

BIOLOGY OF DEEP-SEA SHARKS: A REVIEW

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Introduction

The biology of deep-sea sharks is poorly known compared to that of their shallow-water counterparts. Despite the inherent logistical challenges, the study of deep-sea sharks is a rapidly expanding field. The primary literature was extensively reviewed toward summarizing what is known about the natural history of these elusive elasmobranchs. Preliminary results are presented to provide a broad context for other papers presented in this symposium.

The diversity, distribution, ecology, life history, and diet of 241 species of deep-sea sharks was analyzed according several data categories. Deep-sea sharks were divided into four bathymetric categories:

- paraprofundic (shallow-water species known to penetrate 200 m or deeper);
- mesoprofundic (moderately deep-dwelling species, typically inhabiting depths of 200-600 m);
- holoprofundic (deep-dwelling species, typically inhabiting depths of 600 m or greater); and
- metaprofundic (species inhabiting a wide range of depths encompassing at least two of the previous categories).

Table 1: Phyletic Diversity of Deep-Sea Sharks and their Bathymetric Categories

Order	Species	Deepsea	%	Bathymetric Category			
				Para	Meso	Holo	Meta
Hexanchiformes	5	4	80.0				4
Squaliformes	98	98	100.0	5	28	10	47
Pristiophoriformes	5	3	60.0	1	1	1	
Squatiformes	15	8	53.0	2	2		3
Heterodontiformes	8						
Orectolobiformes	31	1	3.2	1			
Lamniformes	16	11	68.8	2			9
Carcharhiniformes	216	116	53.7	17	36	22	31
Totals	394	241	61.2	28	67	33	94

Diversity

With respect to systematic diversity, of 394 described species of sharks (Compagno 1999), 241 (61.6%) occur in the deep-sea, of which 136 occur deeper than 600 m. All extant shark orders except Heterodontiformes are represented in the deep-sea. In terms of species richness, deep-sea shark taxa are dominated by Squaliformes and Carcharhiniformes, which together account for 214 species of deep-sea sharks.

Of 22 shark ecomorphotypes (Compagno 1990), 17 are represented in the deep-sea; however, the bathic, probenthic, and rhynchobathic ecomorphotypes account for the bulk of deep-sea sharks. These ecomorphotypes are relatively unspecialized, suggesting that shark adaptations to the deep-sea are primarily physiological or biochemical rather than morphological.

Bathymetric Distribution

Depth data were available for 222 species of deep-sea sharks and a surprising diversity of sharks occur at great depth: 136 species occur at 600 m and deeper. Distinct phyletic trends are found among the deepest-dwelling sharks, with squaloids and scyliorhinids being predominant. Only 24 species of deep-sea sharks are known to be vertical migrators.

Table 2: Minimum and Maximum Depths of the 20 Deepest-Dwelling Sharks

Order	Family	Species	Minimum Depth (m)	Maximum Depth (m)
Squaliformes	Somniosidae	<i>Centroscymnus coelolepis</i>	270	3675
Squaliformes	Dalatiidae	<i>Isistius brasiliensis</i>	0	3500
Hexanchiformes	Hexanchidae	<i>Hexanchus griseus</i>	3	2500
Squaliformes	Centrophoridae	<i>Centrophorus squamosus</i>	200	2400
Squaliformes	Etmopteridae	<i>Etmopterus princeps</i>	567	2213
Squaliformes	Somniosidae	<i>Somniosus microcephalus</i>	20	2200
Squaliformes	Etmopteridae	<i>Etmopterus spinax</i>	70	2000
Squaliformes	Dalatiidae	<i>Squaliolus aliae</i>	200	2000
Squaliformes	Somniosidae	<i>Zameus squamulosus</i>	550	2000
Squaliformes	Somniosidae	<i>Somniosus pacificus</i>	0	2000
Carcharhiniformes	Scyliorhinidae	<i>Apristurus microps</i>	700	2000
Carcharhiniformes	Scyliorhinidae	<i>Apristurus kampae</i>	457	1888
Carcharhiniformes	Scyliorhinidae	<i>Apristurus indicus</i>	1061	1840
Squaliformes	Dalatiidae	<i>Dalatias licha</i>	37	1800
Carcharhiniformes	Scyliorhinidae	<i>Apristurus aphyodes</i>	1014	1800
Squaliformes	Centrophoridae	<i>Deania profundorum</i>	275	1785
Carcharhiniformes	Scyliorhinidae	<i>Apristurus manis</i>	658	1740
Squaliformes	Etmopteridae	<i>Centroscyllium fabricii</i>	180	1653
Squaliformes	Somniosidae	<i>Scymnodon ringens</i>	200	1600
Carcharhiniformes	Scyliorhinidae	<i>Apristurus profundorum</i>	1300	1600

Physiological Adaptations

The physiological adaptations of deep-sea sharks have received little attention. With what little information is available, there appears to be some parallels and some potential deviations from the general view of deep-sea fish adaptation. These include aspects of muscle physiology, osmoregulatory strategy, buoyancy, and visual adaptations. This is an area with great potential for future research.

Bioluminescence

Bioluminescence is relatively rare in deep-sea sharks. Only 48 species of deep-sea sharks are known to be bioluminescent versus some 70% of deep-sea teleosts (Bone and Marshall 1982, p 199). Bioluminescence in deep-sea sharks is restricted to two squaloid families, Etmopteridae and Dalatiidae. These are not sister taxa (Shirai 1992, pp 116-117), indicating that bioluminescence in sharks evolved independently twice. Four patterns of bioluminescence in deep-sea sharks were identified, here termed ventral, linear, cloacal, and scapular.

Feeding Biology

Deep-sea sharks are highly opportunistic feeders, taking whatever appropriate-sized prey is most readily available and scavenging whenever the opportunity presents itself. Collectively, these data suggest that the main optimal foraging strategy of most deep-sea sharks is numbers maximization rather than energy maximization.

Reproductive Biology

No data exists on how deep-sea sharks find suitable mates, although pheromones and – at closer range – bioluminescent cues seem reasonable possibilities. No clear reproductive season has been determined for any non-paraprofundic deep-sea shark, whether this is due to a lack of overt seasonal cues in the relatively stable physicochemical environment of the deep-sea or merely an artifact of the paucity of life history data for deep-sea sharks is not clear.

Gestation period is known for only 32 species of deep-sea sharks, averaging 12.9 months and ranging from 5 to 30 months with litter sizes (based on 101 species) ranging from 1 to 301. The compiled data suggest low reproductive output (long gestation, small litter size) is typical for deep-sea sharks, which is probably a reflection of their oligotrophic environment.

Data comparing length at maturity for 101 species of deep-sea sharks found that maturity for both sexes is attained at more than 75% maximum length. The compiled data suggest that deep-sea sharks may attain sexual maturity significantly later in their life spans than shallow-water species (Cortes 2000). Difficulty in accumulating adequate energy reserves, especially in female sharks, in the oligotrophic deep-sea environment may partially account for this.

Conclusions

The biology of deep-sea sharks is a relatively new field. Data is largely limited to those deep-sea sharks (especially squaloids) that are of greatest commercial importance. The paucity of validated life history data on deep-sea sharks precludes wise management of them as a natural resource. Yet the commercial importance of deep-sea sharks is likely to increase in the near future as demand rises for alternate protein and pharmaceutical sources. Commercial incentives and new technologies will undoubtedly accelerate discoveries in the biology of deep-sea sharks. But if deep-sea sharks are to survive commercially driven exploitation, it is imperative that problematic taxonomic issues be resolved, bathymetric and zoogeographic distributions clarified, and life history parameters important to fisheries management be determined accurately and in a timely fashion.

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