

TAXONOMY AND BIOLOGY OF SEAMOUNT FISHES

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ABSTRACT

This study presents a preliminary annotated checklist, a preliminary bibliography, and an analysis of current knowledge of seamount fishes. Based on surveys carried out on sixty seamounts 535 species in 130 Families, 29 Orders and 4 Classes are recognized as seamount fishes. Sufficient information for sustainable management such as growth, maturity, fecundity, and diet is available for only 12 (2%) of the species. Yet 151 (28%) of the species are known to be exploited commercially. Most of the species for which data are available are of low or very low productivity and resilience to exploitation. Fitness strategies of seamount fishes are discussed and compared. The number of species in each ecological niche is low on seamounts signifying vulnerability at the ecosystem level. Of the six seamount fishes evaluated for the purposes of the 2000 IUCN Red List, one was critically endangered, two were vulnerable and three were of lower risk, near-threatened, while other seamount fishes have not yet been assessed. In this study, 62 (12%) seamount fish species are reported from only one seamount, suggesting a high rate of endemism.

WHAT ARE SEAMOUNT FISHES?

Seamounts are typically defined as mountains that rise at least 1000 m from the abyssal floor of the ocean in about 4000 m depth but do not reach the surface (see Kitchingman and Lai, this vol.). Seamount fishes thus are mostly deep-sea fishes with occasional visitors from the epipelagic realm or from the continental shelf or slope. Several seamounts reach within less than 100 m off the surface and their tops are inhabited by coral reefs and associated species typical of coastal areas or oceanic islands. Distinguishing ‘true’ seamount fishes that depend on seamounts as preferred habitat or major feeding or spawning grounds from those that inhabit only the upper zone of shallow seamounts or are opportunistic visitors is the first problem that must be resolved when attempting to review our knowledge of seamount fishes. Here, we have taken a pragmatic approach, marking as ‘strays’ those fishes that have a depth range not exceeding 150 m or that typically close their life-cycles in coastal waters without apparent dependence on seamounts, such as butterfly fishes or surgeon fishes.

HOW MANY SEAMOUNT FISHES ARE THERE?

Deep-sea fishes are often considered to consist of species living below 1000 m, but Weitzman (1997) extended this definition to include species occurring between 500 and 1000 m. He also provided an account of deep-sea fish Orders and Families, albeit without an attempt to estimate their numbers. According to Helfman et al. (1997) "more than 1000 species inhabit the open waters of the deep sea and another 1000 species are benthic". FishBase (Froese and Pauly, 2004) lists 1276 fishes as bathypelagic and 2103 as bathydemersal. Also, only few seamounts have been sampled so far (Stocks, this vol.) and data from only 60 seamounts are used in this study. Thus, the attached preliminary annotated checklist of seamount fishes (Appendix 1) with currently 535 species—although it represents the most comprehensive checklist to-date—is incomplete. We expect the total number to be close to 1000 species. A preliminary list of seamount fishes with localities (Appendix 2), by seamount (Appendix 3), and a list of commercially important seamount fishes (Appendix 4) are also presented, along with a list of references supporting those lists (Appendix 5 and 6).

Of the currently recognized seamount fishes 365 demersal or benthopelagic species live and feed on or close to the bottom whereas 170 pelagic species live and feed in the water column above and around the seamounts.

HOW IMPORTANT IS BIODIVERSITY OF SEAMOUNT FISHES?

The current 535 species of seamount fishes represent only about 2% of the over 28,400 recent fish species on earth. However, seamount fishes belong to 130 (25%) of 515 Families and 29 (47%) of 62 Orders and thus are mostly not closely related to each other, i.e., their genetic diversity is higher than suggested by the low number of species. Many seamount Families are small, with 13 Families consisting only of seamount species and 12 Families with half or more of the members living on seamounts. According to Marshall (1979) and Haedrich (1997), deep-sea fishes tend to be representatives of groups that appeared rather early in the evolution of modern fishes. However, many of them are highly derived and adapted to the particular environment and ecological conditions of the deep sea, such as specialized eyes, highly complex bioluminescent organs, elaborate gas glands and swim bladder constructions, and often remarkable jaws and teeth. Some fish synthesize potentially interesting organic compounds: for example, the luminescent excretion of the Softhead grenadier *Malacocephalus laevis*, which has been used to enhance (= 'lighten') baits used for cod fishing (Cohen et al., 1990). The fauna has persisted over very long time spans and has resisted competitive invasion from more recently evolved and less adapted forms such as the spiny-rayed (perciform) fishes which usually dominate the fish fauna of shallower waters (Marshall, 1979): only 109 (20%) of the listed seamount fishes are perciforms, compared to 35% perciforms in all fishes. Thus, although the number of known seamount fishes is comparatively small, because they encompass a quarter of fish Families, about half of the Orders and many unique adaptations, they represent a relatively large and unique portion of fish biodiversity.

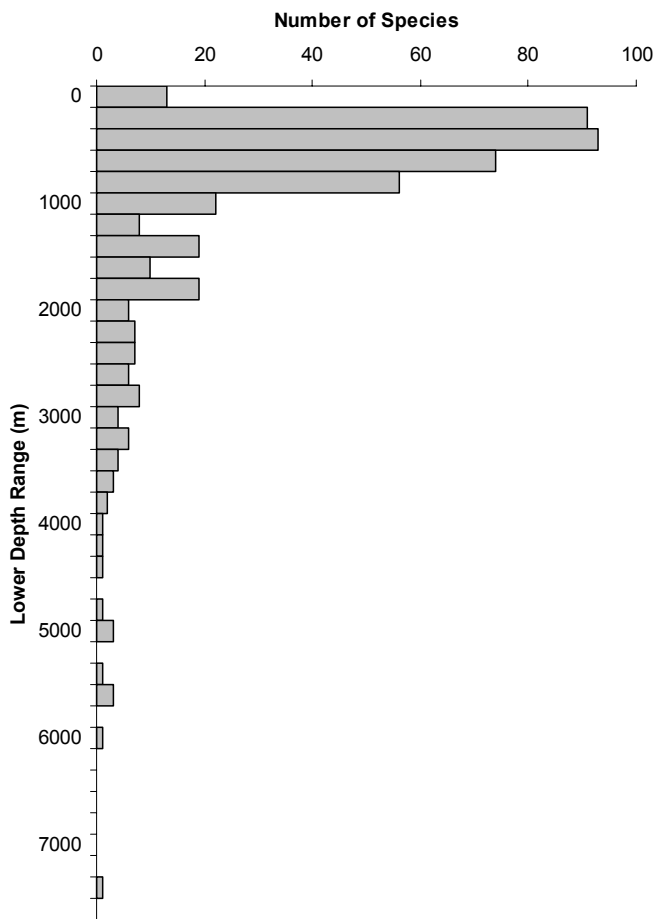


Figure 1. Number of seamount fishes (total = 470) by lower depth range.

HOW DEEP CAN YOU GO?

Depths reported for deep-sea organisms have to be treated as approximations. First of all, the sampling effort has mostly been inadequate and many species are likely to be found outside their current depth ranges in the future. Also, sampling is often done with open nets and thus an occurrence record with a depth range of 1000-3000 m does not mean that the species occupies this range, but rather that it has been captured somewhere in between, resulting in a maximum depth of 'at least 1000 m.' Figure 1 shows the number of species (with know depth distribution) by lower end of their depth range. Below 1000 m zooplankton and thus plankton feeders become scarce, leading to a marked drop in species numbers. Below 3000 m food in general becomes scarce and thus species numbers drop of again. Generally, numbers of species decline with depth and the shape of this decline is likely to be exponential as shown in Figure 1. Thus, the low and uneven shape of the curve below 1000 m is likely to be caused by under-sampling. Or to use a metaphor: the seamount fishes that we know, and thus much of our knowledge of seamount ecosystems, are only the tip of an iceberg.

KNOWLEDGE ABOUT SEAMOUNT FISHES

Many seamount fishes (26%) have been discovered and described only within the last 50 years, mostly by Russian workers such as N.V. Parin (first- or co-author of 39 recent descriptions). If taxonomic surveys of seamounts were to be increased, many new and undescribed species would likely be found.

The biology of most seamount fishes is poorly known, often only assumed from the morphology of the type specimens. Sustainable management of fish stocks requires information on how fast any extracted biomass is replenished. More particularly, data on body growth, length-weight relationships, mean age at maturity, fecundity and natural mortality are needed for stock assessment and management. In the context of ecosystem management additional data on trophic relationships, i.e., food items, diet composition and common predators are needed. Table 1 summarizes existing knowledge. A comprehensive suite is known for only twelve seamount fish species. Despite this lack of information needed for sustainable use, 151 seamount fishes are known to be exploited commercially.

HOW RESILIENT ARE SEAMOUNT FISHES TO EXPLOITATION?

Musick (1999) studied the vulnerability of fishes to extinction. He devised a scheme (Table 2) to assign species to productivity or resilience categories based on available knowledge. The first row in Table 2 gives the vulnerability threshold: if an observed decline measured in biomass or numbers of mature individuals over the longer of 10 years or three generations exceeds the indicated threshold value, the population or species is considered vulnerable to extinction unless explicitly shown otherwise. For example, if the biomass of a seamount fish with very low resilience has been reduced by 70% during the past 10 years, then it is considered vulnerable to extinction; unfortunately, biomass estimates are not available for most seamount fishes. The second row in Table 2 gives the maximum intrinsic rate of population increase (r_{max}), which is difficult to estimate and thus rarely available in fishes, and which is provided here as an output indicating the numerical range of the resilience categories. The minimum time (t_d) a population needs at low density to double in numbers is calculated as t_d (years) = $\ln(2) / r_{max}$ in the third row. The more familiar concept of the interest rate earned on capital is calculated as I (%) = $100 * (e^{r_{max}} - 1)$. Other parameters are defined in the caption of Table 2. The assignment is to the lowest resilience category fitting available data.

Table 2. Ranges of key traits of fishes used to assign species to resilience categories, where vulnerability threshold is as explained in the text, r_{max} is the maximum intrinsic rate of population increase, t_d is the minimum population doubling time in numbers corresponding to r_{max} ; interest rate is the maximum annual interest gained if the population were capital; K is the von Bertalanffy growth parameter; T_m is age at first maturity, and T_{max} is maximum age.

Parameter (unit)	High	Medium	Low	Very low
Vulnerability threshold	0.99	0.95	0.85	0.70
r_{max} (1/year)	> 0.5	0.16 – 0.50	0.05 – 0.15	< 0.05
t_d (years)	<1.4	1.4 – 4.4	4.5 – 14	> 14
Interest rate (%)	> 65	17 – 65	5 – 16	< 5
K (1/year)	> 0.3	0.16 – 0.30	0.05 – 0.15	< 0.05
Fecundity (1/year)	> 10,000	100 – 1000	10 – 100	< 10
T_m (years)	< 1	2 – 4	5 – 10	> 10
T_{max} (years)	1 – 3	4 – 10	11 – 30	> 30

Table 1. Knowledge about seamount fishes presented as number of records in FishBase (as of 03/2004) and number and percentage of species for which information is available.

Topic	Records	Species	Percent
Growth	328	70	13.1
Length Weight	286	109	20.4
Reproduction	126	126	23.6
Maturity	223	93	17.4
Fecundity	42	36	6.7
Natural mortality	51	46	8.6
Food items	1834	236	44.1
Diet composition	238	83	15.5
Predators	330	107	20.0
Commercial	-	151	28.2

Data for at least one of the parameters in Table 2 are available for only 76 seamount species, resulting in 5 (6.6%) species with High, 32 (42%) with Medium, 20 (26%) with Low and 19 (25%) with Very low resilience or productivity. This result may overestimate resilience of seamount fishes because usually it is the 'shallower' and thus 'warmer' species with presumably faster growth and life cycles, for which data are available. In other words, we can expect the percentage of species with low and very low resilience to increase with more knowledge about the 'deeper' seamount fishes because "biochemically, rates of enzymatic and metabolic activity and even levels of ATP-generating enzymes are lower in deep-sea fishes than in shallow-water relatives" (Helfman et al., 1997; p. 301). Also, annual fecundity is often not known and could reduce resilience to Low if < 100 and to Very low if < 10 , as can be assumed to be the case in all sharks, rays and chimaeras and all other live-bearers. Some of the few available growth studies on deep-sea fish suggest very fast growth based on the assumption that the few rings found in otoliths are annual; however, independent verification is lacking and this assumption could be erroneous. In contrast, some of the oldest known fishes occur on seamounts, such as the Yelloweye rockfish (*Sebastes ruberrimus*) with 118 years or the Sablefish (*Anoploma fimbria*) with 114 years.

It should be noted that sustainable exploitation of species with low or very low resilience makes little economic sense. Economically, it is more profitable to catch and sell all of the stock and then move on to exploit other resources, with devastating effects on seamount biodiversity. Unfortunately, this appears to be the pattern adopted by many seamount fisheries (See Watson and Morato, this vol.).

WHAT ARE THE FITNESS STRATEGIES OF SEAMOUNT FISHES?

Evolution favours the traits of those individuals, that under given circumstances, produce the highest number of reproductively successful individuals. To produce successful offspring individuals, have to avoid mortality, feed and grow to reach maturity, mate with best matching partners, and maximize chances of survival for their offspring. Fitness strategies thus have to balance various traits related to predator avoidance, position in the food web, mating success, number of offspring and parental care, if any. Individuals inherit a specific fitness strategy depending on the place of their species in the phylogenetic hierarchy of fishes. For the purpose of this study, we define fitness strategies as combinations of three traits that impact on the above themes and that are highly correlated with other traits and thus can serve as proxies. For these types of analyses to be conducted, information on these traits needs to be available for a high number of species across all phylogenetic groups. The traits selected here were size, trophic level and resilience. To include more species in this exercise we made assumptions about trophic level and productivity for species with no data, based on information available for other members of the same genus or family, resulting in 468 species included in Table 3. As discussed above, this procedure may be biased towards higher resilience categories, i.e., if more data become available a number of species that are now classified as Medium or High are likely to be transferred to lower categories.

The trophic levels utilized by seamount fishes are restricted to low-level predators which feed mostly on zooplankton or benthic invertebrates and to high level predators which feed mostly on other fish. No herbivore or omnivore fishes occur on seamounts. This confirms the observation by Helfman et al. (1997) that "All deep-sea fishes are carnivores...", as can be expected given that seamounts typically do not reach into the zone where plants can grow. Seamount fishes cover the whole range from very low to high resilience and from small to very large sizes.

There are 64 theoretically possible fitness strategies as combinations of the traits mentioned above. Seamount fishes make use of only 16 strategies (Table 3): hagfishes are large high-level predators of low resilience; chimaeras are large low- and high-level predators of low resilience; most (57%) sharks and rays are large high-level predators of low or very low resilience; ray-finned fishes are mostly (62%) medium-sized low- or high-level predators of medium or low resilience. The number of families per fitness strategy increases with the number of respective species, i.e., there is no evidence that species of a certain strategy tend to belong to the same Family.

Two Classes of recent fishes are missing from seamounts: Cephalaspidomorpha (lampreys) are mostly confined to freshwater or are anadromous; they are not known to occur in the deep-sea and thus are not expected to occur on seamounts. Of the Sarcopterygii (lobe-finned fishes), coelacanths occur in deep water and may be found on seamounts in the future.

Table 1. Fitness strategies of seamount fishes. Low-level predators have trophic levels between 2.75 and 3.75; High-level predators have trophic levels higher than 3.75; resilience scores were assigned according to Table 2; length groups were assigned in total length on a logarithmic scale, with Small < 7cm, Medium = 7-45 cm, Large >45 – 300 cm, and Very large > 300 cm; the number of species adopting a certain fitness strategy and the percentage within the respective Class is given, as well as the number of Families to which these species belong.

Class	Trophic group	Resilience	Length group	Species n (%)	Families n	
Myxini (hagfishes)	High-level pred.	Low	Large	2 (100.0)	1	
Holocephali (chimaeras)	Low-level pred.	Low	Large	3 (75.0)	1	
	High-level pred.	Low	Large	1 (25.0)	1	
Elasmobranchii (sharks and rays)	Low-level pred.	Low	Medium	1 (2.9)	1	
			Large	4 (11.4)	2	
	High-level pred.	Very low	Large	2 (5.7)	1	
			Medium	3 (8.6)	1	
			Large	10 (28.6)	4	
		Very low	Large	10 (28.6)	6	
			Very large	2 (5.7)	2	
			Very large	3 (8.6)	3	
	Actinopterygii (ray-finned fishes)	Low-level pred.	High	Small	5 (1.2)	3
				Medium	10 (2.3)	4
Medium				7 (1.6)	4	
Medium				160 (37.5)	45	
Low			Large	17 (4.0)	11	
			Small	1 (0.2)	1	
			Medium	49 (11.5)	17	
			Large	42 (9.8)	20	
High-level pred.		Very low	Large	7 (1.6)	5	
			Medium	43 (10.1)	24	
		Low	Large	26 (6.1)	15	
			Medium	10 (2.3)	7	
			Large	34 (8.0)	23	
			Very low	Large	16 (3.7)	10

If we consider the 16 fitness strategies as evolutionary responses to niches being available at the seamount ecosystem, then it is striking that, across seamounts 6 (38%) such niches are occupied by fewer than 10 species each, and probably less at any particular seamount. Given that we have no knowledge about relative niche importance for the overall functioning of the seamount ecosystem, such lack of redundancy in ecological roles should be taken as a sign of potential ecosystem vulnerability.

Table 4 provides a comparison of fitness strategies at the Class level. Ray-finned fishes are the most numerous group, making use of 14 out of 16 strategies, including 8 strategies without competition from other Classes. Sharks and rays make use of 8 strategies, including two strategies (very large high-level predators of low or very low resilience) without competition from ray-finned fishes. Chimaeras use only two strategies which they share with the other classes. The two species of hagfishes so far found in the upper region of seamounts use only one strategy. Thus, while the strategy of medium sized low-level predators of medium resilience has the highest diversity at the species level, large high-level predators of low resilience have the highest diversity at the Class level.

Table 2. Fitness strategies of seamount fishes by Class. Actino = ray-finned fishes, Elasm = sharks and rays, Holo = chimaeras, and Myxini = hagfishes.

Trophic group	Resilience	Length group	Actino	Elasmo	Holo	Myxini	Species
Low-level pred.	Very low	Large	7	2			9
		Small	1				1
	Medium	Medium	49	1			50
		Large	42	4	3		49
		Small	7				7
		Medium	160				160
		Large	17				17
		Small	5				5
	High	Medium	10				10
		Large	16	10			26
High-level pred.	Very low	Very large		3			3
		Medium	10	3			13
	Low	Large	34	10	1	2	47
		Very large		2			2
	Medium	Medium	43				43
		Large	26				26

DOES SIZE MATTER?

Maximum length of seamount fishes ranges from about 3.7 cm in Garrick (*Cyclothone braueri*) to about 480 cm in the Bluntnose sixgill shark (*Hexanchus griseus*). Most seamount fishes have total lengths between 10 and 100 cm (Figure 2). Interestingly, size ranges appear to decline with depth. Also, sharks, rays, chimaeras and hagfishes all of which are of low or very low resilience, appear to be restricted to depths above 2500 m, i.e., the area where most fishing occurs.

ENDEMISM OF SEAMOUNT FISHES

The data used in this study are ‘presence’ data in the sense that they provide evidence when and where a species has been found on seamounts. Absence of evidence for a species does not necessarily mean its absence, especially when only a few seamounts have been sampled and not all surveys are included in this study. With this restriction in mind, we refrained from classifying fishes as endemic to certain seamounts pending analysis of more data. Currently 62 (12%) species are reported from only one seamount in one subsection (FAO area) of the world ocean. This compares to reports in the literature of 44% endemic fishes on the Nasca and Sala-y-Gomez seamount chain (Parin et al., 1997), 9% on the Great Meteor seamount (Fock et al., 2002) and 5% on the Hawaiian seamounts (Stocks, in press).

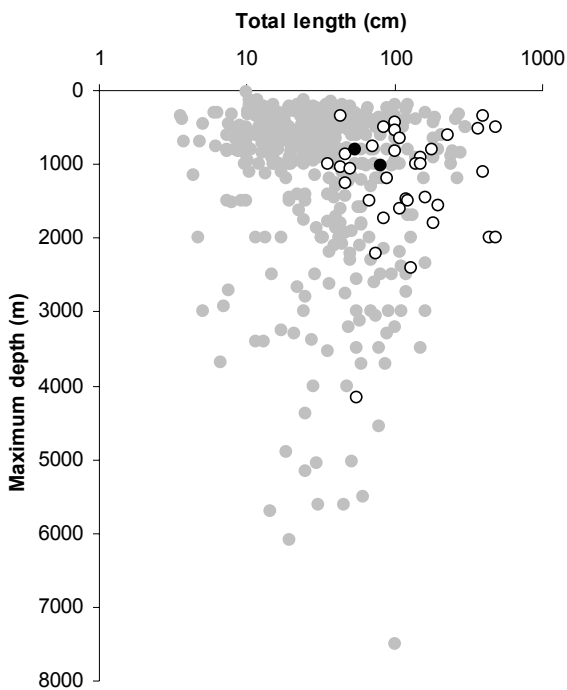


Figure 2. Size and depth distribution of seamount fishes. Grey dots are ray-finned fishes, black dots are hagfishes and circles are chimaeras, sharks and rays.

SEAMOUNT FISHES IN THE IUCN RED LIST

Only 6 seamount fishes are included in the 2000 IUCN Red List (Hilton-Taylor, 2000): *Sebastes paucipinis* is listed as 'critically endangered', *Sphoeroides pachygaster* and *Hexanchus griseus* are listed as 'vulnerable', and *Squalus acanthias*, *Dalatias licha* and *Prionace glauca* are listed as 'lower risk, near threatened.' Other seamount fishes have not been evaluated so far.

APPENDICES

The data and studies on which this analysis of seamount fishes is based are presented in the following Appendices:

1. Preliminary annotated checklist of seamount fishes;
2. Preliminary list of seamount fishes with reported seamounts;
3. Preliminary checklist of fishes by seamount;
4. Preliminary list of commercially important seamount fishes;
5. Reference numbers with citations;
6. Preliminary bibliography of seamount fishes.

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