001). In light of our research, this experience supports the conclusion that fishing on seamount is not sustainable, at current levels and with current methods. A number of seamount populations have already been depleted. More will be depleted and some will go extinct if fishing on seamounts continues at the current, high, or even at more moderate levels.

Our fuzzy-logic, life-history attributes method of estimating intrinsic vulnerability to biomass depletion by fishing (based on Cheung et al. this vol.), followed by evaluation of sensitivity and local extinction risk using simulation, is a relatively new technique, but it may be more informative and robust than previous methods. It provides a quantitative basis for more conservatively management of fisheries for seamount and seamount-aggregating fish in the future.

APPENDICES

The list of fish species occurring for seamounts worldwide prepared by Froese and Sampang (this vol.) was augmented from additional sources:

1. Additions to Froese and Sampang's checklist of seamount fishes.

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