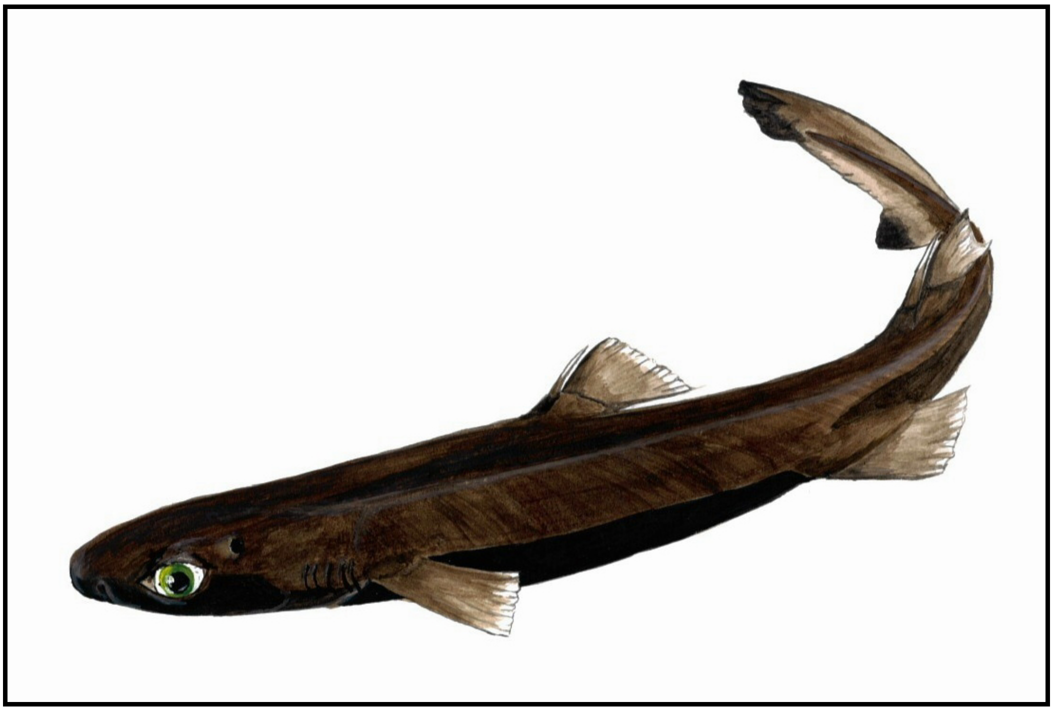
A COLLATION AND SUMMARIZATION OF AVAILABLE DATA ON DEEPWATER CHONDRICHTHYANS: BIODIVERSITY, LIFE HISTORY AND FISHERIES.

A report prepared by the
IUCN SSC Shark Specialist Group
for the
Marine Conservation Biology Institute



Peter M. Kyne[1] & Colin A. Simpfendorfer[2]

[1]School of Biomedical Sciences, University of Queensland, St. Lucia 4072 Qld, Australia; p.kyne@uq.edu.au

[2]School of Earth and Environmental Sciences, James Cook University, Townsville 4811 Qld, Australia; colin.simpfendorfer@jcu.edu.au

15 February 2007

ACKNOWLEDGEMENTS

The collation and summarization of available information on deepwater chondrichthyans was made possible with the support of a number of colleagues who willingly and openly allowed access to their unpublished data, reports, theses and other documents. Sarah Irvine (Australia) provided constant constructive input into the project, assisting with literature, data, contacts, reviewing and editing of the report as well as invaluable discussions on the biology, fisheries and conservation of deepsea chondrichthyans. We sincerely thank Sarah for her constant support. Particular thanks are also extended to Dave Ebert (Pacific Shark Research Center, Moss Landing Marine Laboratories, USA), Malcolm Francis (NIWA, Wellington, New Zealand) and William White (CSIRO Marine and Atmospheric Research, Australia) for their continued support.

We also wish to acknowledge the individual contributions made by M. Shiham Adam (Marine Research Centre, Republic of Maldives), R. Charles Anderson (Republic of Maldives), Paul Brickle (Falkland Islands Fisheries Department), Nick Dulvy (Centre for Environment, Fisheries and Aquaculture Sciences, UK), Ian Fergusson (BBC UK), Brooke Flammang (Harvard University, USA), Michael Gallagher (Irish Sea Fisheries Board, UK), Chris Gburski (NMFS Alaska Fisheries Science Center, USA), Ken Graham (NSW Department of Primary Industries, Australia), Hannes Holtzhausen (National Marine Information and Research Center, Namibia), Agnès Le Port (University of Auckland, New Zealand), Pamela Mace (New Zealand Ministry of Fisheries), Beth Matta (NMFS Alaska Fisheries Science Center, USA), Matt Piasente, Paula Shoulder and Thim Skousen (Australian Fisheries Management Authority, Australia) and James Sulikowski (University of New Hampshire, USA).

We also thank Claudine Gibson, Sarah Fowler, Catherine McCormack and Sarah Valenti of the IUCN Shark Specialist Group for administrative and technical assistance and project direction, Mike Bennett (University of Queensland, Australia) for administrative support, Tom Kashiwagi (University of Queensland, Australia) for assistance with the Japanese literature, Steve Taylor (University of Queensland, Australia) for reviewing sections of the report and Claire Bartron (Murdoch University, Australia) for the cover artwork. Finally, we thank Lance Morgan (MCBI) for project support.

Cover art: Velvet belly *Etmopterus spinax* by Claire Bartron.

TABLE OF CONTENTS

EXECUTIVE SUMMARY

Despite the widespread recognition of the vulnerability of deepwater chondrichthyan fishes (sharks, batoids and holocephalans) to overfishing and their potential inability to recover from depletion, there is a lack of a concise overview of the present status of knowledge concerning the biodiversity and life history of this group. This report provides a global review of this data, together with fisheries information in order to provide a sound summary to inform future research, conservation and management directions.

For the purposes of this project, deepwater chondrichthyans have been defined as those sharks, rays and holocephalans whose distribution is predominantly at, are restricted to, or spend the majority of their lifecycle at, depths below 200m. This depth is generally recognised as the continental and insular shelf edge, and therefore, deepwater species are those occurring on or over the continental and insular slopes and beyond, including the abyssal plains and oceanic seamounts.

Of the global chondrichthyan fauna (1193 species), 581 species are considered to be deepwater (48.7% of the global total). The deepwater fauna is divided between 278 sharks (55.8% of global), 257 batoids (39.8% of global) and 46 holocephalans (93.9% of global). The bulk of the deepwater shark fauna is attributable to the squaloid dogfishes (Order Squaliformes) and scyliorhinid catsharks (Order Carcharhiniformes, Family Scyliorhinidae), together comprising 84.5% of deepsea sharks. Three families of skates (Arhynchobatidae, Rajidae and Anacanthobatidae) dominate the deepwater batoid fauna, together comprising 89.9% of deepsea batoids. A full annotated checklist of deepwater chondrichthyans is incorporated into the report.

The total number of known species is ever increasing as exploratory and taxonomic work ensues. Undescribed taxa, those new or recently identified species yet to be formally treated by science, represent over one fifth (21%) of all known deepwater chondrichthyans and the systematics and inter-relationships of several groups of deepsea chondrichthyans remains unresolved. This high proportion not only highlights the overall lack of knowledge of the deepsea fauna at even the most basic (i.e. taxonomic) level, but also that the deepsea chondrichthyan fauna is far from fully documented.

Chondrichthyans are generally considered to be K-selected species, displaying conservative life history parameters such as relatively slow growth, late age at maturity, low fecundity and low natural mortality, resulting in limited reproductive output. These characteristics place them at risk of overexploitation and population depletion, with an inability to recover from reduced population levels once depleted. An understanding of the biological parameters of a species is important to accurately assess its productivity and thus make inferences concerning its vulnerability to fisheries. This report collated available (published and unpublished) information on the life history of deepwater chondrichthyans. Citations for life history data presented in this summary can be located in the main text of the report.

For the vast majority of deepwater chondrichthyans, details of their life history characteristics are lacking and many groups remain very poorly-known. There is a reasonable amount of information on the biology of some species of dogfish sharks (Squalidae), gulper sharks (Centrophoridae), lanternsharks (Etmopteridae), sleeper sharks (Somniosidae), catsharks (Scyliorhinidae), softnose skates (Arhynchobatidae) and hardnose skates (Rajidae), but in general, our understanding of the deepwater fauna is lagging considerably behind the level of knowledge of some inshore and pelagic chondrichthyans.

Reproductive output in deepwater chondrichthyans is generally limited. For the viviparous squaloid dogfishes, litter sizes are generally small, 6–19 in *Cirrhigaleus*, 1–15 in *Squalus*, 1–7 (mostly 1–2) in *Centrophorus*, 1–17 in *Deania*, 3–40 in *Centroscyllium*, 1–21 in *Etmopterus*, 1–31 in *Centroscymnus*, 1–9 in *Centroselachus*, 8–10 in *Somniosus*, 7–15 in *Oxynotus*, 7–16 in *Dalatias*, nine in *Isistius* and four in *Squaliolus*. Exceptions to the general trend are 59 in *Scymnodalatias albicauda* and 114 in *Echinorhinus cookei*.

Deepwater squaloid dogfishes generally do not have well-defined reproductive seasons and it is difficult to elucidate their reproductive cycle. Gestation periods are generally unknown and many species have a resting period after parturition (ovarian follicles do not develop while gestation proceeds). The large size of preovulatory follicles suggests lengthy vitellogenesis, as the energy demands to develop such large oocytes are high. It seems plausible then, that reproductive cycles are likely biennial or triennial, and this has been confirmed for some species. Lengthy reproductive cycles such as these obviously limit annual fecundity.

For the oviparous deepwater catsharks and skates, fecundity is more difficult to assess as embryos develop in the ocean environment once females have deposited egg cases. Most deepwater species appear to be reproductively active year-round, although there may be seasonal peaks in egg case production. Egg-laying rates are only available from animals held in aquaria. Estimates of annual fecundity for skates have included 10-20 for *Amblyraja radiata*, 90 for *Leucoraja naevus* and 1260 for *Raja binoculata*.

Estimates of age and growth for deepwater chondrichthyans are available for only 31 of the 581 species (12 dogfishes, 1 thresher shark, 17 skates and 1 chimaera). The vast majority of ageing estimates are unvalidated and many are preliminary. Attempts to age deepwater catsharks have proved unsuccessful. There is a continual need for the development of ageing methodologies for deepwater chondrichthyans, as well as research into suitable validation techniques. Maximum age estimates for squaloid sharks (females) include 8 years for *Squalus blainvillei*, 27 for *S. mitsukurii*, 39 for *Centrophorus granulosus*, 46 for *C.* cf. *uyato*, 37 for *Deania calcea*, 30 for *Etmopterus baxteri*, 7 for *E. spinax* and 54 for *Centroselachus crepidater*. The oldest age estimates are 70 years for female and 71 years for male *Centrophorus squamosus*. Maximum age estimates for *Bathyraja* skates range from 16–29 years for females and 15–20 for males and for rajid skates, 8–26 for females and 6–25 for males (with the exception of *Dipturus batis* which has been aged to 50 years). Age estimates are available for a single holocephalan *Chimaera montrosa* (to 26 years for females and 30 years for males).

The number of reproductive years for some deepwater chondrichthyans may be very small, particularly for the skates which may also undergo senescence at large sizes. Combining available information on life history characteristics, calculations can be made on lifetime reproductive output (lifetime fecundity). The lowest calculated is for *Centrophorus granulosus*; a single female will produce a maximum of 12 pups throughout its lifetime.

Available life history data were also combined to assess the productivity of deepwater chondrichthyans using the intrinsic rebound potential method. Suitable data could only be sourced for 13 species (2.2%) of deepwater chondrichthyan. The intrinsic rebound potential values of deepwater chondrichthyans fall at the lower end of the productivity scale of elasmobranchs, and include the lowest levels observed to date. Where the values of deepwater species fell within the range of continental shelf species they often had lower productivities for the same age at maturity. All deepwater species should therefore be considered to have limited productivity and so have limited ability to sustain high levels of fishing pressure and be slow to recover from overfishing. The population doubling times indicate that once a stock has been depleted, it will be decades, and potentially centuries, before it will recover. There was a significant decline in the intrinsic rebound potential of species with increasing maximum depth. This indicates that deeper living species are likely to have decreased abilities to sustain fishing or rebound from population declines. While such an observation is not a surprise, it does provide the ability to predict, within the bounds of confidence intervals, the rebound potentials of species for which only the maximum depth of occurrence is known.

There is a general lack of available trade and landings data for deepwater chondrichthyans. Many deepwater species are taken as bycatch, often discarded, or landed under generic species-codes such as 'shark' or 'other'. The lack of accurate catch data, including the under-reporting of catches, the lack of recording bycatch, poor taxonomic resolution and species-identification, and illegal fishing, makes an assessment of the global catch of deepwater chondrichthyans extremely difficult. Production statistics from FAO fisheries databases were analysed to overview trends in global and regional production. From 1950 to 2004 there was an increasing but fluctuating trend in global production of deepwater chondrichthyans. The global trend was largely influenced by the trends in production figures from the Eastern and Western Atlantic. However, poor data resolution and under-reporting make this analysis of questionable accuracy.

Where data or information are available, intensive fishing has led to the collapse of deepwater squaloid dogfish stocks, particularly *Centrophorus* species. In Australia, fishing has depleted upper slope species, with 98–99% declines for *Centrophorus* species over a twenty-year period. Additionally, severe declines have been documented for other species. One chondrichthyan, *Squalus megalops*, increased in abundance (small, abundant species probably recruiting from the shelf to the slope and benefiting from declines in other species). Recent management arrangements will benefit the conversation of mid-slope species, but pressure is continuing on the upper slope.

In the Northeast Atlantic, less than 20 years of fishing in deep water to the west of the British Isles has led to the depletion of *Centrophorus squamosus* and *Centroscymnus coelolepis* stocks, prompting calls for a zero catch limit for these species. Even with such a regulation in place, bycatch will remain an issue for these species. In the Azores, the poor market value of shark liver oil led to the end of directed fishing for the kitefin shark *Dalatias licha*, but a considerable biomass decline from nearly 30 years of fishing pressure is apparent for the stock. A cessation of fishing suggests that the stock will likely begin to recover, but the overall result appears to suggest local depletion of the population. A liver oil fishery for gulper shark (*Centrophorus* species) in the Maldives was short-lived, commencing in 1980 and closing just over 20 years later due to population depletion. The present status of the stock is unknown, but fishing for gulper sharks has ceased. The resource was probably fished beyond sustainable levels in its early years.

In contrast to the above examples, Namibia is taking a precautionary approach to the development of deepwater shark fisheries. Short-term fishing rights were granted to explore the deepwater shark resource but no commercial licences have yet been granted due to inadequate biomass data to accurately set catch limits.

GENERAL INTRODUCTION

THE CLASS CHONDRICHTHYES

The cartilaginous fishes of the Class Chondrichthyes comprise the sharks, batoids and chimaeras. This diverse group of primarily, but not exclusively, marine predators has a long evolutionary history dating back to the Devonian some 400 million years ago, and possibly earlier. The Class Chondrichthyes is divided into two unequal subclasses, the Holocephali (chimaeras) and the Elasmobranchii (sharks and batoids). The Holocephali contains the single order Chimaeriformes, comprised of the chimaeras, commonly referred to as elephant fishes, ghost sharks, silver sharks, ratfishes and rabbitfishes. The Elasmobranchii is comprised of the typical sharks and the batoids, the latter commonly referred to as the skates and rays. The Elasmobranchii is divided into two superorders, the Squalomorphi and the Galeomorphi. The present systematic arrangement, following Compagno (2001, 2005), places the batoids in a single order, the Rajiformes, within the Squalomorphi. The Squalomorphi thus contain four orders of sharks and one order of batoids, while the Galeomorphi contains four orders of sharks (see box page 8). All nine orders of the Elasmobranchii are represented in the deepwater, as is the single order of the Holocephali. This systematic arrangement, covered in more detail in Compagno (2001), is still somewhat tentative and considerable debate remains as to the correct classification and inter-relationships of the elasmobranch orders, particularly as new molecular data are synthesised and incorporated.

The earliest unquestionable evidence in the fossil record of cartilaginous fishes originates from the Devonian (408.5-362.5mya) (Grogan and Lund 2004). Further scale and spine material from the Silurian (439-408.5mya) has also been attributed to the group, and it has been suggested that chondrichthyan origins may extend back into the Ordovician (510-439mya) or Cambrian (570-510mya). Grogan and Lund (2004) specify, however, that there is no morphological evidence to support attributing Silurian or Ordovician scale material to the Chondrichthyes. In any case, the diversity of form is well-documented from the Devonian and this may be the period of maximal adaptive radiation (Grogan and Lund 2004). Living chondrichthyans occurring today are derived from forms present in the Mesozoic (245-65mya) (Grogan and Lund 2004). Chondrichthyans can thus be considered a highly successful group of fishes given their survival through the major extinction events of the last 400 million years (Compagno 2001, Grogan and Lund 2004).

The Chondrichthyes differ from the presently more diverse bony fishes, or Osteichthyes, in possessing simple endoskeletons of calcified cartilage, thus lacking the bony skeleton of the latter group. It is the mode of mineralization of the endoskeletal tissue along with the modification of the pelvic fin in male chondrichthyans to form claspers (secondary sexual organs utilised for the transport of sperm) that define the Chondrichthyes from all other fish groups (Grogan and Lund 2004). The body form of the group shares many characteristics, but is highly-varied between orders, reflecting adaptations to lifestyle and environment. Compagno (1999) outlines characteristics of chondrichthyan body form in detail.

Living chondrichthyans occupy a diversity of habitats from freshwater lakes and rivers, estuaries, coastal waters, reefs, the open ocean and the deepsea, occurring in waters from the tropics to the Arctic and the Sub-Antarctic. Of interest here are the deepwater chondrichthyans, those adapted to a relatively stable environment, characterised by cold temperature and poor or absent light. The biodiversity, life history characteristics and the impact of, and importance to, fisheries of this suite of specialised sharks, batoids and chimaeras will be addressed within this report.

Orders of the Class Chondrichthyes
(following Compagno 2001)

Subclass Holocephali	
Order Chimaeriformes	Modern Chimaeras
Subclass Elasmobranchii	
Superorder Squalomorphii	Squalomorph Sharks
Order Hexanchiformes	Cow and Frilled Sharks
Order Squaliformes	Dogfish Sharks
Order Squatiniformes	Angelsharks
Order Pristiophoriformes	Sawsharks
Order Rajiformes	Batoids
Superorder Galeomorphii	Galeomorph Sharks
Order Heterodontiformes	Bullhead Sharks
Order Orectolobiformes	Carpetsharks
Order Lamniformes	Mackerel Sharks
Order Carcharhiniformes	Ground Sharks

DEEPWATER CHONDRICHTHYANS – A DEFINITION

For the purposes of this project and report, deepwater chondrichthyans have been defined as those sharks, rays and holocephalans whose distribution is predominantly at, are restricted to, or spend the majority of their lifecycle at, depths below 200m. This depth is generally recognised as the continental and insular shelf edge, and therefore, deepwater species are those occurring on or over the continental and insular slopes and beyond, including the abyssal plains and oceanic seamounts. Incorporated into this definition are benthic and epibenthic species, those occurring on, or associated with, the bottom of the ocean floor; and, pelagic species, those occurring in the water column. Definitions of habitat zones are provided in Section I.

In employing this definition, several species which have been recorded at >200m have not been included in this report. These include coastal, inshore and shelf species which are recorded far less commonly or irregularly in the deepsea. Shelf edge species, such as the undescribed Australian fatspine spurdog *Squalus* sp. D [Last & Stevens, 1994] which occurs at 180-210m, are not included. Several species whose depth range is distributed equally between the continental shelf and upper slope are excluded where they are considered to be predominantly species of the shelf. Examples include the electric rays *Torpedo marmorata* and *T. torpedo*. Similarly, a suite a North Atlantic skates, recorded from inshore to depths of 275-380m are excluded due to their primarily shelf occurrence. These include the sandy skate

Leucoraja circularis, blonde skate *Raja brachyura*, thornback skate *R. clavata*, clearnose skate *R. eglanteria*, brown skate *R. miraletus* and rough skate *R. radula*.

Some particular species which require justification as to their absence from this report are the broadnose sevengill shark *Notorynchus cepedianus*, which although recorded to 570m is primarily a coastal inshore shark of temperate waters; the spiny or piked dogfish *Squalus acanthias*, primarily a shelf species, but which occurs occasionally on the slope and exceptionally to 1446m; the Sparsetooth dogfish *Scymnodalatias oligodon* and the Largetooth cookiecutter shark *Isistius plutodus*, although both occur over very deep water (to 4000m), they have both only ever been recorded in the epipelagic zone (0-200m depth in the water column) (it should be noted though that these species are potential vertical migrators and may also occur in the mesopelagic and bathypelagic zones); the megamouth shark *Megachasma pelagios*, a coastal, shelf and epipelagic species recorded from the pelagic zone to depths of 166m over water to 4600m depth, but never recorded from deep water. One last notable species is the great white shark *Carcharodon carcharias*, a coastal, inshore, shelf and epipelagic offshore species known to undertake considerable migrations. Great whites have rarely been recorded from the continental slope (Compagno 2001), and thus in deepwater, and a reported capture at 1280m (Bigelow and Schroeder 1948a, Compagno 2001) is doubtful (Bonfil et al. 2005). However, more recent research of a shark tagged off South Africa has shown that during transoceanic migration great whites undertake periodic deep dives to depths of up to 980m (Bonfil et al. 2005). It should be noted that this depth is the sensor limit for the tag employed and so it is possible that the tagged shark dived to depths in excess of 980m. While deep dives were regular in occurrence during its migration, with the shark spending 18% of the time at depths of 500-750m, a far greater amount of time (61%) was spent at the surface in water 0-0.5m deep (Bonfil et al. 2005). Thus, given the species' primarily coastal and epipelagic occurrence, it is not further discussed here.

AIMS OF THE PROJECT

The overall aim of the present study is to provide a collation and summarization of the available information and data on the biodiversity, life history and fisheries of deepwater chondrichthyan fishes at the global level.

By examining the present status of knowledge, the project will also address the specific data needs required to provide a global understanding of the vulnerability of deepwater chondrichthyans to fisheries, and to provide a baseline from which to prioritize research, conservation and management. To address the central aim, the report is divided into three Sections. Section I reviews the global biodiversity of deepwater chondrichthyans and provides a checklist of all known living, described and undescribed deepwater species. This annotated checklist incorporates a summary of the known distribution, habitat and depth occurrence of each species, as well as any taxonomic notes where relevant. Section II collates available (published and unpublished) information on life history and provides relevant summaries of biological data including a demographic assessment of the productivity of deepwater chondrichthyans. Section III summarizes global and regional catch data for deepwater chondrichthyans. Regional and fisheries case-studies are presented to illustrate specific examples of catch trends, management or monitoring information.

GENERAL INTRODUCTION LITERATURE

Bigelow, H.B. and Schroeder, W.C. 1948a. Sharks. In: Fishes of the Western North Atlantic. Memoirs of the Sears Foundation for Marine Research (1)1:59-546.

Bonfil, R., Meÿer, M., Scholl, M.C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. and Paterson, M. 2005. Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science 310:100-103.

Compagno, L.J.V. 1999. Systematics and body form. Pp. 43-68. In: Hamlett, W.C. (ed.). Sharks, skates, and rays: the biology of elasmobranch fishes. The John Hopkins University Press, Baltimore and London.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes. No. 1, Vol. 2. FAO, Rome.

Compagno, L.J.V. 2005. Global checklist of living chondrichthyan fishes. Pp. 401-423. In: Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A. and Musick, C.A. (eds.) Sharks, rays and chimaeras: The status of chondrichthyan fishes. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Grogan, E.D. and Lund, R. 2004. The origin and relationships of early Chondrichthyes. Pp. 3-31. In: Carrier, J.C., Musick, J.A. and Heithaus, M.R. (eds.). Biology of sharks and their relatives. CRC Press, Boca Raton.

SECTION I.
BIODIVERSITY AND AN ANNOTATED CHECKLIST OF DEEPWATER CHONDRICHTHYANS

DEEPWATER BIODIVERSITY

The total number of known chondrichthyan species currently stands at 1193; comprising 498 sharks, 646 batoids and 49 holocephalans (numbers calculated from a global checklist updated and modified from Compagno (2005)). These figures include both described and undescribed species. The latter group are those new or recently identified species yet to be formally treated by science and as such do not yet possess a binomial scientific name.

Of the global fauna, some 581 chondrichthyans are considered to be deepwater species (applying the definition outlined in the general introduction of this report), representing 48.7% of the global total. The deepwater fauna is divided between 278 sharks (55.8% of global), 257 batoids (39.8% of global) and 46 holocephalans (93.9% of global). All nine orders of elasmobranch and the single holocephalan order are represented in the deepsea, and Table 1.1 provides a summary of deepwater species (both described and undescribed) by order and family. The bulk of the deepwater shark fauna is attributable to the squaloid dogfishes and scyliorhinid catsharks, together comprising 84.5% of deepsea sharks. Three families of skates (Arhynchobatidae, Rajidae and Anacanthobatidae) dominate the deepwater batoid fauna, together comprising 89.9% of deepsea batoids.

A full annotated checklist of deepwater chondrichthyans appears at the end of this Section.

The total number of known species is ever increasing as exploratory and taxonomic work ensues. Undescribed taxa represent over one fifth (21%) of all known deepwater chondrichthyans. This high percentage illustrates two important points. Firstly, the overall lack of knowledge of the deepsea fauna at even the most basic (i.e. taxonomic) level. Secondly, that the deepsea chondrichthyan fauna is far from fully documented. For example, a recent joint Australian/Indonesian project monitoring the landings of chondrichthyans at various fish markets in Indonesia has revealed several previously unknown deepsea taxa amongst a larger number of new species (White et al. 2006). The majority of fishing in Indonesia is still focused on coastal and pelagic resources, with relatively little deepsea fishing activity. With continuing exploitation of traditional resources, fishing activities will likely move to deeper water around Indonesia, and the discovery of new fauna will likely continue. The checklist of known species will also continue to grow as material is gathered and examined from exploratory research cruises to previously poorly surveyed ocean regions. The 2003 NORFANZ cruise, surveying the seamounts and abyssal plains around the Lord Howe and Norfolk Ridges in the Western Pacific is one such example (Last 2007). Priede et al. (2006) note, however, that the discovery of new species of chondrichthyans at considerable depth (>3000m) is unlikely given present bathymetrical distributions and the apparent inability of chondrichthyans to exploit the deepest habitat zones.

The systematics and inter-relationships of several groups of deepsea chondrichthyans remains unresolved and as these groups are reviewed by taxonomists, the total number of species will ultimately change. One of the more taxonomically complex groups is the gulper sharks of the genus *Centrophorus*. The gulper shark fauna of the Indo-West Pacific is currently under review and many species traditionally considered to be wide-ranging with global distributions are likely species-complexes of regional endemics (W. White pers. comm.). Forms in the Atlantic likely represent distinct species to those in the Indo-West Pacific, for example, the lowfin gulper shark *Centrophorus lusitanicus*. At even a more localised scale, the apparently endemic Australian longnose gulper shark *C. harrissoni* appears to be distinct between the east and the west coasts of the continent (W. White pers. comm.). Resolution of such issues will have a profound effect on conservation and management of gulper sharks, amongst the most exploited of the deepsea sharks.

Another group presently under taxonomic review are the deepwater catsharks of the genus *Apristurus*. This large group has a complex and confused taxonomic history in part due to poor descriptions, lack of comparative material, poorly-defined morphometric characters and the large number of synonyms and undescribed species (Nakaya et al. 2005, Sato 2005). Resolution of the genus is relying on an international collaboration of experts. These studies are incorporating new fauna, some which may prove to be limited range endemics, such as *Apristurus* sp. 1 [Nakaya, Ueki & Sato, 2005] which as presently known, appears to be restricted to the Emperor Seamount chain in the Northwest Pacific (Nakaya et al. 2005).

Finally, the softnose and hardnose skates of the families Arhynchobatidae and Rajidae are considered to be a morphologically conservative, yet highly diverse group (McEachran and Dunn 1998). Indeed, they are two of the largest families of chondrichthyans, yet the phylogeny and inter-relationships of the skates remains unresolved, and the large number of unnamed species of these families in Table 1.1 (40 taxa), together with poor resolution at the generic level of the Australasian fauna in particular (Last and Yearsley 2002) illustrates the complexity of their systematics.

Table 1.1. The diversity of deepwater chondrichthyan fishes by order and family.

	Order	**Family**	**Common name**	**Described species**	**Undescribed species**	**Total species**
Sharks						
	Hexanchiformes	Chlamydoselachidae	Frilled Sharks	1	1	2
		Hexanchidae	Sixgill and Sevengill Sharks	3	0	3
	Squaliformes	Echinorhinidae	Bramble Sharks	2	0	2
		Squalidae	Dogfish Sharks	11	8	19
		Centrophoridae	Gulper Sharks	16	1	17
		Etmopteridae	Lanternsharks	42	5	47
		Somniosidae	Sleeper Sharks	16	1	17
		Oxynotidae	Roughsharks	5	0	5
		Dalatiidae	Kitefin Sharks	9	0	9
	Squatiniformes	Squatinidae	Angelsharks	5	2	7
	Pristiophoriformes	Pristiophoridae	Sawsharks	2	4	6
	Heterodontiformes	Heterodontidae	Bullhead Sharks	1	0	1
	Orectolobiformes	Parascylliidae	Collared Carpetsharks	2	0	2
	Lamniformes	Odontaspididae	Sand Tiger Sharks	2	0	2
		Pseudocarchariidae	Crocodile Sharks	1	0	1
		Mitsukurinidae	Goblin Sharks	1	0	1
		Alopiidae	Thresher Sharks	1	0	1
		Cetorhinidae	Basking Sharks	1	0	1
	Carcharhiniformes	Scyliorhinidae	Catsharks	84	35	119
		Proscylliidae	Finback Catsharks	3	1	4
		Pseudotriakidae	False Catsharks	2	3	5
		Triakidae	Houndsharks	4	2	6
		Carcharhinidae	Requiem Sharks	1	0	1
			Subtotal - sharks	*215*	*63*	*278*
Batoids						
	Rajiformes	Rhinobatidae	Guitarfishes	1	0	1
		Narcinidae	Numbfishes	6	1	7
		Narkidae	Sleeper Rays	4	0	4
		Torpedinidae	Torpedo Rays	7	1	8
		Arhynchobatidae	Softnose Skates	68	16	84
		Rajidae	Hardnose Skates	101	24	125
		Anacanthobatidae	Legskates	18	5	23
		Plesiobatidae	Giant Stingarees	1	0	1
		Urolophidae	Stingarees	2	0	2
		Hexatrygonidae	Sixgill Stingrays	1	0	1
		Dasyatidae	Stingrays	1	0	1
			Subtotal - batoids	*210*	*47*	*257*
Holocephalans						
	Chimaeriformes	Rhinochimaeridae	Longnose Chimaeras	8	1	9
		Chimaeridae	Shortnose Chimaeras	26	11	37
			Subtotal - holocephalans	*34*	*12*	*46*
			Total	**459**	**122**	**581**

BIOGEOGRAPHY

A broad-scale analysis of the biogeographical distribution of deepwater chondrichthyans reveals the highest levels of diversity in the Indo-West Pacific (Table 1.2). The Western and Eastern Atlantic have similar numbers of species, while diversity is lower in the Eastern Pacific. The Arctic and Antarctic regions are depauperate in terms of deepsea fauna. These biogeographical patterns follow general trends of chondrichthyan biogeography and diversity (Musick et al. 2004). The Indo-West Pacific is a large ocean region with a high level of endemism and thus it is not surprising that the highest diversity is recorded there. Lower diversity in the Eastern Pacific is attributable to a general lack of squaloid sharks, as previously recognised by Musick et al. (2004). Table 1.3 displays diversity by FAO Fisheries Areas (the United Nation's Food and Agriculture Organization's Major Fishing Areas for Statistical Purposes - maps of these can be located at ftp://ftp.fao.org/fi/maps/Default.htm#CURRENT), again illustrating high diversity in Fisheries Areas constituting the Indo-West Pacific, as well as in the Western Central Atlantic, a region centred around the tropical Caribbean Sea. (In Tables 1.2 and 1.3 the sum of totals exceeds the known number of deepwater species (581) as wider-ranging species occur in more than one region or Fisheries Area).

Table 1.2. Deepwater chondrichthyan diversity by major ocean region*.

Ocean region	Sharks	Batoids	Holocephalans	Total
Arctic Sea	1	0	0	1
Indo-West Pacific	190	123	28	341
Eastern Pacific	49	41	8	98
Western Atlantic	73	70	8	151
Eastern Atlantic	72	58	12	142
Antarctic seas	1	7	1	9

*Arctic Sea (FAO Area 18); Indo-West Pacific (FAO Areas 51, 57, 61, 71, 81); Eastern Pacific (FAO Areas 67, 77, 87); Western Atlantic (FAO Areas 21, 31, 41); Eastern Atlantic (FAO Areas 27, 34, 37, 47); Antarctic seas (FAO Areas 48, 58, 88).

Table 1.3. Deepwater chondrichthyan diversity by FAO Fisheries Area.

FAO Fisheries Area	Sharks	Batoids	Holocephalans	Total
18 Arctic Sea	1	0	0	1
21 Northwest Atlantic	18	13	3	34
27 Northeast Atlantic	42	23	8	73
31 Western Central Atlantic	59	37	5	101
34 Eastern Central Atlantic	44	21	7	72
37 Mediterranean and Black Sea	19	9	1	29
41 Southwest Atlantic	26	27	3	56
47 Southeast Atlantic	48	25	6	79
48 Antarctic Atlantic	0	4	1	5
51 Western Indian Ocean	68	27	5	100
57 Eastern Indian Ocean	71	32	13	116
58 Antarctic Indian Ocean	1	5	0	6
61 Northwest Pacific	81	37	10	128
67 Northeast Pacific	4	14	1	19
71 Western Central Pacific	79	26	9	114
77 Eastern Central Pacific	32	16	3	51
81 Southwest Pacific	54	39	16	109
87 Southeast Pacific	30	24	5	59
88 Antarctic Pacific	0	2	0	2

ANNOTATED CHECKLIST OF EXTANT DEEPWATER CHONDRICHTHYAN FISHES

Introduction

Systematics and classification

The following checklist contains all known described and undescribed deepwater species of the Class Chondrichthyes. The definition of a deepwater chondrichthyan is outlined in the general introduction of this report. The checklist is based largely upon Compagno and Duffy (2003) *A checklist of deep water chondrichthyans of the world* and Compagno (2005) *Global checklist of living chondrichthyan fishes*. Additionally, the present list contains recent species discoveries and descriptions, synonymy, and taxonomic changes and updates since preparation of the above-mentioned checklists, that is, up until January 2007. Primary literature (in the form of species descriptions and reviews), grey literature (in the form of in internal reports and conference abstracts books) and consultation with researchers possessing expert knowledge of taxonomic groups were used to update the checklist.

Phylogeny and systematic arrangement of the checklist follows Compagno (2001, 2005) with the Holocephali here presented first, followed by the squalomorph sharks (incorporating the batoids) and finally the galeomorph sharks.

Two of the notable discrepancies arising from following Compagno (2001, 2005) between the present checklist and other classifications concern the batoids. Firstly, several authors classify the batoids into numerous orders, but these are here considered suborders within the order Rajiformes. Suborders are not specified in the present checklist but these can be obtained from Compagno (2005). Secondly, the systematics and classification of the skates (suborder Rajoidei) is among the most complex and unresolved and the softnose and hardnose skates are often classified into two subfamilies within the single family Rajidae: the Arhynchobatinae (softnose skates) and the Rajinae (hardnose skates). However, these are here referred to as the families Arhynchobatidae (softnose skates) and Rajidae (hardnose skates).

Differences in the systematics and classification in the present list to that in Compagno (2005) concern recent systematic updates and these are briefly summarised as follows. 1). The classification of the Australasian skate fauna follows Last and Yearsley (2002) (with the exception of familial classification) along with recent descriptions (i.e. New Zealand *Brochiraja*; Last and McEachran 2006); 2). Whereas Compagno (2005) placed several Southwest Atlantic and Southeast Pacific *Bathyraja* into *Rhinoraja* they are here retained in *Bathyraja* due to a lack of explanation for their placement in *Rhinoraja*; and, 3). The systematics of the Indo-West Pacific *Centrophorus* are currently under review and this is reflected in the checklist (W. White pers. comm.).

The scientific name of each species is followed by the authority and year of publication for the description of that species. Parentheses around the authority and year indicate that the species name has changed since the original description. For example, the smallspine spookfish *Harriotta haeckeli* was described by Karrer in 1972 as the binomial name *Harriotta haeckeli* and is thus referred to as *Harriotta haeckeli* Karrer, 1972. The sicklefin chimaera *Neoharriotta pinnata* however, was originally described by Schnakenbeck in 1931 as *Harriotta pinnata* before being reassigned to the new genus *Neoharriotta*; it is thus referred to as *Neoharriotta pinnata* (Schnakenbeck, 1931). Where a species has not yet been formally described, that is, it has not been given a specific name and its description has not been published, it is often assigned a temporary letter or numerical code followed by a name of the researcher or publication which identified the species as distinct and new, and whom may be working on the relationship of this species to its congeners and ultimately its description. An example of this is the dwarf spookfish *Rhinochimaera* sp. A [Didier], a new species of longnose chimaera captured off Japan, under investigation by Dr Dominique Didier-Dagit.

Where a ? follows a generic name, the placement of this species in that particular genera is questionable and thus tentative. Further research may result in placement in another genus, evaluation of a subgenera to generic level or designation of an altogether new genus. Where a ? follows a specific name, the validity of this species is questionable or the use of that specific name may be invalid.

Subgeneric names have been provided for several skates within the families Arhynchobatidae and Rajidae and these may be elevated to generic level where further taxonomic research dictates. An example of this is the proposed elevation of *Zearaja* from a subgenera within *Dipturus* (Last and Gledhill 2006), represented here by the yellownose skate *Dipturus* (*Zearaja*) *chilensis* and the rough skate *Dipturus* (*Zearaja*) *nasutus*.

Distribution and habitat

Each species entry incorporates a summary of its known distribution, a list of FAO Fisheries Areas in which it occurs, habitat zones, bathymetric distribution (depth range) and where relevant, taxonomic notes including recent or commonly used synonyms.

Distribution, habitat and depth information was collated from Compagno and Duffy (2003), global and regional field guides, specifically Last and Stevens (1994), Carpenter and Niem (1998, 1999), Carpenter (2002), Ebert (2003), Compagno et al. (2005) and White et al. (2006), as well as the primary literature, grey literature sources and consultation with experts.

FAO Fisheries Areas (the United Nation's Food and Agriculture Organization's Major Fishing Areas for Statistical Purposes) are outlined below:

18 Arctic Sea
21 Northwest Atlantic
27 Northeast Atlantic
31 Western Central Atlantic
34 Eastern Central Atlantic
37 Mediterranean and Black Sea
41 Southwest Atlantic
47 Southeast Atlantic
48 Antarctic Atlantic
51 Western Indian Ocean
57 Eastern Indian Ocean
58 Antarctic Indian Ocean
61 Northwest Pacific
67 Northeast Pacific
71 Western Central Pacific
77 Eastern Central Pacific
81 Southwest Pacific
87 Southeast Pacific
88 Antarctic Pacific

Maps of these can be located at ftp://ftp.fao.org/fi/maps/Default.htm#CURRENT.

Habitat zones broadly follow Compagno et al. (2005). Benthic habitat zones are defined as follows:

Shelf: continental and insular shelves, 0 to 200m depth. Outer shelf defined as >90m.
Slope: continental and insular slopes, 200 to ~2250m depth, divided into upper slope (200–750m), mid slope (750–1500m) and deep slope (1500–2250m).
Abyssal plains: deep oceanic plains at ~2000–2250 to 6000m depth.
Hadal: benthic zone of deepsea trenches at 6000 to 11000m depth.

Where available, more specific habitat information may be provided, including occurrences on submarine ridges and rises, troughs, plateaus, seamounts, and deepsea reefs and shoals.

Pelagic habitat zones are defined as follows:

Epipelagic: 0 to 200m.
Mesopelagic: 200 to 1000m.
Bathypelagic: 1000 to 4000m.
Hadopelagic: 6000 to 11000m.
No chondrichthyans have ever been observed or recorded in the hadal or hadopelagic zones (Compagno et al. 2005, Priede et al. 2006). Priede et al. (2006) hypothesised that the high-energy demands of chondrichthyans exclude them from the deepest habitat zones.

Class Chondrichthyes.

Subclass Holocephali.

Order Chimaeriformes. Modern Chimaeras.

Family Rhinochimaeridae. Longnose Chimaeras.

***Harriotta haeckeli* Karrer, 1972.** Smallspine spookfish
Patchy in the Southern Ocean and Eastern Atlantic. A record in the Northwest Atlantic requires confirmation. FAO Areas 21(?), 27, 34, 57, 81. Abyssal plains and deepsea troughs. 1114-2603m.

***Harriotta raleighana* Goode & Bean, 1895.** Narrownose or longnose chimaera, bentnose rabbitfish or bigspine spookfish
Wide-ranging but patchy in the Indo-West Pacific and Atlantic. FAO Areas 21, 27, 34, 41, 47, 51, 57, 61, 71, 81. Upper to deep slope, abyssal plains and seamounts. 380-2600m.

***Neoharriotta carri* Bullis & Carpenter, 1966.** Dwarf sicklefin chimaera
Western Central Pacific: southern Caribbean. FAO Area 31. Upper slope. 240-600m.

***Neoharriotta pinnata* (Schnakenbeck, 1931).** Sicklefin chimaera
Eastern Central and Southeast Atlantic: West Africa. FAO Areas 34, 47. Outermost shelf and upper slope. 200-470m.

***Neoharriotta pumila* Didier & Stehmann, 1996.** Arabian sicklefin chimaera
Western Indian: Arabian Sea and Gulf of Aden. FAO Area 51. Outer shelf and upper to mid slope. 100-1120m.

***Rhinochimaera africana* Compagno, Stehmann & Ebert, 1990.** Paddlenose chimaera or spookfish
Patchy in the Western Indian and Northwest Pacific. FAO Areas 51, 61. Upper to mid slope and seamounts. 500-1500m.

***Rhinochimaera atlantica* Holt & Byrne, 1909.** Spearnose chimaera or straightnose rabbitfish
Wide-ranging in the Atlantic. FAO Areas 21, 27, 31, 34, 41, 47. Upper to mid slope. 500-1500m.

***Rhinochimaera pacifica* (Mitsukuri, 1895).** Pacific spookfish or knifenose chimaera
Patchy in the Indo-West Pacific and the Southeast Pacific. FAO Areas 57, 61, 71, 81, 87. Outermost shelf, upper to mid slope, deepsea troughs, deepsea plateaus and seamounts. 191-1290m (mostly >700m).

***Rhinochimaera* sp. A [Didier].** Dwarf spookfish
Northwest Pacific: Japan. FAO Area 61.

Family Chimaeridae. Shortnose Chimaeras.

***Chimaera cubana* Howell-Rivero, 1936.** Cuban chimaera
Western Central Atlantic: Caribbean. FAO Area 31. Upper slope. 234-450m.

***Chimaera jordani* Tanaka, 1905.** Jordan's chimaera
Confirmed from the Northwest Pacific (Japan) and Western Indian, but probably more wide-ranging. FAO Areas 51, 61. Upper to deep slope. 383-1600m.

***Chimaera lignaria* Didier, 2002.** Giant, purple or carpenter's chimaera
Primarily Southwest Pacific: southern Australia and New Zealand. FAO Areas 57, 81. Upper to deep slope, deepsea plateaus and seamounts. 400-1800m (mostly >800m). Includes *Chimaera* sp. D [Last & Stevens, 1994].

***Chimaera monstrosa* Linnaeus, 1758.** Rabbitfish
Wide-ranging in the Northeast Atlantic including the Mediterranean. FAO Areas 27, 34, 37. Shelf and upper to mid slope. 50-1000m (mostly 300-500m).

***Chimaera owstoni* Tanaka, 1905.** Owston's chimaera
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope. 500-1200m.

***Chimaera panthera* Didier, 1998.** Leopard or roundfin chimaera
Southwest Pacific: New Zealand. FAO Area 81. Upper to mid slope, deepsea rises, submarine ridges and seamounts. 327-1020m.

***Chimaera phantasma* Jordan & Snyder, 1900.** Silver chimaera
Wide-ranging but patchy in the Western Pacific and Eastern Indian. FAO Areas 57, 61, 71, 81. Shelf and upper to mid slope. 20-962m. Includes the junior synonym *Chimaera pseudomonstrosa* Fang & Wang, 1932, and *Chimaera* sp. E [Last & Stevens, 1994].

***Chimaera* sp. A [Last & Stevens, 1994].** Southern chimaera
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Upper to mid slope. 300-850m.

***Chimaera* sp. B [Last & Stevens, 1994].** Shortspine or brown chimaera
Western Pacific: Australia and New Zealand. FAO Areas 71, 81. Upper to mid slope. 450-1000m.

***Chimaera* sp. C [Last & Stevens, 1994].** Longspine chimaera
Eastern Indian and Western Pacific: Australia and possibly New Zealand. FAO Areas 57, 71, 81. Upper to mid slope. 440-1300m.

***Chimaera* cf. sp. E [Last & Stevens, 1994; White et al. 2006].** Lombok chimaera
Eastern Indian: Lombok, Indonesia. FAO Area 57. Habitat not documented, but probably slope.

***Chimaera* sp.? [not *africana*, Compagno et al., 1989; Didier].** Cape chimaera
Southeast Atlantic: South Africa. FAO Area 47.

***Hydrolagus affinis* (Capello, 1867).** Atlantic chimaera or smalleyed rabbitfish
Wide-ranging in the North Atlantic. FAO Areas 21, 27, 34. Upper to deep slope, abyssal plains and seamounts. 300-2410m (mostly >1000m).

***Hydrolagus africanus* (Gilchrist, 1922).** African chimaera
Western Indian and probably Southeast Atlantic: southern Africa. FAO Areas 47(?), 51. Upper to mid slope. 300-1300m (mostly 421-750m).

***Hydrolagus alberti* Bigelow & Schroeder, 1951.** Gulf chimaera
Western Central Atlantic: Caribbean and the Gulf of Mexico. FAO Area 31. Upper to mid slope. 348-1100m.

***Hydrolagus alphus* Quaranta, Didier, Long & Ebert, 2006.** Whitespot ghostshark
Southeast Pacific: Galapagos Islands. FAO Area 87. Upper to mid slope. 600-900m.

***Hydrolagus barbouri* (Garman, 1908).** Ninespot chimaera
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope. 250-1100m (most common 600-800m).

***Hydrolagus bemisi* Didier, 2002.** Pale ghostshark
Southwest Pacific: New Zealand. FAO Area 81. Upper to mid slope, deepsea plateaus and rises. 400-1100m (mostly 500-700m).

***Hydrolagus colliei* (Lay & Bennett, 1839).** Spotted ratfish
Northeast and Eastern Central Pacific: Alaska to Mexico. FAO Areas 67, 77. Shelf and upper to mid slope. 0-971m.

***Hydrolagus lemures* (Whitley, 1939).** Blackfin ghostshark
Eastern Indian and Western Central and Southwest Pacific: Australia. FAO Areas 57, 71, 81. Outer shelf and upper slope. 146-510m.

***Hydrolagus lusitanicus* Moura, Figueiredo, Bordalo-Machado, Almeida & Gordo, 2005.**
Northeast Atlantic: Portugal. FAO Area 27. Deep slope. 1600m.

***Hydrolagus macrophthalmus* de Buen, 1959.** Bigeye chimaera.
Southeast Pacific: Chile. FAO Area 87. Habitat data not available.

***Hydrolagus matallanasi* Soto & Vooren, 2004.** Striped Rabbitfish
Southwest Atlantic: southern Brazil. FAO Area 41. Upper slope. 416-736m.

***Hydrolagus mccoskeri* Barnett, Didier, Long & Ebert, 2006.** Galapagos ghostshark
Southeast Pacific: Galapagos Islands. FAO Area 87. Upper slope. 396-506m.

***Hydrolagus mirabilis* (Collett, 1904).** Large-eyed rabbitfish or spectral chimaera
Wide-ranging in the Eastern Atlantic and also in the Western Central Atlantic. FAO Areas 27, 31, 34, 47. Upper to deep slope. 450-1933m (mostly >800m).

***Hydrolagus mitsukurii* (Dean, 1904).** Mitsukurii's chimaera
Northwest and Western Central Pacific: Japan to Philippines. FAO Areas 61, 71. Upper to mid slope. 325-770m. Includes the junior synonym *Hydrolagus deani* (Smith & Radcliffe, 1912).

***Hydrolagus novaezealandiae* (Fowler, 1910).** Dark or New Zealand ghostshark
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 25-950m (most common 150-500m).

***Hydrolagus ogilbyi* (Waite, 1898).** Ogilby's ghostshark
Eastern Indian and Southwest Pacific: southeastern Australia. FAO Areas 57, 81. Outer shelf and upper slope. 120-350m.

***Hydrolagus pallidus* Hardy & Stehmann, 1990.** Pale chimaera
Scattered records in the Northeast Atlantic. FAO Area 27. Mid to deep slope and deepsea troughs. 1200-2075m.

***Hydrolagus purpurescens* (Gilbert, 1905).** Purple chimaera
Northwest Pacific (Japan) and Eastern Central Pacific (Hawaii). FAO Areas 61, 77. Mid to deep slope, deepsea troughs and seamounts. 920-1130m (Japan), 1750-1951m (Hawaii). Includes the probable junior synonym *Hydrolagus eidolon* (Jordan & Hubbs, 1925).

***Hydrolagus trolli* Didier & Séret, 2002.** Pointy-nosed blue chimaera
Wide-ranging but patchy in the Southern Hemisphere. FAO Areas 47, 48, 58(?), 71, 81, 88(?) Upper to mid slope and seamounts. 650-1719m (mostly >1000m).

***Hydrolagus* sp. A [Last & Stevens, 1994; Didier in prep.].** Black ghostshark
Primarily Southwest Pacific: southern Australia and New Zealand. FAO Areas 57, 81. Mid slope and seamounts. 900-1400m.

***Hydrolagus* sp. B [Last & Stevens, 1994; Didier in prep.].** Marbled ghostshark
Western Central and Southwest Pacific: eastern Australia. FAO Areas 71, 81. Upper to mid slope. 450-850m.

***Hydrolagus* sp. E ["*melanophasma*" Compagno/McCosker].** Black ratfish
Eastern Central Pacific: California. FAO Area 77.

***Hydrolagus* sp. F [Chirichigno, 1974].** Peruvian ratfish
Southwest Pacific: Peru. FAO Area 87.

***Hydrolagus* sp. 1. [White et al. 2006].** Striped ghostshark
Eastern Indian: Lombok, Indonesia. FAO Area 57. Habitat not documented, but probably slope.

***Hydrolagus* cf. *lemures* (Whitley, 1939) [White et al. 2006].** Indonesian ghostshark
Eastern Indian: eastern Indonesia. FAO Area 57. Habitat not documented, but probably slope.

Subclass Elasmobranchii.

Superorder Squalomorphii. Squalomorph Sharks.

Order Hexanchiformes. Cow and Frilled Sharks.

Family Chlamydoselachidae. Frilled Sharks.

***Chlamydoselachus anguineus* Garman, 1884.** Frilled shark
Wide-ranging but patchy in temperate and tropical waters of the Atlantic and Indo-Pacific. FAO Areas 27, 31, 34, 47, 57, 61, 77, 81, 87. Shelf and upper to mid slope. 50-1500m.

***Chlamydoselachus* sp. A [Ebert & Compagno]**. Southern African frilled shark
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Shelf and upper to mid slope. 51-1440m.

Family Hexanchidae. Sixgill and Sevengill Sharks.

***Heptranchias perlo* (Bonnaterre, 1788).** Sharpnose sevengill shark or perlon
Wide-ranging but patchy in temperate and tropical waters of the Atlantic and Indo-Pacific. FAO Areas 27, 31, 34, 37, 41, 47, 51, 57, 61, 71, 81. Shelf (occassional) and upper to mid slope. 27-1000m.

***Hexanchus griseus* (Bonnaterre, 1788).** Bluntnose sixgill shark
Wide-ranging but patchy in temperate and tropical waters of the Atlantic and Indo-Pacific. FAO Areas 27, 31, 34, 37, 41, 47, 51, 57, 61, 67, 71, 77, 81, 87. Shelf, upper to deep slope, submarine ridges and seamounts. Mainly deepwater, young inshore in cold water. 0-1875m (500-1100m usual).

***Hexanchus nakamurai* Teng, 1962.** Bigeye sixgill shark
Wide-ranging but patchy in warm-temperate and tropical waters of the Atlantic and Indo-Pacific. FAO Areas 27, 31, 34(?), 37, 47, 51, 57, 61, 71. Shelf (occassional) and upper slope. 90-621m.

Order Squaliformes. Dogfish Sharks.

Family Echinorhinidae. Bramble Sharks.

***Echinorhinus brucus* (Bonnaterre, 1788).** Bramble shark
Wide-ranging but patchy in the Atlantic and Indo-Pacific. FAO Areas 21, 27, 31, 34, 37, 41, 47, 51, 57, 61, 71(?), 81. Shelf (occassional) and upper to mid slope. 18-900m.

***Echinorhinus cookei* (Pietschmann, 1928).** Prickly shark
Patchy in the Eastern, Central and Western Pacific. FAO Areas 57, 61, 71, 77, 81, 87. Shelf and upper to mid slope and seamounts. 11-1100m.

Family Squalidae. Dogfish Sharks.

***Cirrhigaleus asper* (Merrett, 1973).** Roughskin spurdog
Wide-ranging but patchy in warm-temperate and tropical waters of the Atlantic and Indo-Pacific. FAO Areas 31, 41, 47, 51, 57(?), 77. Shelf and upper slope. 73-600m.

***Cirrhigaleus barbifer* Tanaka, 1912.** Mandarin dogfish
Patchy in the Western Pacific. FAO Areas 61, 71, 81. Outer shelf and upper slope. 146-640m. May represent a species complex.

***Squalus blainvillei*? (Risso, 1826).** Longnose spurdog
Nominally from the Eastern Atlantic and the Mediterranean, but not well defined due to confusion with other species and taxonomic issues. FAO Areas 27, 34, 37, 47, 51(?), 61(?), 81(?). Shelf and upper slope. 16->440m. Considerable taxonomic issues (records from elsewhere in the Atlantic and the Indo-Pacific based in part on *S. mitsukurii* or close relatives).

***Squalus brevirostris* Tanaka, 1917.** Japanese shortnose spurdog
Northwest Pacific: Japan and Taiwan. FAO Area 61. Habitat information not available. Tentatively placed on checklist as distinct from *Squalus megalops*.

***Squalus cubensis* Howell-Rivero, 1936.** Cuban dogfish
Warm-temperate waters of the Western Atlantic. FAO Areas 31, 41. Shelf and upper slope. 60-380m.

***Squalus japonicus* Ishikawa, 1908.** Japanese spurdog
Northwest and Western Central Pacific: East Asia. FAO Areas 61, 71. Outer shelf and upper slope. 120-340m.

***Squalus lalannei* Baranes, 2003**. Seychelles spurdog
Western Indian: Seychelles. FAO Area 51. Mid slope. 1000m.

***Squalus megalops* (Macleay, 1881).** Shortnose spurdog
Widespread in temperate and warm-temperate waters of the Indo-West Pacific and Eastern Atlantic. FAO Areas 27, 34, 37, 47, 51, 57, 61, 71, 81. Shelf and upper slope. 0-732m. May represent a species complex.

***Squalus melanurus* Fourmanoir, 1979.** Blacktail spurdog
Western Central Pacific: New Caledonia. FAO Area 71. Shelf and upper slope. 34-480m.

***Squalus mitsukurii* Jordan & Snyder, *in* Jordan & Fowler, 1903.** Shortspine spurdog
Wide-ranging, but patchy in temperate and tropical waters of the Atlantic and Indo-Pacific, but not well defined due to taxonomic issues. FAO Areas 31, 41, 34(?), 47(?), 51, 57, 61, 71, 77, 81, 87. Shelf and upper to mid slope, submarine ridges and seamounts. 4-954m (100-500m usual). Resolution of considerable taxonomic issues is ongoing. Tentatively includes the junior synonyms *Squalus griffini* Phillipps, 1931 and *Squalus probatovi* Myagkov & Kondyurin, 1986.

***Squalus rancureli* Fourmanoir, 1978.** Cyrano spurdog
Western Central Pacific: Vanuatu. FAO Area 71. Upper slope. 320-400m.

***Squalus* sp. A [Last & Stevens, 1994].** Bartail spurdog
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 220-450m.

***Squalus* sp. B [Last & Stevens, 1994].** Eastern highfin spurdog
Western Central and Southwest Pacific: eastern Australia. FAO Areas 71, 81. Upper slope. 240-450m.

***Squalus* sp. C [Last & Stevens, 1994].** Western highfin spurdog
Eastern Indian: western Australia and Indonesia. FAO Area 57. Upper slope. 220-510m.

***Squalus* sp. E [Last & Stevens, 1994].** Western longnose spurdog
Eastern Indian: northwestern Australia and Indonesia; Western Central Pacific: Philippines. FAO Areas 57, 71. Upper slope. 300-510m.

***Squalus* sp. F [Last & Stevens, 1994].** Eastern longnose spurdog
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 220-500m.

***Squalus* sp. 1 [White et al. 2006].** Indonesian greeneye spurdog
Eastern Indian: Indonesia. FAO Area 57. Upper to mid slope. 154-1370m.

***Squalus* sp. 2 [Compagno et al., 2005].** Philippine longnose spurdog
Western Central Pacific: Philippines. FAO Area 71. Shelf and upper slope. <40-385m. Possibly conspecific with dogfishes in the East and South China seas, and *Squalas* sp. E [Last & Stevens, 1994] (Compagno et al. 2005).

***Squalus* sp. 3 [White et al. 2006].** Indonesian shortnose spurdog
Eastern Indian: Indonesia. FAO Area 57. Upper slope. Depth data not available.

Family Centrophoridae. Gulper Sharks.

***Centrophorus acus* Garman, 1906.** Needle dogfish
Northwest Pacific: Japan, Taiwan and Philippines. FAO Areas 61, 71. Outer shelf and upper to mid slope. 150-950m (mostly >200m, possibly to 1786m).

***Centrophorus atromarginatus* Garman, 1913.** Dwarf gulper shark
Patchy in the Indo-West Pacific, but not well defined. FAO Areas 51, 57, 61, 71. Outer shelf and upper slope. 150-450m.

Centrophorus granulosus **(Bloch & Schneider, 1801).** Gulper shark
Wide-ranging but patchy in the Atlantic and Indo-Pacific, but some records may represent additional species. FAO Areas 27, 31(?), 34, 37, 41(?), 47, 51, 57, 61, 71. Shelf and upper to mid slope. 50-1440m (mostly 200-600m). Resolution of taxonomic issues ongoing and as such occurrence and distribution not well defined.

Centrophorus harrissoni **McCulloch, 1915.** Longnose gulper shark
Western Central and Southwest Pacific, Eastern Indian: Australia. FAO Areas 57, 71, 81. Upper to mid slope. 250-790m. Resolution of taxonomic issues ongoing. May represent a species complex.

Centrophorus isodon **(Chu, Meng & Liu, 1981).** Blackfin gulper shark
Patchy in the Indo-West Pacific. FAO Areas 51, 57, 61, 71. Mid slope. 760-770m.

Centrophorus lusitanicus **Bocage & Capello, 1864.** Lowfin gulper shark
Patchy in the Eastern Atlantic and Indo-West Pacific. FAO Areas 27, 34, 51, 61. Upper to mid slope. 300-1400m (mostly 300-600m). Indo-West Pacific form may represent a separate species (*Centrophorus* cf. *lusitanicus* in White et al. 2006).

Centrophorus moluccensis **Bleeker, 1860.** Smallfin gulper shark
Patchy in the Indo-West Pacific. FAO Areas 51, 57, 61, 71, 81. Outer shelf and upper to mid slope. 125-820m. Resolution of taxonomic issues ongoing. May represent a species complex.

Centrophorus niaukang **Teng, 1959.** Taiwan gulper shark
Scattered locations in the Atlantic and Indo-West Pacific. FAO Areas 31, 34, 47, 51, 57(?), 61, 71(?). Outer shelf and upper to mid slope. 98-~1000m. Taxonomic resolution of this species' relationship to *Centrophorus acus* is ongoing.

Centrophorus seychellorum **Baranes, 2003.** Seychelles gulper shark
Western Indian: Seychelles. FAO Area 51. Mid slope. 1000m.

Centrophorus squamosus **(Bonnaterre, 1788).** Leafscale gulper shark
Wide-ranging, but patchy in the Eastern Atlantic and Indo-West Pacific. FAO Areas 27, 34, 47, 51, 61, 71, 81. Upper to deep slope and abyssal plains. 230-2400m.

Centrophorus tessellatus **Garman, 1906.** Mosaic gulper shark
Scattered locations in the Western Atlantic and Pacific, but some records provisional. FAO Areas 31, 61, 77. Upper slope. 260-730m. Taxonomic issues mean that occurrence and distribution are not well defined and as such many records are provisional.

Centrophorus uyato **(Rafinesque, 1810).** Southern dogfish
Patchy in the Eastern and Western Atlantic and the Indo-West Pacific, but inadequately defined due to taxonomic issues. FAO Areas 27, 31, 34, 37, 51, 57, 61, 71. Shelf and upper to mid slope. 50-1400m. Taxonomic issues mean that occurrence and distribution are not well defined and as such many records are provisional. Likely a species complex.

Centrophorus **sp. A [Séret].**
Western Central Pacific: New Caledonia. FAO Area 71.

Deania calcea **(Lowe, 1839).** Birdbeak or shovelnose dogfish
Wide-ranging in the Eastern Atlantic and Indo-West Pacific. FAO Areas 27, 34, 47, 51, 57, 61, 81, 87. Shelf and upper to mid slope. 70-1470m (usually 400-900m). Indonesian form may represent a distinct species (*Deania* cf. *calcea* in White et al. 2006).

***Deania hystricosum* (Garman, 1906).** Rough longnose dogfish
Scattered locations in the Eastern Atlantic and Western Pacific. FAO Areas 27(?), 34, 47, 61, 81(?). Upper to mid slope. 470-1300m.

***Deania profundorum* (Smith & Radcliffe, 1912).** Arrowhead dogfish
Scattered locations in the Atlantic and Indo-West Pacific. FAO Areas 31, 34, 47, 51, 71. Upper to deep slope. 275-1785m.

***Deania quadrispinosum* (McCulloch, 1915).** Longsnout dogfish
Southern regions of the Eastern Atlantic and Indo-West Pacific. FAO Areas 47, 51, 57, 71, 81. Outer shelf and upper to mid slope. 150-1360m (usually <400m).

Family Etmopteridae. Lanternsharks.

***Aculeola nigra* de Buen, 1959.** Hooktooth dogfish
Southeast Pacific: Peru to Chile. FAO Area 87. Outer shelf and upper slope. 110-735m.

***Centroscyllium excelsum* Shirai & Nakaya, 1990.** Highfin dogfish
Northwest Pacific: Emperor Seamount Chain. FAO Area 61. Seamounts. 800-1000m.

***Centroscyllium fabricii* (Reinhardt, 1825).** Black dogfish
Wide-ranging in temperate waters of the Atlantic. FAO Areas 21, 27, 31, 34, 47. Outer shelf and upper to deep slope. 180-1600m (usually >275m, probably to 2250m).

***Centroscyllium granulatum* Günther, 1887.** Granular dogfish
Southeast Pacific: Chile. FAO Area 87. Upper slope. 300-500m.

***Centroscyllium kamoharai* Abe, 1966.** Bareskin dogfish
Indo-West Pacific: Japan, Australia and possibly Philippines. FAO Areas 57, 61, 71(?), 81. Upper to mid slope. 500-1200m (mostly >900m).

***Centroscyllium nigrum* Garman, 1899.** Combtooth dogfish
Patchy in the Central and Eastern Pacific. FAO Areas 77, 87. Upper to mid slope. 400-1143m.

***Centroscyllium ornatum* (Alcock, 1889).** Ornate dogfish
Northern Indian: Arabian Sea and the Bay of Bengal. FAO Areas 51, 57. Upper to mid slope. 521-1262m.

***Centroscyllium ritteri* Jordan & Fowler, 1903.** Whitefin dogfish
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope and seamounts. 320-1100m.

***Etmopterus baxteri* Garrick, 1957.** New Zealand lanternshark
Southern regions of the Eastern Atlantic and Indo-West Pacific. FAO Areas 34(?), 47, 51, 57, 81. Upper to mid slope. 250-1500m. Occurrence and distribution not well defined in the Southeast Atlantic and Western Indian.

***Etmopterus bigelowi* Shirai & Tachikawa, 1993.** Blurred smooth lanternshark
Wide-ranging but patchy in the Atlantic and Indo-Pacific. FAO Areas 31, 34, 41, 47, 51, 57, 61, 71, 81, 87. Outer shelf, upper to mid slope, submarine ridges and seamounts. 163-1000m.

***Etmopterus brachyurus* Smith & Radcliffe, 1912.** Shorttail lanternshark
Indo-West Pacific: Japan, Philippines and Australia. FAO Areas 57, 61, 71. Upper slope. 481m. References to the species off southern Africa refer to the as yet undescribed sculpted lanternshark.

***Etmopterus bullisi* Bigelow & Schroeder, 1957.** Lined lanternshark
Western Central Atlantic: Caribbean. FAO Area 31. Upper to mid slope. 275-824m (mostly >350m).

***Etmopterus burgessi* Schaaf-da Silva & Ebert, 2006.** Broad-snout lanternshark
Northwest Pacific: Taiwan. FAO Area 61. Slope. >300m.

***Etmopterus carteri* Springer & Burgess, 1985.** Cylindrical lanternshark
Western Central Atlantic: Caribbean coast of Colombia. FAO Area 31. Upper slope. 283-356m.

***Etmopterus caudistigmus* Last, Burgess & Séret, 2002.** New Caledonia tailspot lanternshark
Western Central Pacific: New Caledonia. FAO Area 71. Upper to mid slope. 638-793m.

***Etmopterus decacuspidatus* Chan, 1966.** Combtooth lanternshark
Northwest Pacific: South China Sea. FAO Area 61. Upper slope. 512-692m.

***Etmopterus dianthus* Last, Burgess & Séret, 2002.** Pink lanternshark
Western Central Pacific: Australia and New Caledonia. FAO Area 71. Upper to mid slope. 700-880m.

***Etmopterus dislineatus* Last, Burgess & Séret, 2002.** Lined lanternshark
Western Central Pacific: Australia. FAO Area 71. Upper slope. 590-700m.

***Etmopterus evansi* Last, Burgess & Séret, 2002.** Blackmouth lanternshark
Eastern Indian: Australia and Arafura Sea. FAO Areas 57, 71. Shoals and reefs on the upper slope. 430-550m.

***Etmopterus fusus* Last, Burgess & Séret, 2002.** Pygmy lanternshark
Eastern Indian: Australia. FAO Area 57. Upper slope. 430-550m.

***Etmopterus gracilispinis* Krefft, 1968.** Broadband lanternshark
Wide-ranging but patchy in the Western Atlantic and off southern Africa. FAO Areas 21, 31, 41, 47, 51. Outer shelf and upper to mid slope. 70-1000m.

***Etmopterus granulosus* (Günther, 1880).** Southern lanternshark
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Upper slope. 220-637m.

***Etmopterus hillianus* (Poey, 1861).** Caribbean lanternshark
Northwest and Western Central Atlantic including the Caribbean. FAO Areas 21, 31. Upper slope. 311-695m.

***Etmopterus litvinovi* Parin & Kotlyar, *in* Kotlyar, 1990.** Smalleye lanternshark
Southeast Pacific: Nazca and Sala y Gomez Submarine Ridges. FAO Area 87. Submarine ridges. 630-1100m.

***Etmopterus lucifer* Jordan & Snyder, 1902**. Blackbelly lanternshark
Patchy in the Western Pacific, but provisional records from elsewhere require confirmation. FAO Areas 41(?), 47(?), 51(?), 57, 61, 71(?), 81. Outer shelf, upper to mid slope. 158-1357m. Various nominal records require confirmation.

***Etmopterus molleri* (Whitley, 1939).** Slendertail lanternshark
Patchy in the Western Pacific and possibly also the Western Indian (Mozambique). FAO Areas 51(?), 61, 81. Upper slope. 238-655m. Includes the probable junior synonym *Etmopterus schmidti* Dolganov, 1986.

***Etmopterus perryi* Springer & Burgess, 1985.** Dwarf lanternshark
Western Central Atlantic: Caribbean off Colombia. FAO Area 31. Upper slope. 283-375m.

***Etmopterus polli* Bigelow, Schroeder & Springer, 1953.** African lanternshark
Eastern Atlantic: West Africa. Possibly Caribbean off Venezuela. FAO Areas 31(?), 34, 47. Upper to mid slope. 300-1000m.

***Etmopterus princeps* Collett, 1904.** Great lanternshark
Wide-ranging in the North and Central Atlantic. FAO Areas 21, 27, 34. Upper to deep slope, deepsea rises, deepsea plateaus and abyssal plains. 567-4500m.

***Etmopterus pseudosqualiolus* Last, Burgess & Séret, 2002.** False pygmy laternshark
Western Central Pacific: Norfolk and Lord Howe Ridges. FAO Area 71. Submarine ridges. 1043-1102m.

***Etmopterus pusillus* (Lowe, 1839).** Smooth lanternshark
Wide-ranging in temperate and warm-temperate waters of the Atlantic and Indo-West and Central Pacific. FAO Areas 27, 31, 34, 41, 47, 57, 61, 77, 81. Upper to mid (possibly to deep) slope. 274-1000m (possibly to 1998m).

***Etmopterus pycnolepis* Kotlyar, 1990.** Densescale lanternshark
Southeast Pacific: Nazca and Sala y Gomez Submarine Ridges. FAO Area 87. Submarine ridges. 330-763m.

***Etmopterus robinsi* Schofield & Burgess, 1997.** West Indian laternshark
Western Central Atlantic: Caribbean. FAO Area 31. Upper to mid slope. 412-787m.

***Etmopterus schultzi* Bigelow, Schroeder & Springer, 1953.** Fringefin lanternshark
Western Central Atlantic: Gulf of Mexico. FAO Area 31. Upper to mid slope. 220-915m (mostly >350m).

***Etmopterus sentosus* Bass, D'Aubrey & Kistnasamy, 1976.** Thorny lanternshark
Western Indian: East Africa. FAO Area 51. Upper slope. 200-500m.

***Etmopterus spinax* (Linnaeus, 1758).** Velvet belly
Widespread in the Eastern Atlantic and Mediterranean. FAO Areas 27, 34, 37, 47.
Shelf and upper to deep slope. 70-2000m (mostly 200-500m).

***Etmopterus splendidus* Yano, 1988.** Splendid lanternshark
Northwest Pacific: Japan and Taiwan. FAO Area 61. Uppermost slope. 210m.

***Etmopterus unicolor* (Engelhardt, 1912).** Brown lanternshark
Northwest Pacific: Japan, although not well defined with provisional records from southern Africa, Australia and New Zealand. FAO Areas 47(?), 51(?), 57(?), 61, 81(?). Upper to mid slope and seamounts. 402-1380m. Tentatively classified as one species including *Etmopterus compagnoi* Fricke & Koch, 1990 and *Etmopterus* sp. B [Last & Stevens, 1994].

***Etmopterus villosus* Gilbert, 1905.** Hawaiian lanternshark
Eastern Central Pacific: Hawaii. FAO Area 77. Upper to mid slope. 406-911m.

Etmopterus virens **Bigelow, Schroeder & Springer, 1953.** Green lanternshark
Western Central Atlantic: Gulf of Mexico and Caribbean. FAO Area 31. Upper to mid slope. 196-915m (mostly >350m).

Etmopterus **sp. [Compagno].** Guadalupe lanternshark

Etmopterus **sp. [Compagno].** Chilean lanternshark
Southeast Pacific: Chile. FAO Area 87.

Etmopterus **sp. near *baxteri* [Compagno & Ebert].** Giant lanternshark
Southern Africa.

Etmopterus **sp. near *brachyurus* [Compagno & Ebert].** Sculpted lanternshark
Southern Africa.

Etmopterus **sp. near *princeps* [Compagno].**
Southeast Atlantic: Inaccessible Island. FAO Area 47.

Miroscyllium sheikoi **(Dolganov, 1986).** Rasptooth dogfish
Northwest Pacific: off Japan. FAO Area 61. Upper slope of submarine ridges. 340-370m.

Trigonognathus kabeyai **Mochizuki & Ohe, 1990.** Viper dogfish
North and Central Pacific: Japan and Hawaii. FAO Areas 61, 77. Upper slope and seamounts. 270-360m.

Family Somniosidae. Sleeper Sharks.

Centroscymnus coelolepis **Bocage & Capello, 1864.** Portuguese dogfish
Wide-ranging in the Atlantic and Indo-Pacific. FAO Areas 21, 27, 31, 34, 37, 47, 51, 57, 61, 81. Outer shelf, upper to deep slope and abyssal plains. 128-3675m (mostly >400m).

Centroscymnus owstoni **Garman, 1906.** Roughskin dogfish
Wide-ranging, but patchy in the Atlantic, Pacific and Eastern Indian. FAO Areas 31, 34, 41, 47, 57, 61, 81, 87. Upper to mid slope and submarine ridges. 426-1459m (mostly >600m). Includes the junior synonym *Centroscymnus cryptacanthus* Regan, 1906.

Centroselachus crepidater **(Bocage & Capello, 1864).** Longnose velvet dogfish
Wide-ranging, but patchy in the Western Atlantic, Pacific and Western Indian. FAO Areas 27, 34, 47, 51, 57, 61, 81, 87. Upper to deep slope. 270-2080m (mostly >500m).

Proscymnodon macracanthus **(Regan, 1906).** Largespine velvet dogfish
Southeast Pacific: Straits of Magellan (Chile). FAO Area 87. Habitat and depth unrecorded.

Proscymnodon plunketi **(Waite, 1909).** Plunket shark
Patchy in southern regions of the Indo-West Pacific. FAO Areas 51, 57, 81.
Upper to mid slope. 219-1427m (most common 550-732m).

Scymnodalatias albicauda **Taniuchi & Garrick, 1986.** Whitetail dogfish
Patchy in the Southern Ocean. FAO Areas 47, 57, 81. Outer shelf, upper slope and submarine ridges. 150-500m.

Scymnodalatias garricki **Kukuyev & Konovalenko, 1988.** Azores dogfish
Northeast Atlantic: North Atlantic Ridge. FAO Area 27. Mesopelagic over seamounts. 300m.

***Scymnodalatias sherwoodi* (Archey, 1921).** Sherwood dogfish
Southwest Pacific: New Zealand. FAO Area 81. Upper slope. 400-500m.

***Scymnodon ringens* Bocage & Capello, 1864.** Knifetooth dogfish
Northeast and Eastern Central Atlantic. Uncertain from New Zealand in the Southwest Pacific. FAO Areas 27, 34, 81(?). Upper to deep slope. 200-1600m.

***Somniosus antarcticus* Whitley, 1939.** Southern sleeper shark. Patchy in the Southern Ocean. FAO Areas 41, 47, 57, 58, 81, 87. Outer shelf and upper to mid slope. 145-1200m.

***Somniosus longus* (Tanaka, 1912).** Frog shark
Western Pacific: Japan and New Zealand. FAO Areas 61, 81. Upper to mid slope. 250-1160m.

***Somniosus microcephalus* (Bloch & Schneider, 1801).** Greenland shark
Cool temperate and boreal waters of the North Atlantic. FAO Areas 21, 27. Shelf (inshore in Arctic winter) and upper to mid slope. 0-1200m.

***Somniosus pacificus* Bigelow & Schroeder, 1944.** Pacific sleeper shark
Wide-ranging in the North Pacific. FAO Areas 18, 61, 67, 77. Shelf and upper to deep slope (shallower in north, deeper in south of range). 0-2000m.

***Somniosus rostratus* (Risso, 1810).** Little sleeper shark
Northeast Atlantic and the Mediterranean. Uncertain from Cuba in the Western Central Atlantic. FAO Areas 27, 31(?), 34, 37. Outermost shelf and upper to mid slope. 200-2200m.

***Somniosus* sp. A [Compagno, 1984].** Longnose sleeper shark
Northeast Atlantic: off Portugal. FAO Area 27.

***Zameus ichiharai* (Yano & Tanaka, 1984).** Japanese velvet dogfish
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope. 450-830m.

***Zameus squamulosus* (Günther, 1877).** Velvet dogfish
Wide-ranging but patchy in the Atlantic, Southern Indian, Western and Central Pacific. FAO Areas 27, 31, 34, 41, 51, 61, 71(?), 77, 81(?). Upper to mid slope. Also epipelagic and mesopelagic. 550-1450m (when benthic); 0-580m in water up to 6000m deep (when pelagic).

Family Oxynotidae. Roughsharks.

***Oxynotus bruniensis* (Ogilby, 1893).** Prickly dogfish
Indo-West Pacific: New Zealand and Australia. FAO Areas 57, 81. Shelf and upper to mid slope. 45-1067m (most common 350-650m).

***Oxynotus caribbaeus* Cervigon, 1961.** Caribbean roughshark
Western Central Atlantic: Gulf of Mexico and Caribbean (Venezuela). FAO Area 31. Upper slope. 402-457m.

***Oxynotus centrina* (Linnaeus, 1758).** Angular roughshark
Wide-ranging in the Eastern Atlantic and the Mediterranean. FAO Areas 27, 34, 37, 47. Shelf and upper slope. 50-660m (mostly >100m).

***Oxynotus japonicus* Yano & Murofushi, 1985.** Japanese roughshark
Northwest Pacific: Japan. FAO Area 61. Uppermost slope. 225-270m.

Oxynotus paradoxus **Frade, 1929.** Sailfin roughshark
Northeast and Eastern Central Atlantic: Scotland to West Africa. FAO Areas 27, 34. Upper slope. 265-720m.

Family Dalatiidae. Kitefin Sharks.

Dalatias licha **(Bonnaterre, 1788).** Kitefin shark
Wide-ranging but patchy in the Atlantic, Indo-West and Central Pacific. FAO Areas 21, 27, 31, 34, 37, 51, 57, 61, 71, 77, 87. Shelf and upper to deep slope. 37-1800m (mainly >200m).

Euprotomicroides zantedeschia **Hulley & Penrith, 1966**. Taillight shark
Patchy in the South Atlantic: off Brazil and southern Africa. FAO Areas 41, 47. Upper slope. Also epipelagic. 458-641m (when benthic), 0-25m (when pelagic).

Euprotomicrus bispinatus **(Quoy & Gaimard, 1824).** Pygmy shark
Wide-ranging but scattered records in the Atlantic and Indo-Pacific. FAO Areas 41, 47, 51, 57, 61, 71, 77, 81, 87. Epipelagic, mesopelagic and bathypelagic. 0->1500m in water up to 9938m deep.

Heteroscymnoides marleyi **Fowler, 1934.** Longnose pygmy shark
Scattered records in the southern Atlantic, Southeast Pacific and Southwest Indian. FAO Areas 47, 51, 87. Epipelagic and mesopelagic. 0-502m in water 830->4000m deep.

Isistius brasiliensis **(Quoy & Gaimard, 1824).** Cookiecutter or cigar shark
Circumglobal in tropical and warm temperate waters. FAO Areas 31, 34, 41, 47, 51, 57, 61, 67(?), 71, 77, 81, 87. Epipelagic, mesopelagic and bathypelagic. 0-3500m.

Isistius labialis **Meng, Chu & Li, 1985.** South China cookiecutter shark
Northwest Pacific: South China Sea. FAO Area 61. Mesopelagic over slope. 520m.

Mollisquama parini **Dolganov, 1984.** Pocket shark
Southeast Pacific: Nazca Submarine Ridge. FAO Area 87. Submarine ridges. 330m.

Squaliolus aliae **Teng, 1959.** Smalleye pygmy shark
Patchy in the Western Pacific and Eastern Indian. FAO Areas 57, 61, 71, 81. Epipelagic, mesopelagic and bathypelagic near land. 200-2000m.

Squaliolus laticaudus **Smith & Radcliffe, 1912.** Spined pygmy shark
Wide-ranging but scattered records in the Atlantic, Western Pacific and Western Indian. FAO Areas 27, 31, 34, 41, 51, 61, 71. Epipelagic and mesopelagic. 200-500m.

Order Squatiniformes. Angelsharks.

Family Squatinidae. Angelsharks.

Squatina aculeata **Dumeril, *in* Cuvier, 1817.** Sawback angelshark
Eastern Atlantic off West Africa, and the Western Mediterranean. FAO Areas 27, 34, 47. Shelf and upper slope. 30-500m.

Squatina africana **Regan, 1908.** African angelshark
Western Indian: East Africa. FAO Area 51. Shelf and upper slope. 0-494m (mainly 60-300m).

Squatina argentina **(Marini, 1930).** Argentine angelshark
Southwest Atlantic: Brazil to Argentina. FAO Area 41. Shelf and upper slope. 51-320m (mostly 120-320m).

Squatina formosa **Shen & Ting, 1972.** Taiwan angelshark
Western Pacific: Taiwan and Philippines. FAO Areas 61, 71. Outer shelf and upper slope. 183-385m.

Squatina tergocellata **McCulloch, 1914.** Ornate angelshark
Eastern Indian: Australia. FAO Area 57. Outer shelf and upper slope. 130-400m (most common ~300m).

***Squatina* sp. A [Last & Stevens, 1994].** Eastern angelshark
Western Pacific: Australia. FAO Areas 71, 81. Outer shelf and upper slope. 130-315m.

***Squatina* sp. B [Last & Stevens, 1994].** Western angelshark
Eastern Indian: Australia. FAO Area 57. Outer shelf and upper slope. 130-310m.

Order Pristiophoriformes. Sawsharks.

Family Pristiophoridae. Sawsharks.

Pliotrema warreni **Regan, 1906.** Sixgill sawshark
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Shelf and upper slope. 37-500m.

Pristiophorus schroederi **Springer & Bullis, 1960.** Bahamas sawshark
Western Central Atlantic: between Cuba, Florida (USA) and Bahamas. FAO Area 31. Upper to mid slope. 438-952m.

***Pristiophorus* sp. A [Last & Stevens, 1994].** Eastern sawshark
Southwest Pacific: Australia. FAO Area 81. Outer shelf and upper slope. 100-630m.

***Pristiophorus* sp. B [Last & Stevens, 1994].** Tropical sawshark
Western Central Pacific: Australia. FAO Area 71. Upper slope. 300-400m.

***Pristiophorus* sp. C [Compagno et al., 2005].** Philippine sawshark
Western Central Atlantic: Philippines. FAO Area 71. Upper slope. 229-593m.

***Pristiophorus* sp. D [Stehmann].** Dwarf sawshark
Scattered records in the Western Indian. FAO Area 51. Upper slope. 286-500m.

Order Rajiformes. Batoids.

Family Rhinobatidae. Guitarfishes.

Rhinobatos variegatus **Nair & Lal Mohan, 1973.** Stripenose guitarfish
Eastern Indian: Gulf of Mannar, India. FAO Area 57. Upper slope. 366m.

Family Narcinidae. Numbfishes.

Benthobatis kreffti **Rincon, Stehmann & Vooren, 2001.** Brazilian blind torpedo
Southwest Atlantic: Brazil. FAO Area 41. Upper slope. 400-600m.

Benthobatis marcida **Bean & Weed, 1909.** Pale or blind torpedo
Western Central Atlantic: South Carolina (USA) to northern Cuba. FAO Area 31. Upper to mid slope. 274-923m.

Benthobatis moresbyi **Alcock, 1898.** Dark blindray
Western Indian: Arabian Sea. FAO Area 51. Mid slope. 787-1071m.

Benthobatis yangi **Carvalho, Compagno & Ebert, 2003.** Narrow blindray
Northwest and Western Central Pacific: Taiwan. FAO Areas 61, 71. Upper slope (possibly also outer shelf). <300m.

Narcine lasti **Carvalho & Séret, 2002.** Western numbfish
Eastern Indian and Western Central Pacific: Eastern Indonesia and western Australia. FAO Areas 57 and 71. Outermost shelf and upper slope. 178-333m.

Narcine tasmaniensis **Richardson, 1840.** Tasmanian numbfish
Eastern Indian and Southwest Pacific: southeastern Australia. FAO Areas 57, 81.
Shelf (south of range) and upper slope (north of range). 5-640m (in north of range mainly 200-640m).

Narcine **sp. C [Last & Stevens, 1994].** Eastern numbfish
Western Central Pacific: northeastern Australia. FAO Area 81. Upper slope. 200-540m (commonly to 360m).

Family Narkidae. Sleeper Rays.

Heteronarce garmani **Regan, 1921.** Natal sleeper ray
Western India: Mozambique and South Africa. FAO Area 51. Shelf and upper slope. 73-329m.

Heteronarce mollis **(Lloyd, 1907).** Soft sleeper ray
Western Indian: Gulf of Aden. FAO Area 51. Shelf and upper slope. 73-346m.

Typhlonarke aysoni **(Hamilton, 1902).** Blind electric ray
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 46-900m (most common 300-400m).

Typhlonarke tarakea **Phillipps, 1929.** Oval electric ray
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 46-900m (most common 300-400m).

Family Torpedinidae. Torpedo Rays.

Torpedo fairchildi **Hutton, 1872.** New Zealand torpedo ray
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 5-1135m (most common 100-300m).

Torpedo fuscomaculata **Peters, 1855.** Blackspotted torpedo
Western Indian: Mozambique and South Africa. Reports from Western Indian Ocean islands likely refer to similar undescribed species. FAO Area 51. Shelf and upper slope. 0-439m.

Torpedo macneilli **(Whitley, 1932).** Short-tail torpedo ray
Eastern Indian and Western Pacific: Australia. FAO Areas 57, 71, 81. Outer shelf and upper slope. 90-750m.

Torpedo microdiscus **Parin & Kotlyar, 1985.** Smalldisk torpedo
Southeast Pacific: Nazca and Sala y Gomez Submarine Ridges. FAO Area 87. Submarine ridges.

***Torpedo nobiliana* Bonaparte, 1835.** Great, Atlantic, or black torpedo
Wide-ranging in the Eastern and Western Atlantic. FAO Areas 21, 27, 31, 37, 41, 47. Shelf and upper slope. 2-530m.

***Torpedo puelcha* Lahille, 1928.** Argentine torpedo
Southwest Atlantic: Brazil to Argentina. FAO Area 41. Shelf and upper slope. Inshore-600m.

***Torpedo tremens* de Buen, 1959.** Chilean torpedo
Patchy in the Eastern Central and Southeast Pacific. FAO Areas 77, 87. Shelf and upper slope. Inshore-700m.

***Torpedo* sp. A [Last & Stevens, 1994].** Longtail torpedo
Eastern Indian and Western Pacific: Australia. FAO Areas 57, 71, 81. Upper slope. 400-560m.

Family Arhynchobatidae. Softnose Skates.

***Arhynchobatis asperrimus* Waite, 1909.** Longtailed skate
Southwest Pacific: New Zealand FAO Area 81. Outer shelf and upper to mid slope. 90-1070m.

***Bathyraja abyssicola* (Gilbert, 1896).** Deepsea skate
Wide-ranging in the North Pacific. FAO Areas 61, 67, 77. Upper to deep slope and abyssal plains. 362-2906m.

***Bathyraja aguja* (Kendall & Radcliffe, 1912).** Aguja skate
Southeast Pacific: Peru. FAO Area 87. Mid slope. 980m.

***Bathyraja albomaculata* (Norman, 1937).** White-dotted skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper to mid slope. 55-861m.

***Bathyraja aleutica* (Gilbert, 1895).** Aleutian skate
Wide-ranging in the North Pacific. FAO Areas 61, 67, 77. Outer shelf and upper slope. 91-700m.

***Bathyraja andriashevi* Dolganov, 1985.** Little-eyed skate
Northwest Pacific: Japan and Russia. FAO Area 61. Mid to deep slope. 1400-2000m.

***Bathyraja bergi* Dolganov, 1985.** Bottom skate
Northwest Pacific: Japan and Russia. FAO Area 61. Outer shelf and upper to mid slope. 70-900m. Includes the junior synonym *Bathyraja pseudoisotrachys* Ishihara & Ishiyama, 1985.

***Bathyraja brachyurops* (Fowler, 1910).** Broadnose skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 28-604m.

***Bathyraja caeluronigricans* Ishiyama & Ishihara, 1977.** Purpleblack skate
Northwest Pacific: Japan and Russia. FAO Area 61. Upper slope. 200-400m. Possible synonym of *Bathyraja matsubarai* (Ishiyama, 1952).

***Bathyraja cousseauae* Diaz de Astarloa & Mabragaña, 2004.** Cousseau's skate
Southwest Atlantic: Argentina and the Falkland/Malvinas Islands. FAO Area 41. Outer shelf and upper to mid slope. 119-1011m.

Bathyraja diplotaenia **(Ishiyama, 1950).** Duskypink skate
Northwest Pacific: Japan. FAO Area 61. Outer shelf and upper slope. 100-700m.

Bathyraja eatonii **(Günther, 1876).** Eaton's skate
Circum-Antarctic. FAO Areas 48, 58, 88. Shelf, upper to mid slope, deepsea plateaus and submarine ridges. 15-800m.

Bathyraja fedorovi **Dolganov, 1985.** Cinnamon skate
Northwest Pacific: Japan and Russia. FAO Area 61. Upper to deep slope and abyssal plains. 447-2025m.

Bathyraja griseocauda **(Norman, 1937).** Graytail skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper to mid slope. 82-941m.

Bathyraja hesperafricana **Stehmann, 1995.** West African skate
Eastern Central Atlantic: West Africa. FAO Area 34. Mid to deep slope. 750-2000m.

Bathyraja interrupta **(Gill & Townsend, 1897).** Bering skate
Wide-ranging in the North and Eastern Central Pacific, although not well defined due possible misidentifications. FAO Areas 61, 67, 77. Shelf and upper to mid slope. 23-1500m.

Bathyraja irrasa **Hureau & Ozouf-Costaz, 1980.** Kerguelen sandpaper skate
Antarctic Indian: Kerguelen Islands. FAO Area 58. Upper to mid slope. 300-1200m.

Bathyraja isotrachys **(Günther, 1877).** Raspback skate
Northwest Pacific: Russia, Japan and Korea. FAO Area 61. Upper to deep slope. 370-2000m.

Bathyraja kincaidii **(Garman, 1908).** Sandpaper skate
Eastern Central and Northeast Pacific: Baja California north to Gulf of Alaska. FAO Areas 67, 77. Shelf and upper to mid slope. 55-1372m (most common 200-500m).

Bathyraja lindbergi **Ishiyama & Ishihara, 1977.** Commander skate
Northwest Pacific: Japan, Russia and the Bering Sea. FAO Area 61. Outer shelf and upper to mid slope. 120-950m.

Bathyraja longicauda **(de Buen, 1959).** Slimtail skate
Southeast Pacific: Peru and Chile. FAO Area 87. Upper slope. 580-735m.

Bathyraja maccaini **Springer, 1972.** McCain's skate
Southeast Pacific and Antarctic Atlantic: Chile and Antarctica (Orkney and South Shetland islands to the Antarctic Peninsula). FAO Areas 48, 87. Shelf and upper slope. Inshore-500m.

Bathyraja macloviana **(Norman, 1937).** Patagonian skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 53-514m.

Bathyraja maculata **Ishiyama & Ishihara, 1977.** Whiteblotched skate
Northern Pacific: Aleutian Islands and Bering Sea westwards to Japan. FAO Areas 61, 67. Shelf and upper to mid slope. 73-1110m.

Bathyraja magellanica **(Philippi, 1902 or Steindachner, 1903).** Magellan skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 51-600m (mostly <70m in Falklands).

***Bathyraja matsubarai* (Ishiyama, 1952)**. Duskypurple skate
Northwest Pacific: Japan and Russia. Occurrence in the Northeast Pacific requires confirmation. FAO Areas 61, 67(?). Outer shelf and upper to deep slope. 120-2000m.

***Bathyraja meridionalis* Stehmann, 1987.** Darkbelly skate
Primarily Sub-Antarctic in the Atlantic, possibly circum-Antarctic. FAO Areas 41, 48. Upper to deep slope, abyssal plains and seamounts. 300-2240m.

***Bathyraja microtrachys* (Osburn & Nichols, 1916).** Fine-spined skate
Eastern Central Pacific: western USA. FAO Area 77. Deep slope and abyssal plains. 1995-2900m. Validity follows Ebert (2003) as separate from *Bathyraja trachura* (Gilbert, 1892).

***Bathyraja minispinosa* Ishiyama & Ishihara, 1977.** Smallthorn skate
Northern Pacific: Aleutian Islands and Bering Sea westwards to Japan. FAO Areas 61, 67. Outer shelf and upper to mid slope. 150-1420m.

***Bathyraja multispinis* (Norman, 1937).** Multispine skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Outer shelf and upper slope. 82-740m. A record at 1900m off Uruguay requires confirmation.

***Bathyraja murrayi* (Günther, 1880).** Murray's skate
Antarctic Indian: Kerguelen and Heard Islands, but possibly circum-Antarctic. FAO Areas 48(?), 58, 88(?). Shelf and upper slope. 30-650m.

***Bathyraja notoroensis* Ishiyama & Ishihara, 1977.** Notoro skate
Northwest Pacific: Japan. FAO Area 61. Upper slope. ~600m. Possible synonym of *Bathyraja matsubarai* (Ishiyama, 1952).

***Bathyraja pallida* (Forster, 1967).** Pallid skate
Northeast Atlantic: Bay of Biscay. FAO Area 27. Deep slope and abyssal plains. 2200-2500m.

***Bathyraja papilionifera* Stehmann, 1985.** Butterfly skate
Southwest Atlantic: Argentina and the Falkland/Malvinas Islands. FAO Area 41. Upper to deep slope and seamounts. 637-2000m.

***Bathyraja parmifera* (Bean, 1881).** Alaska or flathead skate
Wide-ranging in the North Pacific: Gulf of Alaska to Japan. FAO Areas 61, 67. Shelf and upper to mid slope. 20-1425m. Includes the synonym *Bathyraja simoterus* (Ishiyama, 1967).

***Bathyraja peruana* McEachran & Miyake, 1984.** Peruvian skate
Southeast Pacific: Ecuador to Chile. FAO Area 87. Upper to mid slope. 600-1060m.

***Bathyraja richardsoni* (Garrick, 1961).** Richardson's skate
Patchy in the North Atlantic (Canada and France) and Southwest Pacific (New Zealand). FAO Areas 21, 27, 81. Mid to deep slope, abyssal plains and seamounts. 1110-2500m.

***Bathyraja scaphiops* (Norman, 1937).** Cuphead skate
Southwest Atlantic: Argentina and the Falkland/Malvinas Islands. FAO Area 41. Outer shelf and upper slope. 104-509m (most common 104-159m).

***Bathyraja schroederi* (Krefft, 1968).** Whitemouth skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Mid to deep slope and abyssal plains. 800-2380m.

***Bathyraja shuntovi* Dolganov, 1985.** Narrownose skate
Southwest Pacific: New Zealand. FAO Area 81. Upper to mid slope. 300-1470m.

***Bathyraja smirnovi* (Soldatov & Lindberg, 1913).** Golden skate
Northwest Pacific: Bering Sea to Japan. FAO Area 61. Outer shelf and upper to mid slope. 100-1000m.

***Bathyraja smithii* (Müller & Henle, 1841).** African softnose skate
Southeast Atlantic: Namibia and South Africa. FAO Area 47. Upper to mid slope. 400-1020m.

***Bathyraja spinicauda* (Jensen, 1914).** Spinetail or spinytail skate
Wide-ranging in the Northeast and Northwest Atlantic. FAO Areas 21, 27. Outer shelf and upper to mid slope. 140-1209m (mainly >400m).

***Bathyraja spinosissima* (Beebe & Tee-Van, 1941).** White skate
Eastern Central and Southeast Pacific. Records from the Northwest Pacific may be a separate species. FAO Areas 61(?), 77, 87. Mid to deep slope and abyssal plains. 800-2938m.

***Bathyraja trachouros* (Ishiyama, 1958).** Eremo skate
Northwest Pacific: Japan. FAO Area 61. Upper slope. 300-500m.

***Bathyraja trachura* (Gilbert, 1892).** Roughtail skate
Wide-ranging in the North Pacific. FAO Areas 61, 67, 77. Upper to deep slope and abyssal plains. 400-2550m.

***Bathyraja tzinovskii* Dolganov, 1985.** Creamback skate
Northwest Pacific: Japan and Russia. FAO Area 61. Deep slope and abyssal plains. 1776-2500m.

***Bathyraja violacea* (Suvorov, 1935).** Okhotsk skate
North Pacific: Bering Sea to Japan. FAO Areas 61, 67. Shelf and upper to mid slope. 23-1100m.

***Bathyraja* sp. A [Last & Stevens, 1994].** Abyssal skate
Eastern Indian: western Australia. FAO Area 57. Abyssal plains. 2300m.

***Bathyraja* sp. [Stehmann, 1985, as sp. 2].**
Antarctica.

***Brochiraja aenigma* Last & McEachran, 2006.**
Southwest Pacific: New Zealand FAO Area 81.Upper slope. 660-665m.

***Brochiraja albilabiata* Last & McEachran, 2006.**
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 785-1180m.

***Brochiraja asperula* (Garrick & Paul, 1974).** Prickly deepsea skate
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 350-1010m.

***Brochiraja leviveneta* Last & McEachran, 2006.**
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 960-1015m.

***Brochiraja microspinifera* Last & McEachran, 2006.**
Southwest Pacific: New Zealand. FAO Area 81. Upper to mid slope. 510-900m.

Brochiraja spinifera **(Garrick & Paul, 1974).** Spiny deepsea skate
Southwest Pacific: New Zealand FAO Area 81.Upper slope. 500-750m.

Notoraja tobitukai **(Hiyama, 1940).** Leadhued skate
Northwest Pacific: Japan and Taiwan. FAO Area 61. Shelf and upper to mid slope. 60-900m.

Notoraja*? *ochroderma **McEachran & Last, 1994.** Pale skate
Western Central Pacific: northeatern Australia. FAO Area 71. Upper slope. 400-465m.

Notoraja **(*Insentiraja*) *laxipella*** **Yearsley & Last, 1992.** Eastern looseskin skate
Western Central Pacific: northeastern Australia. FAO Area 71. Mid slope. 800-880m.

Notoraja **(*Insentiraja*) *subtilispinosa*** **(Stehmann, 1985).** Velvet or western looseskin skate
Patchy in the Eastern Indian and Western Central Pacific. FAO Areas 57, 71. Upper to mid slope. 600-1200m.

Notoraja **(*Insentiraja*) sp. C [Last & Stevens, 1994].** Ghost skate
Eastern Indian: western Australia. FAO Area 57. Upper to mid slope. 590-760m.

Notoraja **(subgenus C) sp. A [Last & McEachran, *in* Last & Yearsley, 2002].**
Southwest Pacific: New Zealand FAO Area 81. Mid slope. 845-1095m.

Notoraja **(subgenus C) sp. B [Last & McEachran, *in* Last & Yearsley, 2002].**
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 730-1240m.

Notoraja **(subgenus C) sp. C [Last & McEachran, *in* Last & Yearsley, 2002].**
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 1095-1110m.

Notoraja **(subgenus D) sp. A [Last & McEachran, *in* Last & Yearsley, 2002].**
Southwest Pacific: New Zealand. FAO Area 81. Mid slope. 1000m.

Notoraja **sp. A [Last & Stevens, 1994].** Blue skate
Eastern Indian: western and southern Australia. FAO Area 57. Mid slope. 840-1120m.

Notoraja **sp. D [Last & Stevens, 1994].** Blotched skate
Eastern Indian: southern Australia. FAO Area 57. Mid slope. 820-930m.

Notoraja **sp. E [McEachran & Last, *in* Last & Yearsley, 2002].**
Australia.

Notoraja **sp. [Séret].** Madagascar softnose skate
Western Indian: Madagascar. FAO Area 51.

***Notoraja*? sp. [Séret & Last, *in* Last & Yearsley, 2002].**
Western Central Pacific: New Caledonia. FAO Area 71.

Pavoraja alleni **McEachran & Fechhelm, 1982.** Allen's skate
Eastern Indian: western Australia. FAO Area 57. Upper slope. 200-460m.

Pavoraja nitida **(Günther, 1880).** Peacock skate
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Shelf and upper slope. 30-390m.

Pavoraja **sp. C [Last & Stevens, 1994].** Sandy peacock skate
Eastern Indian: southern Australia. FAO Area 57. Upper slope. 200-520m.

***Pavoraja* sp. D [Last & Stevens, 1994].** Mosaic skate
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 300-400m.

***Pavoraja* sp. E [Last & Stevens, 1994].** False peacock skate
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 210-500m.

***Pavoraja* sp. F [Last & Stevens, 1994].** Dusky skate
Western Pacific: eastern Australia. FAO Areas 71, 81. Upper slope. 360-730m.

***Psammobatis scobina* (Philippi, 1857).** Raspthorn sandskate
Southeast Pacific: Chile. FAO Area 87. Shelf and upper slope. 40-450m.

***Pseudoraja fischeri* Bigelow & Schroeder, 1954.** Fanfin skate
Scattered records in the Western Central Atlantic. FAO Area 31. Upper slope. 412-576m.

***Rhinoraja kujiensis* (Tanaka, 1916).** Dapple-bellied softnose skate
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope. 450-~1000m.

***Rhinoraja longi* Raschi & McEachran, 1991.** Aleutian dotted skate
North Pacific: Aleutian Islands. FAO Area 67. Upper slope. 390-435m.

***Rhinoraja longicauda* Ishiyama, 1952.** White-bellied softnose skate
Northwest Pacific: Japan and Russia. FAO Area 61. Upper to mid slope. 300-1000m.

***Rhinoraja obtusa* (Gill & Townsend, 1897).** Blunt skate
North Pacific: Bering Sea. Habitat and depth information not available.

***Rhinoraja odai* Ishiyama, 1952.** Oda's skate
Northwest Pacific: Japan. FAO Area 61. Upper to mid slope. 300-870m.

***Rhinoraja taranetzi* Dolganov, 1985.** Mudskate
Reasonably wide-ranging in the North Pacific. FAO Areas 61, 67. Shelf and upper to mid slope. 81-1000m. Includes the junior synonym *Bathyraja hubbsi* Ishihara & Ishiyama, 1985.

Family Rajidae. Hardnose Skates.

***Amblyraja badia* Garman, 1899.** Broad skate
Patchy in the North Pacific. FAO Areas 61, 67, 77. Mid to deep slope and abyssal plains. 846-2324m.

***Amblyraja doellojuradoi* (Pozzi, 1935).** Southern thorny skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 51-642m.

***Amblyraja frerichsi* Krefft, 1968.** Thickbody skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Mid to deep slope and abyssal plains. 720-2609m.

***Amblyraja georgiana* (Norman, 1938).** Antarctic starry skate
Circum-Antarctic, including off Chile and the Falkland/Malvinas Islands. FAO Areas 41, 48, 58, 87, 88. Shelf and upper to mid slope. 20-800m.

Amblyraja hyperborea **(Collette, 1879).** Arctic or boreal skate
Wide-ranging but patchy in deep temperate waters. FAO Areas 27, 47, 57, 61, 77, 81. Upper to deep slope and abyssal plains. 300-2500m. Taxonomic issues unresolved, may represent a species complex.

Amblyraja jenseni **(Bigelow & Schroeder, 1950).** Jensen's skate
North Atlantic: Nova Scotia (Canada) to southern New England (USA) and Iceland. FAO Areas 21, 27. Upper to deep slope. 366-2196m.

Amblyraja radiata **(Donovan, 1808).** Thorny skate
Wide-ranging in the North Atlantic and also off South Africa. FAO Areas 21, 27, 47. Shelf and upper to mid slope. 18-1400m (most common 27-439m).

Amblyraja reversa **(Lloyd, 1906).** Reversed skate
Western Indian: Arabian Sea. FAO Area 51. Deep slope. 1500m.

Amblyraja robertsi **(Hulley, 1970).** Bigmouth skate
Southeast Atlantic: South Africa. FAO Area 47. Mid slope. 1350m.

Amblyraja taaf **(Meisner, 1987).** Whiteleg skate
Antarctic Indian: Crozet Islands. FAO Area 58. Outer shelf and upper slope. 150-600m.

Amblyraja **sp. [Stehmann, 1989].** Ashy skate

Breviraja claramaculata **McEachran & Matheson, 1985.** Brightspot skate
Western Central Atlantic: South Carolina to Florida (USA). FAO Area 31. Upper to mid slope. 293-896m.

Breviraja colesi **Bigelow & Schroeder, 1948.** Lightnose skate
Western Central Atlantic: Florida (USA), Bahamas and Cuba. FAO Area 31. Upper slope. 220-415m.

Breviraja marklei **McEachran & Miyake, 1987.** Nova Scotia skate
Northwest Atlantic: Nova Scotia, Canada. FAO Area 21. Upper to mid slope. 443-988m.

Breviraja mouldi **McEachran & Matheson, 1995.** Blacknose skate
Western Central Atlantic: Honduras to Panama. FAO Area 31. Upper to mid slope. 353-776m.

Breviraja nigriventralis **McEachran & Matheson, 1985.** Blackbelly skate
Western Central Atlantic: Panama and the northern coast of South America. FAO Area 31. Upper to mid slope. 549-776m.

Breviraja spinosa **Bigelow & Schroeder, 1950.** Spinose skate
Western Central Atlantic: North Carolina to Florida (USA). FAO Area 31. Upper slope. 366-671m.

Breviraja**? sp. [Stehmann, 1979].**

Dactylobatus armatus **Bean & Weed, 1909.** Skilletskate
Patchy in the Western Central Atlantic. FAO Area 31. Upper slope. 338-685m.

Dactylobatus clarki **(Bigelow & Schroeder, 1958).** Hookskate
Patchy in the Western Central Atlantic. FAO Area 31. Upper to mid slope. 366-915m.

***Dipturus batis* (Linnaeus, 1758).** Gray or blue skate
Formerly wide-ranging in the Northeast and Eastern Central Atlantic, including the Mediterranean, but now extirpated from or reduced in much of its historical range. FAO Areas 27, 34, 37. Outer shelf and upper to mid slope. 100-1000m.

***Dipturus bullisi* (Bigelow & Schroeder, 1962).** Tortugas skate
Patchy in the Western Central Atlantic. FAO Area 31. Upper slope. 183-549m.

***Dipturus campbelli* (Wallace, 1967).** Blackspot skate
Western Indian: Patchy off South Africa and Mozambique. FAO Area 51. Outer shelf and upper slope. 137-403m.

***Dipturus crosnieri* (Séret, 1989).** Madagascar skate
Western Indian: Madagascar. FAO Area 51. Upper to mid slope. 300-850m.

***Dipturus doutrei* (Cadenat, 1960).** Violet or javelin skate
Eastern Central and Southeast Atlantic: West Africa. FAO Areas 34, 47. Outer shelf and upper to mid slope. 163-800m (mostly >400m).

***Dipturus garricki* (Bigelow & Schroeder, 1958).** San Blas skate
Western Central Atlantic: northern Gulf of Mexico and Nicaragua. FAO Area 31. Upper slope. 275-476m.

***Dipturus gigas* (Ishiyama, 1958).** Giant skate
Northwest and Western Central Pacific: Japan to Philippines. FAO Areas 61, 71. Upper to mid slope. 300-1000m.

***Dipturus gudgeri* (Whitley, 1940).** Bight skate
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Outer shelf and upper slope. 160-700m.

***Dipturus innominatus* (Garrick & Paul, 1974).** New Zealand smooth skate
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 15-1310m.

***Dipturus johannisdavesi* (Alcock, 1899).** Travancore skate
Western Indian: Gulf of Aden and India. FAO Area 51. Upper slope. 457-549m.

***Dipturus laevis* (Mitchell, 1817).** Barndoor skate
Northwest Atlantic: Canada and USA. FAO Area 21. Shelf and upper slope. 0-430m.

***Dipturus lanceorostratus* (Wallace, 1967).** Rattail skate
Western Indian: Mozambique. FAO Area 51. Upper slope. 430-439m.

***Dipturus leptocaudus* (Krefft & Stehmann, 1975).** Thintail skate
Southwest Atlantic: Brazil. FAO Area 41. Upper slope. 400-550m.

***Dipturus linteus* (Fries, 1838).** Sailskate
North Atlantic, primarily in the Northeast Atlantic. FAO Areas 21, 27. Upper to mid slope. 150-1200+m.

***Dipturus macrocaudus* (Ishiyama, 1955).** Bigtail skate
Northwest Pacific: Japan, Korea and Taiwan. FAO Area 61. Upper to mid slope. 300-800m.

***Dipturus mennii* Gomes & Paragó, 2001.** South Brazilian skate
Southwest Atlantic: Brazil. FAO Area 41. Outer shelf and upper slope. 133-500m. Includes the likely synonym *Dipturus diehli* Soto & Mincarone, 2001.

***Dipturus nidarosiensis* (Collett, 1880).** Norwegian skate
Northeast Atlantic: Norway, Iceland and the Rockall Trough. FAO Area 27. Upper to mid slope and deepsea rises. 200-1000m.

***Dipturus oregoni* (Bigelow & Schroeder, 1958).** Hooktail skate
Western Central Atlantic: northern Gulf of Mexico. FAO Area 31. Upper to mid slope. 475-1079m.

***Dipturus oxyrhynchus* (Linnaeus, 1758).** Sharpnose skate
Wide-ranging in the Northeast and Eastern Central Atlantic, including the Mediterranean. FAO Areas 27, 34, 37. Shelf and upper to mid slope. 15-900m.

***Dipturus pullopunctata* (Smith, 1964).** Slime skate
Southeast Atlantic: Namibia and South Africa. FAO Area 47. Shelf and upper slope. 15-457m (most common 100-300m).

***Dipturus springeri* (Wallace, 1967).** Roughbelly skate
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Upper slope. 400-740m (mostly 400-500m).

***Dipturus stenorhynchus* (Wallace, 1967).** Prownose skate
Southeast Atlantic and Western Indian: South Africa and Mozambique. FAO Areas 47, 51. Upper to mid slope. 253-761m.

***Dipturus teevani* (Bigelow & Schroeder, 1951).** Caribbean skate
Patchy throughout the Western Central Atlantic. FAO Area 31. Upper slope. 311-732m.

***Dipturus tengu* (Jordan & Fowler, 1903).** Acutenose or tengu skate
Northwest and Western Central Pacific: Japan to Philippines. FAO Areas 61, 71. Shelf and upper slope. 45-300m.

***Dipturus trachydermus* (Krefft & Stehmann, 1974).** Roughskin skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 20-450m.

***Dipturus* (*Zearaja*) *chilensis* (Guichenot, 1848).** Yellownose skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Shelf and upper slope. 28-500m. Includes the junior synonym *Dipturus flavirostris* (Philippi, 1892).

***Dipturus* (*Zearaja*) *nasutus* Banks, *in* Muller & Henle, 1841.** Rough skate
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper to mid slope. 10-1500m.

***Dipturus* (subgenus A) *cerva* (Whitley, 1939).** White-spotted skate
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Shelf and upper slope. 20-470m.

***Dipturus* (subgenus A) *polyommata* (Ogilby, 1910).** Argus skate
Western Pacific: eastern Australia. FAO Areas 71, 81. Outer shelf and upper slope. 90-310m.

***Dipturus* (subgenus A) sp. B [Last & Stevens, 1994 as *Raja* sp. B].** Grey skate
Eastern Indian and Southwest Pacific: southeastern Australia. FAO Areas 57, 81. Upper to mid slope. 330-950m (most common 450-600m).

***Dipturus* (subgenus A) sp. E [Last & Stevens, 1994 as *Raja* sp. E].** Oscellate skate
Eastern Indian: western Australia. FAO Area 57. Uppermost slope. 200-250m.

***Dipturus* sp. C [Last & Stevens, 1994 as *Raja* sp. C].** Graham's skate
Southwest Pacific: eastern Australia. FAO Area 81. Shelf and upper slope. 70-450m (most common 200-380m).

***Dipturus* sp. F [Last & Stevens, 1994 as *Raja* sp. F].** Leyland's skate
Eastern Indian: western Australia. FAO Area 57. Upper slope. 200-440m.

***Dipturus* sp. G [Last & Stevens, 1994 as *Raja* sp. G].** Pale tropical skate
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 225-550m (most common 300-400m).

***Dipturus* sp. H [Last & Stevens, 1994 as *Raja* sp. H].** Blacktip skate
Western Pacific: eastern Australia. FAO Areas 71, 81. Upper slope. 240-650m.

***Dipturus* sp. I [Last & Stevens, 1994 as *Raja* sp. I].** Weng's skate
Eastern Indian and Western Pacific: Australia and Indonesia. FAO Areas 57, 71, 81. Upper to mid slope. 400-1030m (mainly 400-600m).

***Dipturus* sp. J [Last & Stevens, 1994 as *Raja* sp. J].** Southern deepwater skate
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Mid slope. 800-1400m (mainly <1000m).

***Dipturus* sp. K [Last & Stevens, 1994 as *Raja* sp. K].** Queensland deepwater skate
Western Central Pacific: northeastern Australia. FAO Area 81. Upper slope. 440-650m.

***Dipturus* sp. Q [Séret & Last, *in* Last & Yearsley 2002].**
Western Central Pacific: New Caledonia. FAO Area 71.

***Dipturus* cf. *johannisdaviesi* Alcock, 1899 [Séret].**
Indonesia.

***Dipturus* sp. [Stehmann, 1990].**
Eastern Central Atlantic: Mauritania. FAO Area 34.

***Dipturus* sp. [Séret].**
Indonesia.

***Dipturus* sp. [Séret].**
Western Central Pacific: New Caledonia. FAO Area 71.

***Dipturus* sp. [Gomes & Picado, 2001].** North Brazil skate
Southwest Atlantic: Brazil. FAO Area 41.

***Fenestraja atripinna* (Bigelow & Schroeder, 1950).** Blackfin pygmy skate
Western Central Atlantic: North Carolina (USA) to Cuba. FAO Area 31. Upper to mid slope. 366-951m.

Fenestraja cubensis **(Bigelow & Schroeder, 1950).** Cuban pygmy skate
Western Central Atlantic: Florida (USA), Bahamas and Cuba. FAO Area 31. Upper to mid slope. 440-869m.

Fenestraja ishiyamai **(Bigelow & Schroeder, 1962).** Plain pygmy skate
Scattered records in the Western Central Atlantic. FAO Area. FAO Area 31. Upper to mid slope. 503-950m.

Fenestraja maceachrani **(Séret, 1989).** Madagascar pygmy skate
Western Indian: Madagascar. FAO Area 51. Upper to mid slope. 600-765m.

Fenestraja mamillidens **(Alcock, 1889).** Prickly skate
Eastern Indian: Bay of Bengal. FAO Area 57. Mid slope. 1093.

Fenestraja plutonia **(Garman, 1881).** Pluto skate
Patchy in the Western Central Atlantic. FAO Area 31. Upper to mid slope. 293-1024m.

Fenestraja sibogae **(Weber, 1913).** Siboga pygmy skate
Western Central Pacific: Bali Sea, Indonesia. FAO Area 71. Upper slope. 290m.

Fenestraja sinusmexicanus **(Bigelow & Schroeder, 1950).** Gulf of Mexico pygmy skate
Patchy in the Western Central Atlantic. FAO Area 31. Shelf and upper to mid slope. 56-1096m.

Gurgesiella atlantica **(Bigelow & Schroeder, 1962).** Atlantic pygmy skate
Western Atlantic: Central and South America. FAO Areas 31, 41. Upper to mid slope. 247-960m.

Gurgesiella dorsalifera **McEachran & Compagno, 1980.** Onefin skate.
Southwest Atlantic: Brazil. FAO Areas 31, 41. Upper to mid slope. 400-800m.

Gurgesiella furvescens **de Buen, 1959.** Dusky finless skate.
Southeast Pacific: Galapagos Islands and Peru to Chile. FAO Area 87. Upper to mid slope. 300-960m.

Leucoraja compagnoi **Stehmann, 1995.** Tigertail skate
Southeast Atlantic and Western Indian: South Africa. FAO Areas 47, 51. Upper slope. 497-625m.

Leucoraja fullonica **Linnaeus, 1758.** Shagreen skate
Northeast (and marginally into the Eastern Central) Atlantic, including the western Mediterranean. FAO Areas 27, 34, 37. Shelf and upper to mid slope. 30-800m.

Leucoraja garmani **(Whitley, 1939).** Rosette skate
Northwest and Western Central Atlantic: Cape Cod to Florida (USA). FAO Areas 21, 31. Shelf and upper slope. 37-530m.

Leucoraja lentiginosa **(Bigelow & Schroeder, 1951).** Freckled skate
Western Central Atlantic: northern Gulf of Mexico. FAO Area 31. Shelf and upper slope. 53-588m.

Leucoraja leucosticta **Stehmann, 1971.** Whitedappled skate
Eastern Central and Southeast Atlantic: West Africa. FAO Areas 34, 47. Shelf and upper slope. 70-600m.

Leucoraja melitensis **Clark, 1926.** Maltese skate
Southwestern and south-central Mediterranean. FAO Area 37. Shelf and upper to mid slope. 60-800m (more common 400-800m).

Leucoraja naevus **Müller & Henle, 1841.** Cuckoo skate
Reasonably wide-ranging in the Northeast and Eastern Central Atlantic, including the Mediterranean. FAO Areas 27, 34, 37. Shelf and upper slope. 20-500m.

Leucoraja wallacei **Hulley, 1970.** Yellowspot or blancmange skate
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Shelf and upper slope. 70-500m (most common 150-300m).

Leucoraja yucatanensis **(Bigelow & Schroeder, 1950).** Yucatan skate
Western Central Atlantic: Central America. FAO Area 31. Outermost shelf and upper slope. 192-457m.

Leucoraja **sp. O [Last & Stevens, 1994 as *Raja* sp. O].** Sawback skate
Eastern Indian: western Australia. FAO Area 57. Upper slope. 350-420m.

Leucoraja **sp. [Stehmann].** Gabon skate
Eastern Central Atlantic: Gabon. FAO Area 34. Upper slope. 302m.

Malacoraja kreffti **(Stehmann, 1978).** Krefft's skate
Northeast Atlantic: Rockall Trough and Iceland. FAO Area 27. Mid slope and deepsea rises. 1200m.

Malacoraja obscura **Carvalho, Gomes & Gadig, 2006.** Brazilian soft Skate
Southwest Atlantic: Brazil. FAO Area 41. Mid slope. 808-1105m.

Malacoraja senta **(Garman, 1885).** Smooth skate
Northwest Altantic: Canada and USA. FAO Areas 21, 31. Shelf and upper to mid slope. 46-914m.

Malacoraja spinacidermis **(Barnard, 1923).** Prickled or roughskin skate
Wide-ranging but patchy in the Eastern Atlantic. FAO Areas 27, 34, 47. Upper to deep slope. 450-1568m.

Neoraja africana **Stehmann & Séret, 1983.** West African pygmy skate
Eastern Central Atlantic: Gabon and Western Sahara. FAO Area 34. Mid to deep slope. 900-1550m.

Neoraja caerulea **(Stehmann, 1976).** Blue pygmy skate
Northeast Atlantic: Rockall Trough. FAO Area 27. Upper to mid slope and deepsea rises. 600-1262m.

Neoraja carolinensis **McEachran & Stehmann, 1984.** Carolina pygmy skate
Western Central Atlantic: North Carolina to Florida (USA). FAO Area 31. Upper to mid slope. 695-1010m.

Neoraja stehmanni **(Hulley, 1972).** South African pygmy skate
Southeast Atlantic: South Africa. FAO Area 47. Upper to mid slope. 292-1025m (most common >600m).

Okamejei heemstrai **McEachran & Fechhelm, 1982.** Narrow or East African skate
Western Indian: East Africa. FAO Area 51. Upper slope. 200-500m.

***Okamejei* sp. N [Last & Stevens, 1994 as *Raja* sp. N].** Thintail skate
Eastern Indian: western Australia. FAO Area 57. Upper slope. 400-735m.

***Raja africana*? Capape, 1977.** African skate
Disjunct range in the Mediterranean (Tunisia) and Eastern Central Atlantic (Mauritania). FAO Areas 34, 37. Shelf and upper slope. 50-400m. Homonym, requires a replacement name.

***Raja bahamensis* Bigelow & Schroeder, 1965.** Bahama skate
Western Central Atlantic: Florida (USA) and Bahamas. FAO Area 31. Upper slope. 366-411m.

***Raja binoculata* Girard, 1854.** Big skate
Wide-ranging in the Northeast and Eastern Central Pacific (and marinally into the Northwest Pacific). FAO Areas 61, 67, 77. Shelf and upper to mid slope. 3-800m.

***Raja inornata* Jordan & Gilbert, 1880.** California skate
Eastern Central Pacific: western USA and Mexico. FAO Area 77. Shelf and upper to mid slope. 17-671m.

***Raja maderensis* Lowe, 1841.** Madeira skate
Eastern Central Atlantic: Madeira. FAO Area 34. Shelf and upper slope. ?-500m.

***Raja polystigma* Regan, 1923.** Speckled skate
Western Mediterranean. FAO Area 37. Outer shelf and upper slope. 100-400m.

***Raja rhina* Jordan & Gilbert, 1880.** Longnose skate
Wide-ranging in the Northeast and Eastern Central Pacific. FAO Areas 67, 77. Shelf and upper to mid slope. 25-1000m.

***Raja stellulata* Jordan & Gilbert, 1880.** Pacific starry skate
Eastern Central Pacific: USA and Mexico. FAO Area 77. Shelf and upper slope. 18-732m (usually <100m). Records from Alaska and Bering Sea likely other species (i.e. *B. parmifera*).

***Raja straeleni* Poll, 1951.** Biscuit skate
Wide-ranging in the Eastern Central and Southeast Atlantic: West Africa; Western Indian: southern Africa. FAO Areas 34, 47. Shelf and upper slope. 80-690m (mostly 200-300m).

***Rajella annandalei* (Weber, 1913).** Indonesian round or Annandale's skate
Western Central Pacific: eastern Indonesia. FAO Area 71. Upper to mid slope. 400-830m.

***Rajella barnardi* (Norman, 1935).** Bigthorn skate
Wide-ranging in the Eastern Atlantic: West Africa. FAO Areas 34, 47. Outer shelf and upper to deep slope. 102-1700m. Includes the junior synonym *Raja confundens* Hulley, 1970.

***Rajella bathyphila* (Holt & Byrne, 1908).** Deepwater skate
Wide-ranging in the North Atlantic. FAO Areas 21, 27, 34. Upper to deep slope and abyssal plains. 600-2050m (mostly >1000m).

***Rajella bigelowi* (Stehmann, 1978).** Bigelow's skate
Wide-ranging but patchy in the North and Central Atlantic. FAO Areas 21, 27, 31, 34. Upper to deep slope, deepsea rises and abyssal plains. 650-4156m (mostly >1500m).

***Rajella caudaspinosa* (von Bonde & Swart, 1923).** Munchkin skate
Southeast Atlantic and Western Indian: Namibia and South Africa. FAO Areas 47, 51. Upper slope. 310-520m.

***Rajella dissimilis* (Hulley, 1970).** Ghost skate
Patchy in the Eastern Atlantic. FAO Areas 27, 34, 47. Upper to deep slope. 400-1570m.

***Rajella eisenhardti* Long & McCosker, 1999.** Galapagos gray skate
Southeast Pacific: Galapagos Islands. FAO Area 87. Mid slope. 757-907m.

***Rajella fuliginea* (Bigelow & Schroeder, 1954).** Sooty skate
Patchy in the Western Central Atlantic. FAO Area 31. Upper to mid slope. 731-1280m.

***Rajella fyllae* (Luetken, 1888).** Round skate
Wide-ranging in the Northeast and Northwest Atlantic. FAO Areas 21, 27. Outer shelf and upper to deep slope. 170-2050m (average depth range 400-800m).

***Rajella kukujevi* (Dolganov, 1985).** Mid-Atlantic skate
Patchy in the Northeast Atlantic. FAO Area 27. Mid slope. 750-1341m.

***Rajella leopardus* (von Bonde & Swart, 1923).** Leopard skate
Patchy in the Eastern Central and Southeast Atlantic and possibly Western Indian (South Africa). FAO Areas 34, 47, 51(?). Outer shelf and upper to deep slope. 130-1920m.

***Rajella nigerrima* (de Buen, 1960).** Blackish skate
Southeast Pacific: Ecuador to Chile. FAO Area 87. Upper to mid slope. 590-1000m.

***Rajella purpuriventralis* (Bigelow & Schroeder, 1962).** Purplebelly skate
Patchy in the Western Central Atlantic. FAO Area 31. Upper to deep slope. 732-2010m.

***Rajella ravidula* (Hulley, 1970).** Smoothback skate
Eastern Central and Southeast Atlantic: Morocco and South Africa. FAO Areas 34, 47. Mid slope. 1000-1250m.

***Rajella sadowskyii* (Krefft & Stehmann, 1974).** Brazilian skate
Southwest Atlantic and Southeast Pacific: southern South America. FAO Areas 41, 87. Mid slope. 1200m.

***Rajella* sp. P [Last & Stevens, 1994 as *Raja* sp. P].** Challenger skate
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Mid slope. 860-1500m (most common >1100m).

***Rajella* sp. [Stehmann, 1990].** Blanched skate
Northeast Atlantic. FAO Area 27.

***Rajella* sp. [Séret & Ishihara].** Longnose deepwater skate
Western Indian: Malagasy Ridge. FAO Area 51. Submarine ridges.

***Rajella* sp. [Séret].** Madagascar deepwater skate
Western Indian: Madagascar. FAO Area 51.

***Rostroraja alba* (Lacepede, 1803).** White, bottlenose or spearnose skate
Wide-ranging in the Eastern Atlantic, including the western Mediterranean, and the Western Indian (to Mozambique). FAO Areas 27, 34, 37, 47, 51. Shelf and upper slope. 30-600m.

Family Anacanthobatidae. Legskates.

Anacanthobatis americanus **Bigelow & Schroeder, 1962.** American legskate
Western Atlantic: Caribbean and the northern coast of South America. FAO Areas 31, 41. Outermost shelf and upper to mid slope. 183-915m.

Anacanthobatis borneensis **Chan, 1965.** Borneo legskate
Patchy in the Northwest and Western Central Pacific. FAO Areas 61, 71. Upper to mid slope. 475-835m.

Anacanthobatis donghaiensis **(Deng, Xiong & Zhan, 1983).** East China legskate
Northwest Pacific: East China Sea. FAO Area 61. Upper to mid slope. 200-1000m.

Anacanthobatis folirostris **(Bigelow & Schroeder, 1951).** Leafnose legskate
Western Central Atlantic: northern Gulf of Mexico. FAO Area 31. Upper slope. 300-512m.

Anacanthobatis longirostris **Bigelow & Schroeder, 1962.** Longnose legskate
Western Central Atlantic: northern Gulf of Mexico and Caribbean. FAO Area 31. Upper to mid slope. 520-1052m.

Anacanthobatis marmoratus **(von Bonde & Swart, 1924).** Spotted legskate
Western Indian: South Africa and Mozambique. FAO Area 51. Upper slope. 230-322m.

Anacanthobatis melanosoma **(Chan, 1965).** Blackbodied legskate
Northwest and Western Central Pacific: South China Sea. FAO Areas 61, 71. Mid slope. 900-1100m.

Anacanthobatis nanhaiensis **(Meng & Li, 1981).** South China legskate
South China Sea. Validity uncertain.

Anacanthobatis ori **(Wallace, 1967).** Black legskate
Western Indian: Mozambique and Madagascar. FAO Area 51. Mid to deep slope. 1000-1725m.

Anacanthobatis stenosoma **(Li & Hu, 1982).** Narrow legskate
South China Sea. Validity uncertain.

Anacanthobatis **sp. A [Last & Stevens, 1994].** Western legskate
Eastern Indian: western Australia. FAO Area 57. Upper to mid slope. 420-1120m (mostly <800m).

Anacanthobatis **sp. B [Last & Stevens, 1994].** Eastern legskate
Western Central Pacific: northeastern Australia. FAO Area 81. Upper to mid slope. 680-880m.

Anacanthobatis **sp. C [Last & Séret, *in* Last & Yearsley, 2002].**
Australia, Indonesia. Mid slope. 1100-1160m.

Anacanthobatis **sp. [Last].** Giant legskate

Anacanthobatis **sp. [Last & Compagno].** Andaman smooth legskate
Eastern Indian: Andaman Islands. FAO Area 57.

***Cruriraja andamanica* (Lloyd, 1909).** Andaman legskate
Patchy in the Indian Ocean: Tanzania and the Andaman Sea. FAO Areas 51, 57. Upper slope. 274-511m.

***Cruriraja atlantis* Bigelow & Schroeder, 1948.** Atlantic legskate
Western Central Atlantic: Florida (USA) to Cuba. FAO Area 31. Upper to mid slope. 512-778m.

***Cruriraja cadenati* Bigelow & Schroeder, 1962.** Broadfoot legskate
Western Central Atlantic: Florida (USA) and Puerto Rico. FAO Area 31. Upper to mid slope. 457-896m.

***Cruriraja durbanensis* (von Bonde & Swart, 1924).** Smoothnose legskate
Southeast Atlantic: South Africa. FAO Area 47. Mid slope. 860m. Note types collected off Northern Cape Province of South Africa, not off KwaZulu-Natal as suggested by the specific name.

***Cruriraja parcomaculata* (von Bonde & Swart, 1924).** Roughnose legskate
Southeast Atlantic and Western Indian: Namibia and South Africa. FAO Areas 47, 51. Outer shelf and upper slope. 150-620m.

***Cruriraja poeyi* Bigelow & Schroeder, 1948.** Cuban legskate
Scattered records throughout the Western Central Atlantic. FAO Area 31. Upper to mid slope. 366-870m.

***Cruriraja rugosa* Bigelow & Schroeder, 1958.** Rough legskate
Western Central Atlantic: Gulf of Mexico and Caribbean. FAO Area 31. Upper to mid slope. 366-1007m.

***Cruriraja triangularis* Smith, 1964.** Triangular legskate
Western Indian: South Africa and Mozambique. FAO Area 51. Upper slope. 220-675m.

Family Plesiobatidae. Giant Stingarees.

***Plesiobatis daviesi* (Wallace, 1967).** Deepwater stingray or giant stingaree
Patchy in the Indo-West Pacific. FAO Areas 51, 57, 61, 71, 77, 81. Shelf (single record at 44m off Mozambique) and upper slope. 44-680m (mostly 275-680m).

Family Urolophidae. Stingarees.

***Urolophus expansus* McCulloch, 1916.** Wide stingaree
Eastern Indian: southern Australia. FAO Area 57. Outer shelf and upper slope. 140-420m (mainly 200-300m).

***Urolophus piperatus* Séret & Last, 2003.** Coral Sea stingaree
Western Central Pacific: northeastern Australia. FAO Area 81. Upper slope and deep reefs. 280-350m.

Family Hexatrygonidae. Sixgill Stingrays.

***Hexatrygon bickelli* Heemstra & Smith, 1980.** Sixgill stingray
Wide-ranging but patchy in the Indo-West and Central Pacific. FAO Areas 47, 51, 57, 61, 71, 77. Upper to mid slope (although some shallow water and beach stranding records). 362-1120m.

Family Dasyatidae. Whiptail Stingrays.

Dasyatis brevicaudata **(Hutton, 1875).** Shorttail or smooth stingray
Patchy in the Indo-West Pacific (New Zealand, Australia and southern Africa). FAO Areas 47, 57, 71, 81. Inshore and shelf in Australia and New Zealand, outermost shelf and upper slope off South Africa. Intertidal-160m (NZ, Australia), 180-480m (southern Africa).

Superorder Galeomorphii. Galeomorph Sharks.

Order Heterodontiformes. Bullhead Sharks.

Family Heterodontidae. Bullhead Sharks.

Heterodontus ramalheira **(Smith, 1949).** Whitespotted bullhead shark
Western Indian: East Africa and Arabian Sea. FAO Area 51. Outer shelf and uppermost slope. 40-275m (mostly >100m).

Order Orectolobiformes. Carpetsharks.

Family Parascylliidae. Collared Carpetsharks.

Cirrhoscyllium japonicum **Kamohara, 1943.** Saddled carpetshark
Northwest Pacific: Japan. FAO Area 61. Uppermost slope. 250-290m.

Parascyllium sparsimaculatum **Goto & Last, 2002.** Ginger carpetshark
Eastern Indian: Australia. FAO Area 57. Upper slope. 245-435m.

Order Lamniformes. Mackerel Sharks.

Family Odontaspididae. Sand Tiger Sharks.

Odontaspis ferox **(Risso, 1810).** Smalltooth sand tiger or bumpytail raggedtooth
Wide-ranging but patchy in the Atlantic, including the Mediterranean, and the Indo-Pacific. Possibly circumglobal in warm-temperate and tropical waters. FAO Areas 27, 31, 34, 37, 51, 57, 61, 77, 81. Shelf and upper slope. 13-850m.

Odontaspis noronhai **(Maul, 1955).** Bigeye sand tiger
Scattered records in the Central and Southwest Atlantic and the Central Pacific. Possibly circumglobal in deep tropical seas. FAO Areas 31, 34, 41, 71, 77. Upper to mid slope as well as mesopelagic. 600-1000m.

Family Pseudocarchariidae. Crocodile Sharks.

Pseudocarcharias kamoharai **(Matsubara, 1936).** Crocodile shark
Cosmopolitan in tropical and warm temperate waters. FAO Areas 31, 34, 41, 47, 51, 57, 61, 71, 77, 81, 87. Epipelagic and mesopelagic. 0-590m.

Family Mitsukurinidae. Goblin Sharks.

Mitsukurina owstoni **Jordan, 1898.** Goblin shark
Wide-ranging but patchy in the Atlantic and the Indo-Pacific. FAO Areas 27, 31, 34, 47, 51, 57, 61, 77, 81. Shelf, upper to mid slope and seamounts. 0-1300m (mainly 270-960m).

Family Alopiidae. Thresher Sharks.

***Alopias superciliosus* (Lowe, 1839). Bigeye thresher**
Cosmopolitan in tropical and warm temperate waters. FAO Areas 21, 27, 31, 34, 37, 41, 47, 51, 57, 61, 71, 77, 81, 87. Shelf, epipelagic and mesopelagic. 0-732m (mostly >100m).

Family Cetorhinidae. Basking Sharks.

***Cetorhinus maximus* (Gunnerus, 1765).** Basking shark
Cosmopolitan in cold to warm-temperate waters. FAO Areas 21, 27, 31, 34, 37, 41, 47, 57, 61, 67, 77, 81, 87. Shelf and upper to mid slope, epipelagic and mesopelagic. 0-904m.

Order Carcharhiniformes. Ground Sharks.

Family Scyliorhinidae. Catsharks.

***Apristurus albisoma* Nakaya & Séret, 1999.** White catshark
Western Central Pacific: Norfolk and Lord Howe Ridges. FAO Area 71. Submarine ridges. 935-1564m.

***Apristurus aphyodes* Nakaya & Stehmann, 1998.** White ghost catshark
Northeast Atlantic: Atlantic Slope. FAO Area 27. Mid to deep slope. 1014-1800m.

***Apristurus brunneus* (Gilbert, 1892).** Brown catshark
Eastern Pacific: Alaska to Mexico, and possibly Southeast Pacific. FAO Areas 67, 77, 87(?). Shelf and upper to mid slope. 33-1298m.

***Apristurus canutus* Springer & Heemstra, *in* Springer, 1979.** Hoary catshark
Western Central Pacific: Caribbean Islands and Venezuela. FAO Area 31. Upper to mid slope. 521-915m.

***Apristurus exsanguis* Sato, Nakaya & Stewart, 1999.** Pale catshark
Southwest Pacific: New Zealand. FAO Area 81. Upper to mid slope and submarine ridges. 573-1200m.

***Apristurus fedorovi* Dolganov, 1985.** Stout catshark
Northwest Pacific: Japan. FAO Area 61. Mid slope. 810-1430m.

***Apristurus gibbosus* Meng, Chu & Li, 1985.** Humpback catshark
Northwest Pacific: South China Sea off southern China. FAO Area 61. Mid slope. 913m.

***Apristurus herklotsi* (Fowler, 1934).** Longfin catshark
Northwest and Western Central Pacific: Japan, China and Philippines. FAO Areas 61, 71. Upper to mid slope. 520-910m.

***Apristurus indicus* (Brauer, 1906).** Smallbelly catshark
Western Indian: Arabian Sea. Records off southern Africa probably erroneous. FAO Area 51. 1289-1840m.

***Apristurus internatus* Deng, Xiong & Zhan, 1988.** Shortnose demon catshark
Northwest Pacific: East China Sea off China. FAO Area 61. Upper slope. 670m.

***Apristurus investigatoris* (Misra, 1962).** Broadnose catshark
Eastern Indian: Andaman Sea. FAO Area 57. Mid slope. 1040m.

***Apristurus japonicus* Nakaya, 1975.** Japanese catshark
Northwest Pacific: Japan. FAO Area 61. Mid slope. 820-915m.

***Apristurus kampae* Taylor, 1972.** Longnose catshark
Eastern Pacific: USA and Mexico. Provisional from the Galapagos Islands. FAO Areas 77, 87(?). Outer shelf and upper to deep slope. 180-1888m.

***Apristurus laurussoni* (Saemundsson, 1922).** Iceland catshark
Wide-ranging but patchy in the North and Central Atlantic. FAO Areas 21, 27, 31, 34. Upper to deep slope. 560-2060m. Includes the junior synonyms *Apristurus atlanticus* (Koefoed, 1932) and *Apristurus maderensis* Cadenat & Maul, 1966.

***Apristurus longicephalus* Nakaya, 1975.** Longhead catshark
Patchy in the Indo-West Pacific. FAO Areas 51, 57, 61, 71. Upper to mid slope and submarine ridges. 500-1140m.

***Apristurus macrorhynchus* (Tanaka, 1909).** Flathead catshark
Northwest Pacific: Japan, China and Taiwan. FAO Area 61. Upper to mid slope. 220-1140m.

***Apristurus macrostomus* Meng, Chu, & Li, 1985.** Broadmouth catshark
Northwest Pacific: South China Sea off China. FAO Area 61. Mid slope. 913m.

***Apristurus manis* (Springer, 1979).** Ghost catshark
Patchy records in the North and Southeast Atlantic. FAO Areas 21, 27, 47. Upper to deep slope. 658-1740m.

***Apristurus melanoasper* Iglésias, Nakaya & Stehmann, 2004.** Black roughscale catshark
Patchy in the Northeast and Northwest Atlantic. FAO Areas 21, 27. Upper to deep slope. 512-1520m (mostly >1000m).

***Apristurus microps* (Gilchrist, 1922).** Smalleye catshark
Patchy in the North and Southeast Atlantic. FAO Areas 21, 27, 47. Upper to deep slope. 700-2200m.

***Apristurus micropterygeus* Meng, Chu & Li, *in* Chu, Meng, & Li, 1986.** Smalldorsal catshark.
Northwest Pacific: South China Sea off China. FAO Area 61. Mid slope. 913m.

***Apristurus nasutus* de Buen, 1959.** Largenose catshark
Eastern Pacific: patchy off Central and South America. Eastern Central Atlantic record probably erroneous. FAO Areas 77, 87. Upper to mid slope. 400-925m.

***Apristurus parvipinnis* Springer & Heemstra, *in* Springer, 1979.** Smallfin catshark
Western Central Atlantic: Gulf of Mexico, Caribbean and northern South America. FAO Area 31. Upper to mid slope. 636-1115m.

***Apristurus pinguis* Deng, Xiong & Zhan, 1983.** Fat catshark
Northwest Pacific: East China Sea. FAO Area 61. Upper to mid slope. 200-1040m.

***Apristurus platyrhynchus* (Tanaka, 1909).** Spatulasnout catshark
Patchy in the Northwest and Western Central Pacific. FAO Areas 61, 71. Upper to mid slope. 594-985m. Includes the junior synonyms *Apristurus acanutus* Chu, Meng & Li, *in* Meng, Chu & Li, 1985 and *Apristurus verweyi* (Fowler, 1934).

***Apristurus profundorum* (Goode & Bean, 1896).** Deepwater catshark
Northwest Atlantic off USA, possibly Eastern Central Atlantic off West Africa. FAO Areas 21, 34(?). Deep slope. ~1500m. Nominal records from the Indian Ocean require confirmation.

***Apristurus riveri* Bigelow & Schroeder, 1944.** Broadgill catshark
Western Central Atlantic: Gulf of Mexico, Caribbean and northern South America. FAO Area 31. Upper to mid slope. 732-1461m.

***Apristurus saldanha* (Barnard, 1925).** Saldanha catshark
Southeast Atlantic: southern Africa. FAO Area 47. Upper to mid slope. 344-1009m.

***Apristurus sibogae* (Weber, 1913).** Pale catshark
Western Central Atlantic: Indonesia. FAO Area 31. Upper slope. 655m.

***Apristurus sinensis* Chu & Hu, *in* Chu, Meng, Hu & Li, 1981.** South China catshark
Western Pacific: South China Sea. FAO Areas 61, 71. Upper to mid slope. 537-1000m.

***Apristurus spongiceps* (Gilbert, 1895).** Spongehead catshark
Patchy in the Western and Central Pacific: Indonesia and Hawaii. FAO Areas 71, 77. Upper to mid slope. 572-1482m.

***Apristurus stenseni* (Springer, 1979).** Panama ghost catshark
Eastern Central Pacific: Panama. FAO Area 77. Mid slope. 915-975m.

***Apristurus* sp. A [Last & Stevens, 1994].** Freckled catshark
Eastern Indian and Southwest Pacific: Australia and possibly New Zealand. FAO Areas 57, 81. Mid slope. 940-1290m.

***Apristurus* sp. B [Last & Stevens, 1994].** Bigfin catshark
Eastern Indian and Western Pacific: Australia and possibly New Caledonia. FAO Areas 57, 71, 81. Upper to mid slope. 730-1000m.

***Apristurus* sp. C [Last & Stevens, 1994].** Fleshynose catshark
Eastern Indian and Southwest Pacific: Australia and New Zealand. FAO Areas 57, 81. Mid slope. 900-1150m.

***Apristurus* sp. D [Last & Stevens, 1994].** Roughskin catshark
Eastern Indian and Southwest Pacific: Australia and New Zealand. FAO Areas 57, 81. Mid slope. 840-1380m.

***Apristurus* sp. E [Last & Stevens, 1994].** Bulldog catshark
Eastern Indian and Southwest Pacific: southeastern Australia. FAO Areas 57, 81. Mid slope. 1020-1500m.

***Apristurus* sp. F [Last & Stevens, 1994].** Bighead catshark
Eastern Indian: Australia. FAO Area 57. Mid slope. 1030-1050m.

***Apristurus* sp. G [Last & Stevens, 1994].** Pinocchio catshark
Eastern Indian and Western Pacific: Australia and possibly New Zealand. FAO Areas 57, 71, 81. Upper to mid slope and seamounts. 590-1000m.

***Apristurus* sp. 1 [Nakaya, Ueki & Sato, 2005].**
Northwest Pacific: Emperor Seamount Chain. FAO Area 61.

***Apristurus* sp. 2 [Nakaya, Ueki & Sato, 2005].**
Northwest Pacific: Ogasawara Islands. FAO Area 61.

Apristurus **sp. [Séret].**
Western Central Pacific: New Caledonia. FAO Area 71.

Apristurus **sp. [Séret].**
Western Central Pacific: Philippines. FAO Area 71.

Apristurus **sp. [Séret].**
Indonesia.

Apristurus **sp. [Compagno & Ebert].** White-edged catshark
Eastern Central Pacific: California (USA). FAO Area 77.

Apristurus **sp. [Compagno & Ebert].** Black wonder catshark
Southern Africa.

Apristurus **sp. [Compagno].** Gray ghost catshark
Western Indian: Melville Ridge. FAO Area 51. Submarine ridges.

Asymbolus pallidus **Last, Gomon & Gledhill, *in* Last, 1999.** Pale spotted catshark
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 270-400m.

Asymbolus **sp. [Séret].** New Caledonia spotted catshark
Western Central Pacific: New Caledonia. FAO Area 71.

Bythaelurus*? *alcocki **(Garman, 1913).** Arabian catshark
Eastern Indian: Arabian Sea. FAO Area 51. Mid slope. 1134-1262m. Original and only specimen has been lost, and thus placement of the species in this genus is tentative.

Bythaelurus canescens **(Günther, 1878).** Dusky catshark
Southeast Pacific: Peru and Chile. FAO Area 87. Upper slope. 250-700m.

Bythaelurus clevai **(Séret, 1987).** Broadhead catshark
Eastern Indian: Madagascar. FAO Area 51. Upper slope. 400-500m.

Bythaelurus dawsoni **(Springer, 1971).** Dawson's catshark
Southwest Pacific: New Zealand. FAO Area 81. Shelf, upper to mid slope. 50-790m (most common 300-700m).

Bythaelurus hispidus **(Alcock, 1891).** Bristly catshark
Eastern Indian: India and the Andaman Islands. FAO Area 57. Upper to mid slope. 293-766m.

Bythaelurus immaculatus **(Chu & Meng, *in* Chu, Meng, Hu & Li, 1982).** Spotless catshark
Northwest Pacific: South China Sea. FAO Area 61. Upper to mid slope. 534-1020m.

Bythaelurus lutarius **(Springer & D'Aubrey, 1972).** Mud catshark
Western Indian: patchy off East Africa. FAO Area 51. Upper to mid slope. 338-766m.

Bythaelurus **sp. A [Last & Stevens, 1994].** Dusky catshark
Eastern Indian: northwestern Australia. FAO Area 57. Mid slope. 900m.

Bythaelurus **sp. B [Compagno, McCosker & Long].** Galapagos catshark
Southeast Pacific: Galapagos Islands. FAO Area 87. Upper slope. 400-600m.

***Cephaloscyllium fasciatum* Chan, 1966.** Reticulated swellshark
Patchy in the Eastern Indian and Western Pacific. FAO Areas 57, 61, 71. Upper slope. 219-450m.

***Cephaloscyllium isabellum* (Bonnaterre, 1788).** Draughtsboard shark
Southwest Pacific: New Zealand. FAO Area 81. Shelf and upper slope. Inshore-690.

***Cephaloscyllium silasi* (Talwar, 1974).** Indian swellshark
Western Indian: India. FAO Area 51. Upper slope. ~300m.

***Cephaloscyllium sufflans* (Regan, 1921).** Balloon shark
Western Indian: South Africa and Mozambique. FAO Area 51. Shelf and upper slope. 40-440m.

***Cephaloscyllium* sp. 1 [Compagno et al., 2005].** Philippine swellshark
Western Central Pacific: Philippines. FAO Area 71. Habitat information not documented.

***Cephaloscyllium* sp. A [Last & Stevens, 1994].** Whitefin swellshark
Eastern Indian and Southwest Pacific: southern Australia. FAO Areas 57, 81. Upper slope. 240-550m.

***Cephaloscyllium* sp. B [Last & Stevens, 1994].** Saddled swellshark
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 380-590m.

***Cephaloscyllium* sp. D [Last & Stevens, 1994].** Narrowbar swellshark
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 440m.

***Cephaloscyllium* sp. E [Last & Stevens, 1994].** Speckled swellshark
Eastern Indian and Western Central Pacific: Australia and Indonesia. FAO Areas 57, 71. Upper slope. 390-700m.

***Cephaloscyllium* sp. [Stewart].** Tiger swellshark
Southwest Pacific: New Zealand. FAO Area 81.

***Cephaloscyllium* sp. [Randall].** New Guinea swellshark
Western Central Pacific: Papua New Guinea. FAO Area 71.

***Cephaloscyllium* sp. [Compagno, 1988].** Dwarf balloon shark
Western Indian: East Africa. FAO Area 51.

***Cephaloscyllium* sp. [Séret].** New Caledonia swellshark
Western Central Pacific: New Caledonia. FAO Area 71.

***Cephaloscyllium* sp. [Ritter].** Red Sea swellshark
Western Indian: Red Sea. FAO Area 51.

***Cephalurus cephalus* (Gilbert, 1892).** Lollipop catshark
Eastern Central Pacific: Mexico. FAO Area 77. Outer shelf and upper to mid slope. 155-927m.

***Cephalurus* sp. A [Compagno, 1988].** Southern lollipop catshark
Southeast Pacific: Peru and Chile. FAO Area 87.

***Galeus antillensis* Springer, 1979.** Antilles catshark

Western Central Atlantic: Straits of Florida and the Caribbean. FAO Area 31. Upper slope. 293-658m.

***Galeus arae* (Nichols, 1927).** Roughtail catshark
Northwest and Western Central Atlantic: USA, Gulf of Mexico, Caribbean and Central America. FAO Areas 21, 31. Upper slope. 292-732m.

***Galeus atlanticus* (Vaillant, 1888).** Atlantic sawtail catshark
Patchy in the Northeast Atlantic and Mediterranean. FAO Areas 27, 37. Upper slope. 400-600m.

***Galeus boardmani* (Whitley, 1928).** Australian sawtail catshark
Eastern Indian and Western Pacific: southern Australia. FAO Areas 57, 71, 81. Outer shelf and upper slope. 150-640m.

***Galeus cadenati* Springer, 1966.** Longfin sawtail catshark
Western Central Atlantic: off Panama and Colombia. FAO Area 31. Upper slope.439-548m.

***Galeus eastmani* (Jordan & Snyder, 1904).** Gecko catshark
Patchy in the Northwest Pacific. FAO Area 61. Habitat information not available.

***Galeus gracilis* Compagno & Stevens, 1993.** Slender sawtail catshark
Eastern Indian and Western Central Pacific: patchy across northern Australia. FAO Areas 57, 71. Upper slope. 290-470m.

***Galeus longirostris* Tachikawa & Taniuchi, 1987.** Longnose sawtail catshark
Northwest Pacific: Japan. FAO Area 61. Upper slope. 350-550m.

***Galeus melastomus* Rafinesque, 1810.** Blackmouth catshark
Wide-ranging in the Northeast and Western Central Atlantic and the Mediterranean. FAO Areas 27, 34, 37. Shelf and upper to mid slope. 55-1440m (mainly 200-500m).

***Galeus mincaronei* Soto, 2001.** Brazillian sawtail catshark
Southwest Atlantic: southern Brazil. FAO Area 41. Deep reefs on upper slope. 236-600m.

***Galeus murinus* (Collett, 1904).** Mouse catshark
Northeast Atlantic: Iceland and the Faeroe Islands. FAO Area 27. Upper to mid slope. 380-1250m.

***Galeus nipponensis* Nakaya, 1975.** Broadfin sawtail catshark
Northwest Pacific: Japan. FAO Area 61. Upper slope and submarine ridges. 362-540m.

***Galeus piperatus* Springer & Wagner, 1966.** Peppered catshark
Eastern Central Pacific: Gulf of California. FAO Area 77. Upper to mid slope. 275-1326m.

***Galeus polli* Cadenat, 1959.** African sawtail catshark.
Wide-ranging in the Eastern Atlantic off West Africa. FAO Areas 34, 47. Outer shelf and upper slope. 159-720m.

***Galeus schultzi* Springer, 1979.** Dwarf sawtail catshark
Western Central Pacific: Philippines. FAO Area 71. Shelf (one record) and upper slope. 50-431m (single record at 50m, usually 329-431m).

***Galeus springeri* Konstantinou & Cozzi, 1998.** Springer's sawtail catshark
Western Central Atlantic: Greater and Lesser Antilles. FAO Area 31. Upper slope. 457-699m.

***Galeus* sp. B [Last & Stevens, 1994].** Northern sawtail catshark
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 310-420m.

***Galeus* sp. 1 [Compagno et al., 2005].** Philippine sawtail catshark
Western Central Pacific: Philippines. FAO Area 71. Habitat information not documented.

***Galeus* sp. [Séret & Last, 1997].** Indonesian sawtail catshark
Indonesia.

***Holohalaelurus favus* Human, 2006.** Honeycomb or Natal izak
Western Indian: southern Africa. FAO Area 51. Upper to mid slope. 200-1000m.

***Holohalaelurus grennian* Human, 2006.** East African spotted catshark
Scattered records in the Western Indian off East Africa. FAO Area 51. Upper slope. 238-300m.

***Holohalaelurus melanostigma* (Norman, 1939).** Tropical izak catshark
Western Indian off East Africa. FAO Area 51. Upper slope. 607-658m.

***Holohalaelurus punctatus* (Gilchrist & Thompson, 1914).** African spotted catshark
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Upper slope. 220-420m.

***Holohalaelurus regani* (Gilchrist, 1922).** Izak catshark
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Shelf and upper to mid slope. 40-910m (mainly ~100-300m).

***Parmaturus campechiensis* Springer, 1979.** Campeche catshark
Western Central Atlantic: Bay of Campeche in the Gulf of Mexico. FAO Area 31. Mid slope. 1097m.

***Parmaturus macmillani* Hardy, 1985.** New Zealand filetail
Southwest Pacific: New Zealand; Western Indian: south of Madagascar. FAO Areas 51, 81. Submarine ridges. 950-1003m (may also occur deeper).

***Parmaturus melanobranchius* (Chan, 1966).** Blackgill catshark
Western Pacific: East and South China Seas. FAO Areas 61, 71. Upper to mid slope. 540-835m.

***Parmaturus pilosus* Garman, 1906.** Salamander shark
Northwest Pacific: Japan and East China Sea. FAO Area 61. Upper to mid slope. 358-895m.

***Parmaturus xaniurus* (Gilbert, 1892).** Filetail catshark
Eastern Central Pacific: southern USA and Mexico. FAO Area 77. Outer shelf and upper to mid slope. Juveniles mesopelagic. 91-1251m.

***Parmaturus* sp. A. [Last & Stevens, 1994].** Shorttail catshark
Western Central Pacific: northeastern Australia. FAO Area 71. Deepsea plateaus. 590m.

***Parmaturus* sp. [Séret].** Indonesian filetail catshark
Indonesia.

***Parmaturus* sp. [McEachran].** Gulf of Mexico filetail
Western Central Atlantic: Gulf of Mexico. FAO Area 31.

***Pentanchus profundicolus* Smith & Radcliffe, 1912.** Onefin catshark
Western Central Pacific: Philippines. FAO Area 71. Upper to mid slope. 673-1070m.

***Schroederichthys maculatus* Springer, 1966.** Narrowtail catshark
Western Central Atlantic: patchy off Central and northern South America. FAO Area 31. Outermost shelf and upper slope. 190-410m.

***Schroederichthys saurisqualus* Soto, 2001.** Lizard catshark
Southwest Atlantic: southwestern Brazil. FAO Area 41. Outer shelf (sporadic) and deep reefs on the upper slope. 122-500m.

***Schroederichthys tenuis* Springer, 1966.** Slender catshark
Restricted range in the Western Atlantic off Suriname and northern Brazil. FAO Areas 31, 41. Shelf and upper slope. 72-450m.

***Scyliorhinus boa* Goode & Bean, 1896.** Boa catshark
Western Central Atlantic: Caribbean and northern South America. FAO Area 31. Upper slope. 229-676m.

***Scyliorhinus capensis* (Smith, *in* Müller & Henle, 1838).** Yellowspotted catshark
Southeast Atlantic and Western Indian: southern Africa. FAO Areas 47, 51. Shelf and upper slope. 26-695m (mostly 200-400m).

***Scyliorhinus cervigoni* Maurin & Bonnet, 1970.** West African catshark
Eastern Atlantic off West Africa. FAO Areas 34, 47. Shelf and upper slope. 45-500m.

***Scyliorhinus comoroensis* Compagno, 1989.** Comoro catshark
Western Indian: Comoro Islands. FAO Area 51. Upper slope. 200-400m.

***Scyliorhinus haeckelii* (Ribeiro, 1907).** Freckled catshark
Western Atlantic: off South America. FAO Areas 31, 41. Deep reefs on the shelf and upper slope. 37-439m (mostly >250m).

***Scyliorhinus hesperius* Springer, 1966.** Whitesaddled catshark
Western Central Atlantic: Central America and Colombia. FAO Area 31. Upper slope. 274-457m.

***Scyliorhinus meadi* Springer, 1966.** Blotched catshark
Western Central Atlantic: USA, Gulf of Mexico, Cuba and Bahamas. FAO Area 31. Upper slope. 329-548m.

***Scyliorhinus retifer* (Garman, 1881).** Chain catshark
Northwest and Western Central Atlantic: USA, Gulf of Mexico and Caribbean. FAO Areas 21, 31. Shelf and upper to mid slope. 75-754m.

***Scyliorhinus torrei* Howell-Rivero, 1936.** Dwarf catshark
Western Central Atlantic: Florida (USA), Bahamas, Cuba and the Lesser Antilles. FAO Area 31. Upper slope. 229-550m (most >366m).

Family Proscylliidae. Finback Catsharks.

***Eridacnis barbouri* (Bigelow & Schroeder, 1944).** Cuban ribbontail catshark
Western Central Atlantic: Florida Straits and Cuba. FAO Area 31. Upper slope. 430-613m.

***Eridacnis radcliffei* Smith, 1913.** Pygmy ribbontail catshark
Wide-ranging but patchy in the Indo-West Pacific. FAO Areas 51, 57, 61, 71. Shelf, upper to mid slope. 71-766m.

***Eridacnis sinuans* (Smith, 1957).** African ribbontail catshark
Western Indian off East Africa. FAO Area 51. Outermost shelf and upper slope. 180-480m.

***Proscyllium* sp. A [Compagno et al., 2005].** Clown or magnificant catshark
Eastern Indian: Andaman Sea. FAO Area 57. Edge of the outer shelf. >200m.

Family Pseudotriakidae. False Catsharks.

***Gollum attenuatus* (Garrick, 1954).** Slender smoothhound
Southwest Pacific: New Zealand. FAO Area 81. Outer shelf, upper slope and seamounts. 129-724m (most common 300-600m).

***Gollum* sp. A [Compagno et al., 2005].** Sulu gollumshark
Western Central Pacific: Philippines. FAO Area 71. Habitat not documented but presumably slope.

***Gollum* sp. B [Compagno et al., 2005].** Whitemarked gollumshark
Western Central Pacific: New Caledonia. FAO Area 71. Habitat not documented but presumably slope.

***Pseudotriakis microdon* Capello, 1868.** False catshark
Wide-ranging but patchy in the Atlantic, Indo-West and Central Pacific. FAO Areas 21, 27, 34, 51, 57, 71, 77, 81. Shelf (occassional) and upper to deep slope. 200-1900m.

New genus and species [Compagno, Stehmann & Anderson]. Pygmy false catshark
Western Indian: Arabian Sea and Maldives. FAO Area 51. Mid slope. ?-1120m.

Family Triakidae. Houndsharks.

***Hemitriakis abdita* Compagno & Stevens, 1993.** Darksnout or deepwater sicklefin houndshark
Western Central Pacific: northeastern Australia. FAO Area 71. Upper slope. 225-400m.

***Iago garricki* Fourmanoir, 1979.** Longnose houndshark
Patchy in the Eastern Indian and Western Central Pacific. FAO Areas 57, 71. Upper slope. 250-475m.

***Iago omanensis* (Norman, 1939).** Bigeye houndshark
Northern Indian including the Red Sea; possibly in the Bay of Bengal (although this may represent a distinct species). FAO Areas 51, 57(?). Shelf and upper to mid (possibly to deep) slope. <110-1000+m (possibly to 2195m in Red Sea).

***Iago* sp. A [Compagno].** Lowfin houndshark
Patchy in the Northern Indian. FAO Areas 51, 57. Outer shelf and upper slope. Also epipelagic and mesopelagic. >183m (when benthic), 0-330m in water 500-2000m deep (when pelagic).

***Iago* sp. [Compagno].** Bengal smallgill houndshark
Eastern Indian: India. FAO Area 57.

***Mustelus canis insularis* (Mitchell, 1815).** Dusky smoothhound (island subspecies)
Western Central Atlantic: Caribbean and northern South America. FAO Area 31. Outer shelf and upper to mid slope. 137-808m (mostly >200m). Shelf subspecies (*M. c. canis*) prefers shallow waters (generally <18m).

Family Carcharhinidae. Requiem Sharks.

***Carcharhinus altimus* (Springer, 1950).** Bignose shark
Wide-ranging but patchy in tropical and warm-temperate waters of the Atlantic and Indo-Pacific. FAO Areas 31, 34, 37, 51, 57, 61, 71, 77, 87. Shelf and upper slope. 25-430m (mostly >90m, young shallower, to 25m).

SECTION I LITERATURE

Carpenter, K.E. (ed). 2002. The living marine resources of the Western Central Atlantic. Volume 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras. FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Carpenter, K.E. and Niem, V.H. (eds.). 1998. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks. FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Carpenter, K.E. and Niem, V.H. (eds.). 1999. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes. No. 1, Vol. 2. FAO, Rome.

Compagno, L.J.V. 2005. Global checklist of living chondrichthyan fishes. Pp. 401-423. In: Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V., Simpfendorfer, C.A. and Musick, C.A. (eds.) Sharks, rays and chimaeras: The status of chondrichthyan fishes. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Compagno, L.J.V and Duffy, C.A.J. 2003. A checklist of deep water chondrichthyans of the world. IUCN SSG Deepwater Shark Workshop, Portobello, New Zealand, 29 November 2003.

Compagno, L., Dando, M. and Fowler, S. 2005. A field guide to sharks of the world. Collins, London.

Ebert, D.A. 2003. Sharks, rays and chimaeras of California. University of California Press, Berkeley.

Last, P.R. 2007. The state of chondrichthyan taxonomy and systematics. Marine and Freshwater Research 58:7-9.

Last, P.R. and Gledhill, D.C. 2006. The Maugean skate (*Zearaja* sp.) – a micro-endemic, Gondwanan relict from Tasmanian estuaries. Abstract. 2006 Joint Meeting of Ichthyologists and Herpetologists, New Orleans, USA, 12-17 July 2006.

Last, P.R. and McEachran, J.D. 2006. New softnose skate genus *Brochiraja* from New Zealand (Rajidae: Arhynchobatinae) with description of four new species. New Journal of Marine and Freshwater Research 40:65-90.

Last, P.R. and Stevens, J.D. 1994. Sharks and rays of Australia. CSIRO Publishing, Melbourne.

Last, P.R. and Yearsley, G.K. 2002. Zoogeography and relationships of Australasian skates (Chondrichthyes: Rajidae). Journal of Biogeography 29:1627-1641.

McEachran, J.D. and Dunn, K.A. 1998. Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chondrichthyes: Rajidae). Copeia 1998(2): 271-290.

Musick, J.A., Harbin, M.M. and Compagno, L.J.V. 2004. Historical zoogeography of the selachii. Pp. 33-78. In: Carrier, J.C., Musick, J.A. and Heithaus, M.R. (eds.). Biology of sharks and their relatives. CRC Press, Boca Raton.

Nakaya, K., Ueki, M. and Sato, K. 2005. Taxonomic review of the genus *Apristurus* (Carchariniformes: Scyliorhinidae) from the Western North Pacific. Abstract. The 7th Indo-Pacific Fish Conference, Taipei, Taiwan, 16-20 May 2005.

Priede, I.G., Froese, R., Bailey, D.M., Aksel Bergstad, O., Collins, M.A., Erik Dyb, J., Henriques, C., Jones, E.G. and King, N. 2006. The absence of sharks from abyssal regions of the world's oceans. Proceedings of the Royal Society Series B 273(1592):1435-1441.

Sato, K. 2005. Comparative morphology and phylogeny of the genus *Apristurus* and related genera. Abstract. The 7th Indo-Pacific Fish Conference, Taipei, Taiwan, 16-20 May 2005.

White, W.T., Last, P.R., Stevens, J.D., Yearsley, G.K., Fahmi and Dharmadi. 2006. Economically important sharks and rays of Indonesia. Australian Centre for International Agricultural Research, Canberra.

SECTION II.
LIFE HISTORY OF DEEPWATER CHONDRICHTHYANS

Introduction to the life history characteristics of chondrichthyans

The chondrichthyans are generally considered to be K-selected species, displaying conservative life history parameters such as relatively slow growth, late age at maturity, low fecundity and low natural mortality (Hoenig and Gruber 1990, Musick 1999). This results in a limited reproductive output, putting their energy into a few well-developed young which resemble miniature adults at birth. As such, the productivity of many chondrichthyans falls within the range of other long-lived animals, such as many large mammals (Cahmi et al. 1998), and is in contrast to r-selected species whose life history strategy is to produce large numbers of offspring with a limited lifespan (Hoenig and Gruber 1990). The restricted life history characteristics of the chondrichthyans place them at risk of overexploitation and population depletion, with an inability to recover from reduced population levels once depleted. This vulnerability is generally heightened in the deepsea, a relatively stable, cold water environment where food resources are more limited. Subsequently growth rates are slower and recruitment to the population is reduced.

An understanding of several biological parameters is important to accurately assess the productivity of an individual species and thus make inferences concerning its vulnerability to fisheries. These parameters include size and age at maturity, fecundity, longevity and reproductive periodicity. For the vast majority of deepwater species, this data is lacking, highlighting a significant gap in our knowledge base. Section II of this report collates available (published and unpublished) information on the life history of deepwater chondrichthyans and provides an assessment of the productivity of the group.

Provided here are brief introductions to the reproductive biology and age and growth of chondrichthyan fishes, including basic methodological backgrounds to the information provided in the life history accounts which follow. Methods for undertaking the assessment of the productivity of deepwater chondrichthyans are provided at the beginning of that assessment.

In all chondrichthyans, fertilization is internal although they display a diversity of reproductive modes. The terminology of reproductive modes and the descriptions following are taken from Musick and Ellis (2005). In oviparous species, egg-laying can be either single oviparity (a single egg case deposited from each oviduct) or multiple oviparity (multiple egg cases retained in the oviduct for an extended period of embryonic development before laying). In viviparous chondrichthyans, the most basic form is yolk-sac viviparity where fertilized ova develop *in utero*, and the embryo obtains nutrition from a single yolk-sac. This form of viviparity together with both forms of oviparity are considered lecithotrophic modes of reproduction, whereby there is no additional maternal nutritional input other than that provided in the ovulated egg. The vast majority of the deepwater fauna is lecithotrophic (oviparity or viviparous forms). The remaining reproductive modes are matrotrophic, whereby embryos rely on additional maternal nutritional input for at least part of their development. The matrotrophic modes are histotrophy (embryos obtain nutrition from a histotroph or 'uterine milk' secreted by trophonemata in the maternal uteri), oophagy (embryos subsist on unfertilised ova ovulated by the mother; this includes the advanced form known as adelphophagy whereby one embryo in each uterus feeds on its sibling embryos before relying on ovulated ova) and placental viviparity (a placental attachment is formed between the embryo and the maternal uterus).

For viviparous species, uterine litter sizes provided throughout this Section are based on counts of ova (ovulated oocytes) or developing embryos in the uteri. Where uterine litter sizes are not available, ovarian fecundities, based on counts of the number of developing or developed follicles (oocyte surrounded by granulosa cells), may be provided. However, these estimates may not reflect actual uterine fecundity and hence an accurate measure of reproductive output if all oocytes are not ovulated and fertilized. Therefore, ovarian fecundity can provide a proxy for reproductive output but will generally always be higher than uterine fecundity for viviparous species. For example, Irvine (2004) noted that mean litter size was 3-4 less than mean ovarian fecundity in *Etmopterus baxteri*, with atretic follicles observed in some early pregnancies. Yano (1995) found a similar disparity between uterine and ovarian fecundity in *Centroscyllium fabricii*. Fecundity is more difficult to determine in oviparous species and again, ovarian fecundity can provide a proxy. Continuous sampling can reveal the length of any egg-laying period, although most deepwater oviparous species appear to deposit egg cases throughout the year. Egg-laying rates can generally only be determined from fish held in aquaria and these may not translate to actual rates in the wild as temperature is a contributing factor (Holden et al. 1971). Furthermore, the success of incubation and natural mortality will influence the actual number of offspring entering the population.

In order to determine the annual fecundity (and indeed the lifetime fecundity) of a species, its reproductive periodicity needs to be elucidated. Many coastal and shelf species display seasonal reproductive cycles and with sampling of a population throughout the year, the seasonal pattern of follicle development, copulation, ovulation, gestation and parturition can be determined. This allows the length of the reproductive cycle (follicle development, ovulation, gestation and parturition) to be resolved and the reproductive periodicity can be determined as biannual, annual, biennial or perhaps longer. However, the majority of deepwater species exhibit an aseasonal reproductive cycle, with asynchronicity within the population. This makes a determination of the gestation period difficult and thus reproductive periodicity for most species remains unknown, although follicle and embryo development rates and sizes indicate a long cycle. Aseasonality in the reproductive biology of deepwater species may be related to the relative stability of their environment (Wetherbee 1996). For many deepwater squaloid sharks there is a resting period between parturition and the next ovulation, extending the reproductive cycle (Irvine 2004, Irvine et al. 2006b). Where litter sizes are known, together with age at maturity and longevity, one can calculate possible lifetime fecundities based on the number of reproductive years and assuming different reproductive periodicities (i.e. biennial or triennial) (Irvine 2004).

The sexual maturity of chondrichthyans is determined by the anatomical, morphological or histological examination of external (male) and internal (male and female) reproductive characters. Where the size at 50% maturity (L_{50}; the size at which 50% of the population is mature) is available this is presented. Maturity is also expressed as a % of the maximum size (L_{max}) reached for the species (by sex – most chondrichthyans are sexually dimorphic with females growing to larger sizes than males, although the scyliorhinid catsharks tend to deviate from this trend). Maximum sizes given in the particular study are used for these calculations and not maximums recorded in the literature to avoid differences between populations, geographical locations or the effects of fishing. Holden (1974) observed that mean size at maturity occurs in female elasmobranchs at an average of 77% of asymptotic size (range 60-90%). From a more comprehensive review of 164 species of sharks, Cortés (2000) determined that sexual maturity occurs at about 75% of L_{max} in both sexes. The deepwater species examined here are generally in agreement with these figures, although there are some exceptions.

Sharks and rays have traditionally been aged by examining seasonal changes in the deposition of growth bands in their vertebrae. Band counts can be correlated to age where the pattern of deposition has been shown to be annual (processes termed verification and validation). For most sharks and rays examined, growth bands have been shown to be laid down annually, although there are exceptions (angel sharks *Squatina* spp and wobbegongs *Orectolobus* spp). Vertebral ageing of deepsea chondrichthyans has generally been unsuccessful and alternative methods have had to be developed, most still in their infancy. Skates can be aged using caudal thorns (Gallagher and Nolan 1999) and the internal and external examination of the dorsal spines of dogfishes (Order Squaliformes) and holocephalans (Order Chimaeriformes) has proved useful for estimating age (Sullivan 1977, Tanaka 1990, Irvine 2004, Irvine et al. 2006b). Further research is required to develop alternative ageing techniques for deepwater sharks, particularly those lacking dorsal spines. Neural arches have shown potential for estimating age in sixgill sharks (Order Hexanchiformes) (McFarlane et al. 2002) and radiometric ageing has been trialled on some dogfishes (Fenton 2001).

Age estimates presented for many species here have not been validated and thus should be viewed as preliminary. Irvine et al. (2006a) notes that most traditional validation techniques are impractical for deepwater sharks. A correlation between external dorsal spine band counts and the results of radiometric age estimates (Fenton 2001) in *Centroselachus crepidater* allowed Irvine (2006b) to assume that external bands were laid down annually.

Age and growth data presented in this Section include parameters for the von Bertalanffy growth model (VBGM) (von Bertalanffy 1938) which provides estimates of L_∞, the asymptotic or maximum length (or width for some batoids), k, the growth coefficient, and t_0, the age or time when length theoretically equals zero. Parameter estimation from the VBGM can be effected by the sample size and the size distribution of the data applied. See Goldman (2004) for further information and a recent review of age and growth in sharks and rays. While the VBGM can provide an estimate of maximum theoretical age, it is maximum observed ages (longevity) that are presented in the age and growth summary tables in this Section.

Measurements used throughout this Section are as follows:

TL = Total Length; standard length measurement for sharks, skates and several other batoid groups, from the tip of the snout to the posterior tip of the tail (caudal fin).

PCL = Precaudal Length; standard length measurement, primarily for sharks, from the tip of the snout to the origin of the upper caudal fin.

DW = Disc Width; standard width measurements for batoids, between the outer margins of the pectoral fins (the 'disc' or 'wings').

PL = Pelvic Length; length measurement for skates, from the tip of the snout to the posterior margin of the pelvic fins (Francis et al. 2001).

BDL = Body Length; standard measurement for holocephalans, dorsal edge of gill opening to origin of upper caudal fin (Didier and Rosenberger 2002).

PSCFL = Pre-Supracaudal Fin Length; a modified precaudal length measurement for holocephalans, from the tip of the snout to the origin of the supracaudal fin (Moura et al. 2004).

FAMILY LIFE HISTORY ACCOUNTS

PART 1. SHARKS

Order Hexanchiformes. Cow and Frilled Sharks.

Hexanchoid sharks are classified as yolk-sac viviparous (Musick and Ellis 2005).

Family Chlamydoselachidae. Frilled Sharks.

The frilled shark *Chlamydoselachus anguineus* was the focus of a study into its reproductive biology in Suruga Bay, Japan by Tanaka et al. (1990). No mature males were caught during the study and thus an assessment of male maturity was not possible (smallest mature male was 1178mm TL). Females were observed to mature at 1400–1500mm TL and with a maximum size of 1960mm TL (Gudger and Smith 1933) this equates to 71-75%TL_{max}. No defined reproductive cycle was found and reproductive activity may occur throughout the year. Fecundity was reported as 2–10 (average 6) embryos per litter, with young born at ~550mm TL (Tanaka et al. 1990). It is highly probably that the gestation period is very long, with Compagno (in prep. a) indicating a one to two year cycle, compared to Tanaka et al. (1990) who suggested at least 3.5 years based on growth rates of embryos held in artificial conditions.

Bass et al. (1975) comment on the maturity of *C. anguineus* off southern Africa, which is referrable to *Chlamydoselachus* sp. A [Ebert & Compagno]. They reported maturity in males at ~970mm TL and in females at 1350mm TL.

Family Hexanchidae. Sixgill and Sevengill Sharks.

Of the deepwater hexanchid sharks, there is a sound amount of information available on the biology of the bluntnose sixgill shark *Hexanchus griseus*, but little data is available for the sharpnose sevengill shark *Heptranchias perlo* or the bigeye sixgill shark *Hexanchus nakamurai*.

The reproductive biology of *H. griseus* has been examined off California, USA (Ebert 1986), in the Mediterranean (Capapé et al. 2004, Kabasakal 2004) and off southern Africa (Ebert 2002). Given a general lack of material, accurate determination of female maturity has been difficult (Ebert 2002), but it has been estimated at 4210mm TL off California (Ebert 1986), by 4200mm TL off southern Africa (Ebert 2002) and from 3940mm TL in the Mediterranean (Capapé et al. 2004). Ebert (2002) estimated female maturity at 87%TL_{max}, based on the largest maximum size in the literature (4820mm TL, Bigelow and Schroeder 1948). Kabasakal (2004) however, report *H. griseus* of up to 5500mm TL in the Mediterranean, and thus maturity there is reached in females from 72%TL_{max}. Male maturity is reported as 3090mm TL off Hawaii (Crow et al. 1996), ~3100mm TL off southern Africa (Ebert 2002) and ~3000mm TL in the Mediterranean (Capapé et al. 2004). Near-term embryos have been documented at 680–736mm TL off California (Ebert 1986) and free-swimming neonates at 610–930mm TL off southern Africa (Ebert 2002) and 556–680mm TL in the Mediterranean (Capapé et al. 2004). Henderson et al. (2003) reported on small numbers of *H. griseus* taken off Ireland, all of which were immature, including a free-living individual of 660mm TL.

Hexanchus griseus is one of the most fecund elasmobranchs with litter sizes documented up to 108 pups (Vaillant 1901). Some variation in litter sizes has been reported, such as 70 and 47 by Desbrosses (1938), 51 by Ebert (1986) and 100, 33 and 2 by Kabasakal (2004). Furthermore, Capapé et al. (2004) and Ebert (2002) observed large numbers (57–128) of follicles in the ovaries of females. The litter size of two presented by Kabasakal (2004), as well as some of the other lower litter sizes may be the result of captured gravid females aborting near-term embryos, with has been observed in this species (Ebert 1986). The reproductive cycle has been postulated to be least one year (Capapé et al. 2004), but the precise duration of gestation is unknown, although it is likely to be extended.

Ebert (1986) attempted to use traditional ageing methodologies on vertebral centra to age *H. griseus*, but these were unsuccessful. McFarlane et al. (2002) examined the suitability of using the neural arches to age this species and noted their potential given observed distinct and regular bands, the number of which increased with total length. However, the authors emphasized that their work was preliminary and that further research needs to include validation of their method, in order to determine if bands are laid down annually. Compagno (in prep. a) notes that the species is probably long-lived.

During a study of the reproductive biology of *H. perlo* off Kyushu, Japan (Tanaka and Mizue 1977), 218 females were observed, of which only a single gravid female with 11 embryos was found. The embryos measured an average of 242mm TL and were considered to be near-term. Bigelow and Schroeder (1948) reported litter sizes of 9–20 from Cuba (including L. Howell-Rivero, pers. comm. in Bigelow and Schroeder 1948). Tanaka and Mizue (1977) indicate that the species has no defined reproductive cycle off Japan. Females mature at 950–1050mm TL off Japan (Tanaka and Mizue 1977), while a 932mm TL female from Cuba was also mature (Bigelow and Schroeder 1948). With a maximum size of 1390mm TL (a record of 2140mm TL may be erroneous) (Bigelow and Schroeder 1948, Compagno et al. 2005), female maturity is reached from 67%TL_{max}.

Hexanchus nakamurai is a very poorly-known species that is reportedly born at 400–430mm TL; females mature at ~1420mm TL; males mature at ~1230mm TL (Springer and Waller 1969, Compagno in prep. a). A litter size of 13 has been reported for the species (Compagno in prep. a).

Order Squaliformes. Dogfish Sharks.

Squaloid species are yolk-sac viviparous, the majority being lecithotrophic, while a few have been shown to have limited matrotrophic input (limited histotrophs) (Musick and Ellis 2005). Guallart and Vicent (2001) confirmed the gulper shark *Centrophorus granulosus* as strictly lecithotrophic.

Family Echinorhinidae. Bramble Sharks.

Echinorhinid sharks are poorly-known and data on their biology is available only from incidental observations. Bramble shark *Echinorhinus brucus* are born at 400–500mm TL with maturity at 2000–2200mm TL for females and, although uncertain, <1500mm TL for males (Compagno in prep. a). Litter sizes of 15–26 embryos have been reported (Cadenat and Blanche 1981, Compagno in prep. a)

In contrast to the recorded fecundity of *E. brucus*, Crow et al. (1996) reported on a very high litter size of 114 pups from an individual prickly shark *E. cookei* from Hawaii. The smallest mature male of this species reported by Crow et al. (1996) was 1830mm TL, but a male of 2260mm TL from California was immature (Compagno in prep. a). Size at female maturity is uncertain, but reported at >2540mm TL and <2990mm TL. Regional variation in size at maturity is possible for the species (Compagno in prep. a). Size at birth is 450mm TL (Compagno in prep. a).

Family Squalidae. Dogfish Sharks.

There is little information on the biology of the two species of *Cirrhigaleus*, largely related to a lack of available specimens for study. The distribution and occurrence of each species remains poorly-defined, especially for the western Pacific mandarin dogfish *C. barbifer*. Fischer et al. (2006) noted that for the roughskin spurdog *C. asper* off northeastern Brazil, maturity in females and males occurs at ~1110mm TL and 910mm TL, respectively. These values were similar to those reported by Compagno (in prep. a) of 890–1180mm TL and 850–900mm TL for females and males, respectively. Size at birth is 250–280mm TL (Compagno in prep. a) and fecundity has been reported at 12–19 (Fischer et al. 2006) and 18-22 (Compagno in prep. a). Duffy et al. (2003) reported on a limited number of *C. barbifer* specimens from New Zealand waters and found males to mature at 900–950mm TL and females at 1090–1190mm TL. Two gravid females have been observed from New Zealand, with litter sizes of 6–10 (Duffy et al. 2003).

The wide-ranging, commercially-exploited piked or spiny dogfish *Squalus acanthias* whose occurrence is primarily on the continental and insular shelves is one of the most studied species of chondrichthyan fishes. There is considerable regional variation in biological parameters for the species, but it has been aged to 70 years (McFarlane and Beamish 1987), and its reported gestation period of up to 24 months is amongst the longest in the animal kingdom. Of the deepwater *Squalus* species there is considerable biological data available for two species, which occur commonly on the shelf as well as the upper-mid slopes, the shortnoes spurdog *S. megalops* and the shortspine spurdog *S. mitsukurii*. While limited information is also available for some other species, particularly the longnose spurdog *S. blainvillei*, the Japanese spurdog *S. japonicus* and the eastern longnose spurdog *Squalus* sp. F [Last & Stevens, 1994], several species are very poorly-known, including those with limited distributions, i.e. the Seychelles endemic *S. lalannei* and the New Caledonian endemic *S. melanurus*. Several undescribed species from Australia and Indonesia (Last and Stevens 1994, White et al. 2006) are presently under description (W. White pers. comm). As noted in Section I of this report, the taxonomy of several nominal *Squalus* species remains unresolved, particularly *S. blainvillei* and *S. mitsukurii*. As such, biological data presented for those species from different regions may turn out to represent data from distinct forms.

Reproductive and age and growth parameters for *Squalus* spp are summarized in Tables 2.1 and 2.2, respectively.

There is considerable geographical variation in the size at maturity for *Squalus* species, including for populations from the same region, i.e. *S. mitsukurii* from the Northwest Pacific (Taniuchi et al. 1993). Similarly, *S. megalops* off southeastern Australia reaches a considerably smaller adult size with both sexes maturing at smaller sizes there compared to populations studied of South Africa and Brazil (Watson and Smale 1998, Graham 2005, Braccini et al. 2006, Hazin et al. 2006). Regional variation in elasmobranch reproductive parameters is common, but some part of the variation in *Squalus* species may be a result of unresolved taxonomic issues.

Squalus dogfishes are characterised by very small fecundities, the largest observed for the deepwater species being 15 for *S. mitsukurii* off Choshi, Japan (Taniuchi et al. 1993). Several species, however, have much smaller litter sizes, such as 1–4 for *S. megalops* off Australia and South Africa (Watson and Smale 1998, Graham 2005, Braccini et al. 2006) and 2–6 for *S. blainvillei* in the Mediterranean (Sion et al. 2003). Within these ranges, litter sizes smaller than the maximum were more common. For example, Braccini et al. (2006) found that 69.3% of gravid females examined had a litter size of two, 30.0% a litter size of three and only 0.7% had a litter size of four. Litter sizes of two and three were also more common (46.9% and 43.9% of gravid females, respectively) for *S. megalops* off South Africa, and litter size is

Table 2.1. Reproductive biology of deepwater *Squalus* species.

Species	Location	TL_{max} (mm)	Maturity (mm TL)	Maturity $\%TL_{max}$	Litter size	Size at birth (mm TL)	Reference
Squalus blainvillei	Western Mediterranean	♀ 785 ♂ 664	601 (L_{50}) 450-510	77 68-77	2-6	190-220	Sion et al. (2003)
Squalus japonicus	Choshi, Japan, NW Pacific	♀ 950 ♂ 700	740-759 700	78-80 --	2-8 (5.3)	--	Chen et al. (1981)
	Nagasaki, Japan, NW Pacific	♀ 758 ♂ 640	560-579 500	74-76 78	2-8 (3.9)	--	Chen et al. (1981)
Squalus megalops	Agulhas Bank, South Africa, SE Atlantic	♀ 782 ♂ 572	500 (L_{50}) 400 (L_{50})	64 70	2-4	232-277	Watson & Smale (1998)
	Andaman Is., Eastern Indian	♀ 766 ♂ --	--	--	5-7	--	Soundararajan & Dam Roy (2004)
	SE Australia	♀ 630 ♂ 510	480 (L_{50}) 380 (L_{50})	76 75	1-3 (2.1)	190-240	Graham (2005)
	SE Australia	♀ 635 ♂ 470	459-495 ($L_{50's}$) 373-398 ($L_{50's}$)	72-78 79-85	2-4	191-244	Braccini et al. (2006)
	NE Brazil, SW Atlantic	♀ 890 ♂ 645	590 (L_{50}) 430-460	66 67-71	1-8	200-230	Hazin et al. (2006)
Squalus mitsukurii	Choshi, Japan, NW Pacific	♀ -- ♂ --	960-999 680-719	--	4-15 (8.8)	--	Taniuchi et al. (1993)
	Masseiba, Japan, NW Pacific	♀ -- ♂ --	--	--	6-9 (7.1)	--	Taniuchi et al. (1993)
	Ogasawara Is., Japan, NW Pacific	♀ -- ♂ --	720-759 520-559	--	2-9 (4.5)	--	Taniuchi et al. (1993)
	Hancock Seamount, NW Pacific	♀ -- ♂ --	680-719 520-559	--	--	--	Taniuchi et al. (1993)
	Hancock Seamount, NW Pacific	♀ 910 ♂ 820	690 (L_{50}) 480 (L_{50})	76 58	1-6	210-260	Wilson & Seki (1994)
	La Plata, SW Atlantic	♀ 840 ♂ 660	520-600 510-550	63-71 77-83	--	--	Lucifora et al. (1999)
	NE Brazil, SW Atlantic	♀ 943 ♂ 730	778 (L_{50}) 650	83 89	3-11	>225	Fischer et al. (2006)
Squalus cf. *mitsukurii*	SE Australia	♀ 960 ♂ 840	805 630	84 75	4-10	--	Graham (2005) (also Daley et al. 2002)
Squalus sp. B	SE Australia	♀ 860 ♂ 740	-- <620	-- <84	--	--	Graham (2005)
Squalus sp. F	SE Australia	♀ 730 ♂ 620	630 ~500	86 81	2-7	>220	Graham (2005)

often related to maternal size, larger females able to carry more embryos (Watson and Smale 1998, Braccini et al. 2006).

Squalus species do not appear to have defined reproductive seasonality, exhibiting aseasonal reproduction (Chen et al. 1981, Graham 2005, Hazin et al. 2006). Braccini et al. (2006) demonstrated that *S. megalops* off Australia has an ovarian cycle and gestation period of two years, and consequently noted that only 50% of mature females will contribute to annual recruitment in any given year. The duration of reproductive cycles and gestation in other species have not been determined, although Chen et al. (1981) suggested that gestation in *S. japonicus* lasted about one year. Given the results of Braccini et al. (2006), as well as data from *S. acanthias*, it is likely that many other squalids exhibit biennial reproductive cycles.

Ageing studies have demonstrated maximum ages for deepwater *Squalus* of 32 years for female *S. megalops* (Watson and Smale 1999) and 27 years for female *S. mitsukurii* (Wilson and Seki 1994, Tanicuhi and Tachikawa 1999). Relatively late ages at maturity for females are also characteristic of the group. Age estimates for *S. blainvillei* were much lower, reaching a maximum age of 8 years with maturity at 5.1 and 3.3 years for females and males, respectively (Cannizzaro et al. 1995). Maximum age estimates for the deeper water *Squalus* species are considerably less than the highest estimate for *S. acanthias* of 70 years from the Northeast Pacific (McFarlane and Beamish 1987). This is a considerably larger *Squalus* than the deeper water species, reaching 1600mm TL in the NE Pacific (Compagno in prep. a).

Table 2.2. Age and growth of squalid sharks. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years). Band count method: Ext DS, external dorsal spine band count; Vert, vertebral band count.

Species	**Location**	**Method**	**VBGM parameters**			**t_{max}**	**A_{mat}**	**Reference**
			L_∞	**k**	**t_0**			
Squalus blainvillei	Western Mediterranean	Vert	♀ 1179	0.102	-1.380	8	5.1	Cannizzaro et al. (1995)
			♂ 960	0.135	-1.397	8	3.3	
Squalus megalops	Agulhas Bank, South Africa, SE Atlantic	Ext DS	♀ 932	0.03	-8.1	32	15	Watson & Smale (1999)
			♂ 526	0.09	-6.9	29	9	
Squalus mitsukurii	Sala y Gomez Seamount, SE Pacific	Ext DS	♀ --	--	--	16	--	Litvinov (1990)
			♂ --	--	--	14	--	
	Hancock Seamount, NW Pacific	Ext DS	♀ 1070	0.041	-10.09	27	15	Wilson & Seki (1994)
			♂ 660	0.155	-4.64	18	4	
	Hancock Seamount, NW Pacific	Ext DS	♀ 831	0.103	-2.94	17	14-16	Taniuchi & Tachikawa (1999)
			♂ 645	0.252	-0.430	12	6-7	
	Choshi, Japan, NW Pacific	Ext DS	♀ 1628	0.039	-5.21	21	19-20	Taniuchi & Tachikawa (1999)
			♂ 1093	0.066	-5.03	20	10-11	
	Ogasawara Is., Japan, NW Pacific	Ext DS	♀ 1112	0.051	-5.12	27	15-17	Taniuchi & Tachikawa (1999)
			♂ 880	0.060	-5.57	21	9-10	

Family Centrophoridae. Gulper Sharks.

The leafscale gulper shark *Centrophorus squamosus* in the Northeast Atlantic is one of the most studied deepwater chondrichthyan fishes. A reasonable amount of data is also available for the gulper shark *C. granulosus* and the birdbeak dogfish *Deania calcea*, again from the Atlantic, with limited information on a handful of other species. However, most species remain very poorly-known, particularly in the Indo-West Pacific, the center of their diversity. As noted in Section I of this report, the taxonomy of *Centrophorus* species remains unresolved. Many gulper sharks are presently considered wide-ranging species, but revision of the genus is indicating that several of these are likely narrow range endemics, with separation of taxa between the Atlantic and the Indo-West Pacific (W. White. pers. comm.).

Reproductive and age and growth parameters for centrophorid sharks are summarized in Tables 2.3 and 2.4, respectively.

Centrophorus species are amongst, if not, the most unproductive of chondrichthyan fishes. Fecundity is low, with litter sizes of 1–2 for most species examined, the exception being a litter size of 7 recorded for *C. squamosus* by Bañón et al. (2006). Daley et al. (2002) found that litter size in Australian *C.* cf. *uyato* was invariably one in 37 gravid females examined, and only a single embryo has been noted in *C. granulsosus* (Golani and Pisanty 2000, Guallart and Vicent 2001). *Centrophorus* have a continuous reproductive cycle with follicles continuing to develop as gestation ensues and at the time of ovulation the follicles are very large (Guallart and Vicent 2001, Daley et al. 2002, McLaughlin and Morrissey 2005). Irvine (2004) suggests that to allow for maturation of oocytes to these large ovulatory sizes in species with continuous reproductive sizes, a long gestation period is required. A two year gestation period has been demonstrated for *C. granulosus* (Guallart and Vincent 2001) and a three year gestation period has been hypothesized for *C.* cf. *uyato* (McLaughlin and Morrissey 2005). Fecundity of *Deania* species is higher than *Centrophorus*, with litter sizes of 1–17 for *D. calcea* and 8–17 for *D. quadrispinosum* (Clarke et al. 2002b, Daley et al. 2002, Irvine 2004). *Deania* is also recognised as having an extended gestation period, probably with a two or three year reproductive cycle that is non-continuous (i.e. with a resting period between parturition and the development of new oocytes) (Daley et al. 2002).

Coupled with a limited reproductive potential, centrophorids have also been estimated to reach considerable ages with a late onset of maturity. Clarke et al. (2002a) suggest that female *C. squamosus* from the Northeast Atlantic live to at least 70 years and mature at 35 years, while Fenton (2001) provided a preliminary age estimate of 46 years for *C.* cf. *uyato* from Australia (although this included only immature individuals). Age estimates for *C. acus* from Japan were considerably lower at 18 years for females and 17 years for males (Tanaka 1990). Female *Deania calcea* was estimated to reach similar maximum ages of 37 and 35 years off southern Australia (Irvine 2004) and in the Northeast Atlantic (Clarke et al. 2002b), respectively. This species also exhibited late maturity, at 21.5 for Australia and 25 years for the Northeast Atlantic (Clarke et al. 2002b, Irvine 2004). It should be noted though that these ageing studies have not been validated, and also that sample size distributions may influence age estimates, and thus some may not be completely reliable (Irvine 2004).

Taking the available life history data on *C. granulosus* (litter size of one, 2 year gestation period, female age at maturity of 16.5 years and longevity of 39 years), and assuming continuous breeding from maturity to maximum age with no senescence, a single female *C. granulosus* will produce a maximum of 12 pups throughout its lifetime. Irvine (2004) calculated lifetime fecundity for *D. calcea*, utilising a mean litter size of 8 and the number of reproductive years as 15.5, and applying either a two or three year reproductive cycle. If the species reproduces biennially, Irvine (2004) calculated that the lifetime fecundity of a female *D. calcea* is 62 pups, and if it reproduces triennially, lifetime fecundity would be 20.4 pups.

Table 2.3. Reproductive biology of centrophorid sharks. A litter size value in parentheses is the mean value. Where uterine litter size is not available ovarian fecundity may be given (*ovarian*).

Species	Location	TL_{max} (mm)	Maturity (mm TL)	Maturity $\%TL_{max}$	Litter size	Size at birth (mm TL)[1]	Reference
Centrophorus acus	Suruga Bay, Japan, NW Pacific	♀ 1608 ♂ 1165	>1535, <1608 1000-1050	-- 86-90	5 *ovarian*	--	Yano & Tanaka (1986)
	Andaman Is., Eastern Indian	♀ 1108 ♂ 875	--	--	1-2	404-440	Soundararajan & Dam Roy (2004)
Centrophorus granulosus	Israel, Eastern Mediterranean	♀ 950 ♂ 825	<795 <725	84 88	1	>336	Golani & Pisanty (2000)
	Gulf of Valencia, Western Mediterranean	--	--	--	1	273-372mm PCL	Guallart & Vicent (2001)
Centrophorus harrissoni	SE Australia	♀ 1120 ♂ 960	~1000 800-850	89 83-89	1-2	~400	Daley et al. (2002)
Centrophorus moluccensis	SE Australia	♀ 930 ♂ 780	690-880 520-710	-- --	1-2	<320	Daley et al. (2002)
Centrophorus squamosus	West of British Isles, NE Atlantic	♀ 1400 ♂ 1200	1240 (L_{50}) 980 (L_{50})	89 82	7-11 *ovarian*	--	Girard & Du Buit (1999)
	West of British Isles, NE Atlantic	♀ -- ♂ --	-- --	--	6-11 (8.1) *ovarian*	--	Clarke et al. (2001)
	Rockall Trough & Porcupine Bank, NE Atlantic	♀ 1450 ♂ 1220	1280 (L_{50}) 1010 (L_{50})	88 83	--	--	Clarke et al. (2002a)
	Galicia, Spain, NE Atlantic	♀ 1440 ♂ 1210	1250 (L_{50}) 1010 (L_{50})	87 83	7	>400	Bañón et al. (2006)
Centrophorus cf. *uyato*	SE Australia	♀ 1120 ♂ 930	~1000 ~800	89 86	1	440-450	Daley et al. (2002)
Centrophorus cf. *uyato*	Cayman Trench, Jamaica, Western Central Atlantic	♀ -- ♂ --	800-900 <812	--	1-2	--	McLaughlin & Morrissey (2005)
Deania calcea	Rockall Trough & Porcupine Bank, NE Atlantic	♀ 1170 ♂ 1090	1060 (L_{50}) 850 (L_{50})	91 78	8-14	--	Clarke et al. (2002b)
	SE Australia	♀ 1220 ♂ 940	~1000 ~800	82 85	1-17 (7)	280-330	Daley et al. (2002)
	SE Australia	♀ 1140 ♂ 910	970 760	85 84	5-10	>310	Irvine (2004)
Deania quadrispinosum	SE Australia	♀ 1180 ♂ 960	1020-1100 800-900	86-93 83-94	8-17	~250	Daley et al. (2002)

[1] Unless specified as precaudal length (PCL).

Table 2.4. Age and growth of centrophorid sharks. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years). Band count method: Int DS, internal dorsal spine band count; Ext DS, external dorsal spine band count; RadioM, radiometric ageing.

Species	**Location**	**Method**	**VBGM parameters**			**t_{max}**	**A_{mat}**	**Reference**
			L_∞	**k**	**t_0**			
Centrophorus acus	Suruga Bay, Japan, NW Pacific	Int DS	♀ 1262 ♂ 1172	0.155 0.173	-0.485 -1.403	18 17	-- 10	Tanaka (1990)
Centrophorus granulosus	Western Mediterranean	Int DS	♀ 1094 ♂ 917	0.096 0.107	-5.48 -9.78	39 25	16.5 8.5	Guallart (1998)
Centrophorus squamosus	Rockall Trough and Porcupine Bank, NE Atlantic	Int DS	♀ -- ♂ --	-- --	-- --	70 71	35 30	Clarke et al. (2002a)
Centrophorus cf. *uyato*	Australia	RadioM	♀ + ♂	--	--	46*	--	Fenton (2001)
Deania calcea	Rockall Trough and Porcupine Bank, NE Atlantic	Int DS	♀ 1193 ♂ 935	0.077 0.135	-0.933 -0.165	35 32	25 --	Clarke et al. (2002b)
	SE Australia	Ext DS	♀ 1225 ♂ --	0.051 --	-5.11 --	37 33	21.5 13.5	Irvine (2004)

*No mature specimens were aged.

Family Etmopteridae. Lanternsharks.

The lanternsharks are the most diverse family of squaloid sharks, with 47 species, all of which inhabit deepwater. Endemism is high in this family; many have restricted ranges, while others are more wide-ranging and global in their distribution. The vast majority of species are poorly-known, particularly the more localised species. For example, the smalleye lanternshark *Etmopterus litvinovi* has only been recorded from two isolated ridges in the Southeast Pacific while the rare cylindrical lanternshark *E. carteri* has only ever been located from a small area and narrow depth range on the upper slope off the Caribbean coast of Colombia. A group of 6 Australian and New Caledonian *Etmopterus* spp are known only from their original description (Last, Burgess and Séret 2002), a situation not uncommon amongst the deepwater squaloids. The biology of these species and many other etmopterids is virtually unknown.

Reproductive and age and growth parameters for etmopterid sharks are summarized in Tables 2.5 and 2.6, respectively.

While there is biological information for two species of *Centroscyllium* and several *Etmopterus*, primarily from studies conducted in the NE Atlantic and southern Australia, the sole members of the three other etmopterid genera (*Aculeola*, *Miroscyllium* and *Trigonognathus*) are very poorly-known. Acuña et al. (2003) reports an average litter size of 10 in the hooktooth dogfish *Aculeola nigra* from off Chile and Yano et al. (2003) noted that litter size in the viper dogfish *Trigonognathus kabeyai* from southern Japan is likely to be <26 given the observed number of mature follicles (25–26) in two females.

Litter sizes for *Centroscyllium* are generally higher (maximum 40 in *C. fabricii*; Yano 1995) than those in *Etmopterus* (maximum 21 in *Etmopterus* sp. B; Daley et al. 2002), although in all species examined thus far, fecundity is restricted with mean litter sizes in the range of 9–

16 embryos (Table 2.5). Irvine (2004) found strong correlations between maternal size and the number of follicles and the number of embryos and within the New Zealand lanternshark *E. baxteri* from southern Australia and Yano (1995) found similar results for the black dogfish *C. fabricii* from Greenland.

Etmopterids do not appear to have well-defined reproductive seasons, and have a non-continuous reproductive cycle with an apparent resting stage after parturition. This is supported by observations that follicles do not continue to develop throughout gestation (i.e. gravid females do not possess developing or mature oocytes) and the finding of numerous large females with inactive reproductive tracts (Yano 1995, Daley et al. 2002, Irvine 2004). With species exhibiting aseasonal reproductive cycles, the duration of any resting stage after parturition and prior to next ovulation is difficult to assess as each reproductive stage occur can be found in any month sampled (Irvine 2004). Furthermore, gestation period has not been calculated.

Age estimates are available for only two species of lanternshark, and these are unvalidated and thus should be considered as preliminary (Gennari et al. 2002, Sion et al. 2002, Irvine et al. 2006a). Irvine et al. (2006a) estimated age from both internal and external bands on the second dorsal spine of *E. baxteri*. While there were considerable differences in age estimations between these techniques (see Table 2.6), Irvine et al. (2006b), in an aging study of the somniosid *Centroselachus crepidater*, suggested that internal bands may underestimate age. Similarly, for *E. baxteri*, internal bands become unreadable as internal dentine appears to stop forming in adult fish (Irvine et al. 2006a). As such, count estimates from external bands are more reliable, and for *E. baxteri* this technique gives a maximum age of 57 years for females and 48 years for males, with age at 50% maturity of 30 years for females and 20 years for males (Irvine et al. 2006a). Vertebral band counts for the velvet belly *E. spinax* from the Mediterranean present 7 bands for the largest individuals (Gennari et al. 2002, Sion et al. 2002). There is a considerable size difference between *E. spinax* which rarely reaches >450mm TL (although can reach 600mm TL) and *E. baxteri* with reaches 880mm TL (Compagno et al. 2005).

Irvine (2004) calculated lifetime fecundity for *E. baxteri*, utilising a mean litter size of 6-12 (variable with maternal size) and the number of reproductive years as 27, and applying either a two or three year reproductive cycle. If the species reproduces biennially, Irvine (2004) calculated that the lifetime fecundity of a female *E. baxteri* is 128 pups, and if it reproduces triennially, then the lifetime fecundity would be 81 pups.

Table 2.5. Reproductive biology of etmopterid sharks. A litter size value in parentheses is the mean value. Where uterine litter size is not available ovarian fecundity may be given (*ovarian*).

Species	**Location**	**TL$_{max}$ (mm)**	**Maturity (mm TL)**	**Maturity %TL$_{max}$**	**Litter size**	**Size at birth (mm TL)**	**Reference**
Centroscyllium fabricii	Greenland, NE Atlantic	♀ 898 ♂ 760	~650 ~550	72 72	4-40 (16.4)	165-192	Yano (1995)
	Iceland, NE Atlantic	♀ 1060 ♂ --	703 (L_{50}) 573 (L_{50})	66 --	--	--	Jabobsdóttir (2001)
Centroscyllium kamoharai	SE Australia	♀ 630 ♂ 540	~550 ~440	87 81	3-22 (12)	--	Daley et al. (2002)
Etmopterus baxteri	New Zealand, SW Pacific	♀ 788 ♂ 697	640-690 550-580	81-88 79-83	9-15 (12.7)	<200	Wetherbee (1996)*
	SE Australia	♀ 830 ♂ 740	600-650 500-600	72-78 68-81	6-16 (10)	210-230	Daley et al. (2002)*
	SE Australia	♀ 870 ♂ 720	630 (L_{50}) 540 (L_{50})	72 75	1-16 (8.8)	220-240	Irvine (2004)
Etmopterus princeps	Iceland, NE Atlantic	♀ 890 ♂ --	622 (L_{50}) 573 (L_{50})	70 --	--	--	Jabobsdóttir (2001)
Etmopterus pusillus	Portugal, NE Atlantic	♀ 502 ♂ 479	436 (L_{50}) 381 (L_{50})	87 80	--	--	Coelho & Erzini (2005)
Etmopterus spinax	Portugal, NE Atlantic	♀ 407 ♂ 338	309 (L_{50}) 254 (L_{50})	76 75	--	--	Coelho & Erzini (2005)
	Mediterranean	♀ 460 ♂ 370	--	--	6-18	90-110	Serena et al. (2006)
Etmopterus sp. B	SE Australia	♀ 730 ♂ 620	~600 ~500	82 81	2-21 (12)	150-180	Daley et al. (2002)
Trigonognathus kabeyai	Kumano-nada Sea and Ogasawara Is., Japan, NW Pacific	♀ 539 ♂ 470	~520 ~430	-- --	25-26 *ovarian*	--	Yano et al. (2003)

*Referred to in Wetherbee (1996) and Daley et al. (2002) as *E. granulosus*, this is correctly *E. baxteri*.

Table 2.6. Age and growth of etmopterid sharks. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years). Band count method: Int DS, internal dorsal spine band count; Ext DS, external dorsal spine band count; Vert, vertebral band count.

Species	Location	Method	VBGM parameters			t_{max}	A_{mat}	Reference
			L_∞	k	t_0			
Etmopterus baxteri	SE Australia	Ext DS	♀ 681 ♂ 606	0.040 0.082	-4.51 -1.43	57 48	30 20	Irvine et al. (2006a)
	SE Australia	Int DS	♀ 693 ♂ 596	0.116 0.163	-1.56 -2.00	26 22	11.5 10.5	Irvine et al. (2006a)
Etmopterus spinax	Western Mediterranean	Vert	--	--	--	7	--	Gennari et al. (2002)
	Western Mediterranean	Vert	--	--	--	7	5	Sion et al. (2002)

Family Somniosidae. Sleeper Sharks.

The small squaloid family Somniosidae includes the relatively well-studied Portuguese dogfish *Centroscymnus coelolepis*, a group of species (*C. owstoni*, *Centroselachus crepidater* and *Proscymnodon plunketi*) for which there is reasonable biological information, and some very poorly-known species, particularly from the genera *Scymnodalatias*, *Scymnodon* and *Zameus*. The vast majority of information on the biology of the family comes from the Northeast Atlantic and southeastern Australia. The systematics of *Somniosus* species has recently been reviewed (Yano et al. 2004) and there remains only a single undescribed species in the family, the longnose sleeper shark *Somniosus* sp. A. However, the only known specimen of this species, from off Portugal, was destroyed in a fire (Yano et al. 2004, Compagno in prep. a).

Reproductive and age and growth parameters for somniosid sharks are summarized in Tables 2.7 and 2.8, respectively.

Details of the reproductive biology of the large *Somniosus* species is sketchy, although they are known to mature at very large sizes (~4500mm TL in female *S. microcephalus*, ~4350mm TL in female *S. antarcticus* and ~3700mm TL in female *S. pacificus*) (Ebert et al. 1987, Yano et al. 2007). Very large numbers of follicles have been reported for *Sominosus* spp, 372+ for *S. pacificus* (Ebert et al. 1987) and up to 2931 in *S. microcephalus* (Yano et al. 2007). Actual reported litter sizes are considerably smaller, 8 in *S. rostratus* (a smaller *Somniosus* reaching 1140mm TL) (Barrull and Mate 2001) and at least 10 in *S. microcephalus* (see Yano et al. 2007). Litter sizes in other somniosids range from 1–9 in *C. crepidater*, 1–29 in *C. coelolopis*, 5–31 in *C. owstoni* to moderately high (59) in *Scymondalatias albicauda* (Table 2.7). Yano and Tanaka (1988) found that fecundity increased with maternal size in *C. coelolepis*.

The lack of developing or preovulatory follicles in gravid or post-partum female somniosids indicates that there is a resting phase after parturition prior to the next pregnancy. This has been shown in such species as *P. plunketi*, *C. crepidater*, *C. owstoni* and *C. coelolepis* (Daley et al. 2002, Irvine 2004). The length of these resting periods remains undetermined as they are difficult to assess in species with aseasonal reproductive cycles, as is the case with somniosids (Irvine 2004). However, the length of the gestation period in sleeper sharks is thought to be long (1–2 years) and the existence of a resting period results in a probable reproductive cycle of 2–3 years.

Irvine et al. (2006b) reported female *C. crepidater* to 54 years and males to 34 years. Irvine et al. (2006b) trialled the application of both internal and external dorsal spine band counts to age this species and was able to validate the annual formation of external bands using the preliminary radiometric age estimates of Fenton (2001). Thus, age estimates from internal bands (27 years in females, 22 in males) were inaccurate and grossly underestimated age (Irvine 2004, Irvine et al. 2006b). Preliminary age estimates for *P. plunketi* are 39 years in females and 32 years in males (Irvine 2004) (Table 2.8). *Somniosus* lack dorsal spines and an examination of vertebrae and neural arches could not identify any bands that may represent growth (S. Irvine, pers. comm.).

While Irvine et al. (2006b) estimated age at 50% maturity (A_{50}) in female *C. crepidater* to be 20 years, maturity actually occurred over a wide range of ages (12–42 years), Furthermore, the youngest gravid female was found to be 27 years old while the youngest carrying near-term embryos was 29 years. This has relevance when considering the reproductive productivity of a species, as it is these older females, several years beyond the estimate of A_{50}, that are contributing to the population (Irvine et al. 2006b).

Irvine (2004) calculated lifetime fecundities for *C. crepidater* (utilising a mean litter size of 6 and 34 reproductive years) and *P. plunketi* (utilising mean litter size of 17 and 10 reproductive years; see Irvine 2004 for details). If these species reproduce biennially, Irvine (2004) calculated that the lifetime fecundity of a female *C. crepidater* is 102 pups and of a female *P. plunketi* is 85 pups and if these species reproduce triennially the lifetime fecundity of a female *C. crepidater* is 68 pups and of a female *P. plunketi* is 56 pups (Irvine 2004).

Table 2.7. Reproductive biology of somniosid sharks. A litter size value in parentheses is the mean value. Where uterine litter size is not available ovarian fecundity may be given (*ovarian*).

Species	Location	TL_{max} (mm)	Maturity (mm TL)	Maturity $\%TL_{max}$	Litter size	Size at birth (mm TL)	Reference
Centroscymnus coelolepis	Suruga Bay, Japan, NW Pacific	♀ 1132 ♂ 924	950-999 (L_{50}) ~700	84-88 76	15-29	~300-350	Yano & Tanaka (1988)
	West of British Isles, NE Atlantic	♀ 1220 ♂ 1080	1020 (L_{50}) 860 (L_{50})	84 80	8-19 (14)	--	Girard & Du Buit (1999)
	West of British Isles, NE Atlantic	♀ -- ♂ --	--	--	8-21 (13.8)	--	Clarke et al. (2001)
	SE Australia	♀ 1200 ♂ 1010	~1100 850-900	92 84-89	8-19 (12)	>320	Daley et al. (2002)
	Portugal, NE Atlantic	♀ 1220 ♂ 1000	985 (L_{50}) ~900	81 90	1-25 (9.9)	233-300	Veríssimo et al. (2003)
	SE Australia	♀ 1120 ♂ 1000	990 (L_{50}) 820 (L_{50})	88 82	10-19 (15.5) *ovarian*	--	Irvine (2004)
	Galicia, Spain, NE Atlantic	♀ 1220 ♂ 1000	1110-1150 880-970	-- --	5-22 (14)	270-290	Bañón et al. (2006)
Centroscymnus owstoni	Suruga Bay, Japan, NW Pacific	♀ 1168 ♂ 882	1000-1049 (L_{50}) 700-749 (L_{50})	86-90 79-85	16-31	~300-350	Yano & Tanaka (1988)
	SE Australia	♀ 1200 ♂ 960	~950 ~750	79 78	5-13	250-320	Daley et al. (2002)
	SE Australia	♀ 1150 ♂ 940	1000 (L_{50}) ~700	87 74	8-19 (12) *ovarian*	--	Irvine (2004)
Centroselachus crepidater	SE Australia	♀ 1030 ♂ 940	~820 ~620	80 66	3-9 (6)	320	Daley et al. (2002)
	NE Atlantic	♀ 870 ♂ 690	680 520	78 75	1-9	--	Nolan & Hogan (2003)
	SE Australia	♀ 1010 ♂ 880	840 (L_{50}) 640 (L_{50})	83 73	4-8 (6)	~310	Irvine (2004)
Proscymnodon plunketi	SE Australia	♀ 1540 ♂ 1330	~1400 ~1080	91 81	7-27 *ovarian*	--	Daley et al. (2002)
	SE Australia	♀ 1550 ♂ 1290	1320 (L_{50}) 1110-1120	85 86-87	19-43 (28) *ovarian*	--	Irvine (2004)
Scymnodalatias albicauda	SE Atlantic	♀ 1110 ♂ --	--	--	59	--	Nakaya & Nakano (1995)
Somniosus pacificus	California, Eastern Central Pacific	♀ 4300 ♂ --	~3700 --	--	372+ *ovarian*	<740	Ebert et al. (1987)
Somniosus rostratus	Western Mediterranean	♀ 1000 ♂ --	--	--	8	--	Barrull & Mate (2001)

Table 2.8. Age and growth of somniosid sharks. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years). Band count method: Int DS, internal dorsal spine band count; Ext DS, external dorsal spine band count; RadioM, radiometric ageing.

Species	Location	Method	VBGM parameters			t_{max}	A_{mat}	Reference
			L_∞	k	t_0			
Centroselachus crepidater	SE Australia	Ext DS	♀ 961 ♂ 732	0.072 0.141	-6.13 -2.99	54 34	20 ~9	Irvine et al. (2006b)
	SE Australia	Int DS	♀ 932 ♂ 706	0.163 0.362	-1.92 -1.51	27 22	-- --	Irvine (2004)
	SE Australia	RadioM	♀+♂	--	--	43	--	Fenton (2001)
Proscymnodon plunketi	SE Australia	Ext DS	♀ -- ♂ --	-- --	-- --	39 32	29 18	Irvine (2004)

Family Oxynotidae. Roughsharks.

The roughsharks are a poorly-known group of deepwater dogfishes. There is some basic published data on the angular roughshark *Oxynotus centrina* from the Mediterranean and eastern Atlantic, but little information available on the other four species. *Oxynotus centrina* has been reported with litters of 10-15 with a reproductive cycle that is suggested to last around one year (Capapè et al. 1999, Megalofonou and Damalas 2004). Maturity occurs at 650mm TL and 600mm TL for females and males, respectively, which corresponds to 83% and 94% of TL_{max} in the study (Capapè et al. 1999). Size at birth is suggested to be 210–240mm TL (Capapè et al. 1999).

Last and Stevens (1994) reports a litter size of seven from a single female *O. bruniensis*, endemic to the Australasian region. There is no information available on the biology of *O. caribbeaus*, *O. japonicus* or *O. paradoxus*.

Family Dalatiidae. Kitefin Sharks.

Biological information on the largely pelagic kitefin sharks is limited, and the nine deepwater species are generally very poorly-known. A few species, such as the taillight shark *Euprotomicroides zantedeschia*, longnose pygmy shark *Heteroscymnoides marleyi*, the South China cookiecutter shark *Isistius labialis* and the pocket shark *Mollisquama parini* are known only from a handful of specimens (*I. labialis* and *M. parini* are each known only from single specimens).

The kitefin shark *Dalatias licha* reaches at least 1590mm TL and possibly over 1800mm TL (Compagno in prep. a). Preliminary maturity estimates suggest that males from southern Australia mature at 1090–1130mm TL (Daley et al. 2002) and females mature at ~1200mm TL (Last and Stevens 1994). Other members of this family are very small, including the world's smallest shark, the smalleye pygmy shark *Squaliolus aliae*, which reaches a maximum size of 220mm TL (Last and Stevens 1994). Some species such as *Isistius* and *Squaliolus* are vertical migrators, moving up the water column at night and returning to deeper water during the day. Litter sizes in the family, like most other squaloid species are small. For *D. licha* Compagno (in prep. a) reported 10–16 and in four gravid females Daley et al. (2002) observed litter sizes of 7–11. A litter size of nine has been reported for *Isistius brasiliensis* (Gadig and Gomes 2002) and four has been reported in *Squaliolus laticaudus* (Cunha and

Gonzalez 2006). Daley et al. (2002) suggests that *D. licha* has a non-continuous reproductive cycle.

Order Squatiniformes. Angelsharks.

Family Squatinidae. Angelsharks.

The angelsharks included in this report are all marginal deepwater species that occur on the shelf and upper slope. The deepest recorded is 500m for the sawback angelshark *Squatina aculeata* from the Atlantic and 494m for the African angelshark *S. africana*. Of the species included here two Australian endemics remain undescribed (Last and Stevens 1994) and are relatively poorly-known, as is *S. africana* and the Taiwan angelshark *S. formosa*. Reproductive parameters for the remaining outer shelf and upper slope squatinid sharks are summarized in Table 2.9.

Squatinids are yolk-sac viviparous (Musick and Ellis 2005) and their reproductive potential is limited. All have small litter sizes and extended gestation periods with possible biennial reproductive cycles in at least some species. Litter sizes in the upper slope species range from 2 to 12 and Bridge et al. (1998) suggested that gestation in *S. tergocellata* lasts 6–12 months with a probable biennial reproductive cycle, while Capapé et al. (2005) provided evidence for a ~12 month gestation in S. *aculeata*. A female breeding cycle of at least 2 years has been suggested for *S. argentina* (Vooren and Klippel 2005).

Table 2.9. Reproductive biology of outer shelf and upper slope squatinid sharks. A litter size value in parentheses is the mean value.

Species	Location	TL_{max} (mm)	Maturity (mm TL)	Maturity $\%TL_{max}$	Litter size	Size at birth (mm TL)	Reference
Squatina aculeata	Senegal, EC Atlantic and Tunisia, Mediterranean	♀ 1750 ♂ 1520	1370-1430 1200-1220	78-82 79-80	8-12 (11.1)	303-350	Capapé et al. (2005)
Squatina argentina	Southern Brazil, SW Atlantic	♀ 1380 ♂ --	~1200 ~1200	87 --	7-11	--	Vooren & Klippel (2005)
Squatina tergocellata	Southern Australia, Eastern Indian	♀ 1400 ♂ 1025	1150-1250 810-910	82-89 79-89	2-9 (4.5)	~325-415	Bridge et al. (1998)

Order Pristiophoriformes. Sawsharks.

Family Pristiophoridae. Sawsharks.

The deepwater sawsharks are poorly-known, with several species remaining undescribed. All species have relatively restricted distributions. Sawsharks are yolk-sac viviparous and Bass et al. (1975) reported a litter of seven embryos in a sixgill sawshark *Pliotrema warreni*, but noted that the female had apparently aborted several other embryos upon capture. Ovarian fecundity from a larger number of females was 7–17 (average 12.5) (Bass et al. 1975). Maturity is reached in females by ~1100mm TL and in males by ~830mm TL, representing 81% and 74% of TL_{max} reported by Bass et al. (1975), respectively. The species is more common on the shelf in some parts of its distribution (including possible shallower water pupping grounds), but occurs more regularly in deeper water in other areas (Compagno in prep. a).

Data from southern Australian shelf *Pristiophorus* species (*P. cirratus* and *P. nudipinnis*) indicate litter sizes of 6–19 pups produced every other year (biennial reproductive cycle) (Compagno et al. 2005). The biology of the truly deepwater Bahamas sawshark *Pristiophorus schroederi*, along with undescribed *Pristiophorus* species from the Indo-West Pacific, however, is essentially unknown (Compagno in prep. a).

Order Heterodontiformes. Bullhead Sharks.

Family Heterodontidae. Bullhead Sharks.

The whitespotted bullhead shark *Heterodontus ramalheira* is unique amongst the family in having a preference for deeper waters than its congeners, which are generally shallow inner shelf species (Compagno 2001). Bullhead sharks are oviparous, but there is no information on the biology of this rare species (Compagno 2001).

Order Orectolobiformes. Carpetsharks.

Family Parascylliidae. Collared Carpetsharks.

The two deepwater species of the small shark family Parascylliidae are very poorly-known. Both are rare restricted range endemics known from narrow depth ranges on the upper slope. These species are oviparous but there are no other details on their biology (Compagno 2001). The ginger carpetshark *Parascyllium sparsimaculatum* is known only from three female specimens (Last and Stevens 1994, Goto and Last 2002).

Order Lamniformes. Mackerel Sharks.

Family Odontaspididae. Sand Tiger Sharks.

Sand tiger sharks are oophagous, and although litter sizes have not been documented in either of the deepwater species, the smalltooth sand tiger *Odontaspis ferox* or the bigeye sand tiger *O. noronhai*, they are likely two, given the mode of reproduction and data from the inshore sand tiger shark *Carcharias taurus*. This latter species displays a modified form of oophagy whereby the largest embryo in each uterus consumes its sibling embryos before relying on ova ovulated by the mother (Musick and Ellis 2005). This form of oophagy is termed adelphophagy or uterine cannibalism and has only been confirmed for *C. taurus* (Musick and Ellis 2005). The reproductive productivity of *C. taurus* is low (2 pups every other year) (Compagno 2001, Lucifora et al. 2002) and it is likely that productivity in the deepwater odontaspidids is similarly restricted.

Fergusson et al. (in press) report that nowhere in its wide but scattered distribution is *O. ferox* abundant. They report maturity in females at ~3000–3500mm TL (73–85% TL_{max}) and in males ~2000–2500mm TL (58–73% TL_{max}), and suggest a size at birth of ~1000mm TL. There are no particular details available concerning the biology of *O. noronhai*, although Compagno (2001) suggests maturity in females at ~3200–3250mm TL.

Family Pseudocarchariidae. Crocodile Sharks.

Despite its widespread distribution, locally common occurrence in some regions and its regular bycatch in pelagic longline fisheries, the biology of the crocodile shark *Pseudocarcharias kamoharai* has not been examined in detail. Most information has come from the incidental capture of gravid females. As with other lamnoid sharks, it is oophagous and in the case of the crocodile shark, two embryos develop in each uterus by feeding on ova in uterine egg capsules (litter size is thus four) (Fujita 1981, Compagno 2001). Maturity has been reported at 740mm TL in males and 890mm TL in females, with a maximum size of 1100mm TL (Compagno 2001).

Family Mitsukurinidae. Goblin Sharks.

The biology of the rare goblin shark *Mitsukurina owstoni* remains very poorly-known due to its infrequent capture and observation (Duffy 1997). Although widely-distributed, a fair proportion of records for the species come from Japan (Duffy 1997). However, an exceptional capture of >100 individuals occurred in Taiwan over a two week period in 2003 (Duffy et al. 2004).

The species' mode of reproduction is unknown as gravid females have never been observed by scientists, but as with other lamnoid sharks, the species is probably oophagous with small litter sizes (Compagno 2001, Duffy et al. 2004). The goblin shark is one of the largest species of elasmobranch, Parsons et al. (2002) reporting that it grows to 5400–6170mm TL. Mature males of 2640, 3200 and 3840mm TL and a mature female of 3350mm TL have been reported (Compagno 2001).

Family Alopiidae. Thresher Sharks.

Like other lamnoids, thresher sharks are oophagous (Gilmore 1993, Musick and Ellis 2005). The reproductive biology of the bigeye thresher *Alopias superciliosus* is reasonably well documented (see review in Gilmore 1993). A litter size of two (one embryo per uteri) has been confirmed for the species (Gubanov 1979, Gilmore 1983, 1993, Moreno and Morón 1992, Chen et al. 1997), although litter sizes of 3 or 4 also occur less regularly (Compagno 2001).

Chen et al. (1997) found gravid females throughout the year off Taiwan in the Northwest Pacific, with no defined mating or pupping season. Similarly, Moreno and Morón (1992) could not find evidence of a well defined breeding season in the Eastern Central Atlantic, although they suggested a possible preferential pupping season in autumn-winter. Without defined reproductive seasonality it is difficult to determine gestation period, although it has been estimated as 12 months in the bigeye thresher (Holden 1974). Diel vertical migration patterns in *A. superciliosus* (Nakano et al. 2003, Weng and Block 2004) are discussed later in this Section (see page 104).

Estimates of maturity and size at birth vary regionally and these are summarized in Gilmore (1993) and Chen et al. (1997). Size at maturity equates to 76–79%TL_{max} in females and to 67–79 TL_{max} in males, and size at birth ranges from 600–1400mm TL (Chen et al. 1997). Verified age estimates for *A. superciliosus* from Taiwan gives longevities of 20 years and 19 years for females and males, respectively (Liu et al. 1998) (Table 2.10).

Table 2.10. Age and growth parameters for *Alopias superciliosus* from Taiwan, Northwest Pacific (Liu et al. 1998). von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years).

	VBGM parameters				
Sex	**L_∞**	**k**	**t_0**	**t_{max}**	**A_{max}**
♀	2246	0.092	-4.21	20	12.3-13.4
♂	2188	0.088	-4.24	19	9-10

Family Cetorhinidae. Basking Sharks.

The basking shark is an apparently social, highly migratory species occurring in coastal, pelagic and deepwater habitats (Compagno 2001, Francis and Duffy 2002). Basking sharks generally appear in inshore waters in spring and depart in autumn and a lack of observations in winter led to the belief that they migrated to deep water to undertake a winter hibernation. However, basking sharks tracked over extended periods (up to 6.5 months) have shown that they do not hiberate, but undertake horizontal and vertical (>750m) movements to exploit prey concentrations (Sims et al. 2003). Furthermore, around New Zealand, basking sharks have been demonstrated to overwinter, probably on or near the bottom, in deep slope waters (to 904m) (Francis and Duffy 2002) and they are thus included here due to their occurrence in these deep habitats.

The biology of the species is very poorly-known with few gravid females ever observed, and Compagno (2001) suggests that these may be separated either geographically or bathymetrically from the more regularly observed individuals. It is probable that basking sharks are oophagous, as with other lamnoids (Compagno 2001). Sund (1943) reported a litter size of six from a single shark. Exact size at maturity is unknown, but females >8000mm TL are mature, while maturity in males occur somewhere between ~4000 and 7000mm TL (Compagno 2001). Size at birth may be ~1500–1700mm TL (Compagno 2001).

Order Carcharhiniformes. Ground Sharks.

Family Scyliorhinidae. Catsharks.

Despite the diversity of the family Scyliorhinidae (119 deepwater species) there is very little information available on their general biology. Data on the large, solely deepsea genus *Apristurus* (47 species) is particularly lacking, and there is very little information on deep water species of the genera *Asymbolus, Cephaloscyllium* or *Pentanchus*.

Of the species of catsharks for which reproductive mode has been confirmed, the majority are oviparous. It should be noted that the reproductive mode of several catsharks remains unknown, for example Ebert et al. (2006) notes that while oviparity has been shown to occur in 13 *Galeus* species, and viviparity in a single species, there are three species in the genera for which the reproductive mode is unknown. Viviparity (yolk-sac) is known only from a small number of species, and has been confirmed from the broadhead catshark *Bythaelurus clevai*, the mud catshark *B. lutarius*, the lollipop catshark *Cephalurus cephalus* and the African sawtail catshark *Galeus polli* (Springer 1979, Séret 1987, Balart et al. 2000, Compagno et al. 2005, Ebert et al. 2006, Francis 2006). Despite earlier reports of viviparity in Dawson's catshark *B. dawsoni* and the roughtail catshark *Galeus arae*, these species have since been shown to be oviparous (Konstantinou et al. 2000, Francis 2006). Furthermore, a report of viviparity in the Saldanha catshark *Apristurus saldanha* by Myagkov and Kondyurin (1978) is in error, and that manuscript is referrable to *G. polli* (Ebert et al. 2006). Reproductive parameters for the oviparous scyliorhinid sharks are summarized in Tables 2.11.

Ebert et al. (2006) reported on the reproductive biology of the viviparous *G. polli* from off southern Africa. Maturity (L_{50}) in females occurred at 296mm TL (69%TL_{max}) and in males at 303mm TL (84%TL_{max}); litter size was 5-13, increasing with maternal length; and a size at birth of ~120-150mm TL (Ebert et al. 2006). Restricted seasonal sampling limited assessment of the species' reproductive cycle (Ebert et al. 2006). Of 11 gravid female *C. cephalus* collected from Pacific México, Balart et al. (2000) observed litter sizes of two in eight individuals and a litter of one embryo in the remaining three. These embryos are retained in very thin-walled egg capsules until birth. Compagno et al. (2005) reports a size at birth of ~100mm TL, maturity at ~190mm TL and the maximum size of the species, as specified by

Balart et al. (2000) is 295mm TL for females and 298mm TL for males. Both *Bythaelurus clevai* and *B. lutarius* produce small litters of two (one embryo per uterus) (Compagno et al. 2005).

Both single and multiple oviparity can occur amongst the *Galeus* species, but only single oviparity is known in *Apristurus*, *Parmaturus* and *Scyliorhinus* (Cross 1988, Ebert et al. 2006). Of the multiple oviparous sawtail sharks, *G. melastomus* can possess up to 13 egg cases in the uteri at one time, while *G. atlanticus* has been observed to carry up to nine egg cases in the uteri at one time (Muñoz-Chápuli and Perez Ortega 1985, Iglésias et al. 2002). For the oviparous *Bythaelurus*, only single oviparity has been observed, while *Halaelurus* are multiple oviparous (Compagno et al. 2005, Francis 2006).

For oviparous species, estimates of fecundity are difficult as egg-laying periods and rates are mostly unknown. Ovarian fecundity may provide a proxy, but as noted previously, the relationship between the number of follicles and actual reproductive output is not clear. Castro et al. (1988) determined egg-laying rates in *Scyliorhinus retifer* held in captivity with pairs of egg cases laid at intervals of 14.1-16.7 days (average ~15.3 days). Taking this average and assuming continuous, year-round egg-laying activity, this would result in an annual production of 46 egg cases. This is a relatively high reproductive output for a chondrichthyan. Richardson et al. (2000) suggested that fecundity is high in *H. regani*, based on the proportion of mature females carrying egg cases and a continuous reproductive cycle. Fecundity in other scyliorhinids may however, be low, particularly the viviparous and multiple oviparous species, where embryos or egg cases are retained for extended periods in the uterus.

Catsharks generally reproduce throughout the year, and while most species lack significant patterns of reproductive seasonality, there are often seasonal peaks in egg production. (Ebert et al. 2006). Richardson et al. (2000) suggested continuous year-round reproduction in *Holohalaelurus regani* with no significant difference observed in the proportion of mature females carrying egg cases between seasons, similar to the situation observed in *Bythaelurus dawsoni* (Francis 2006). Cross (1988) suggested that *A. brunneus* and *P. xaniurus* may be reproductively active throughout the year, although in *A. brunneus* more females carried egg cases in December to May than June to November. Both *G. eastmani* and *G. nipponensis* from Suruga Bay, Japan reproduced throughout the year, but with *G. nipponensis* showing a higher incidence of carrying egg cases in December and January (Horie and Tanaka 2000). Off southern Portugal, *G. melastomus* is reproductively active year-round but with bimodal peaks, in summer and winter (Costa et al. 2005).

Estimates of maturity for *G. melastomus* have shown a high degree of consistency in the western and central Mediterranean (Tursi et al. 1993, Ungaro et al. 1997, Rey et al. 2004), but maturity appears to occur at a considerably larger size in the NE Atlantic, demonstrated by a study off Portugal (Costa et al. 2005). It should be noted that Table 2.11 provides a summary of only a handful of maturity estimations for *G. melastomus* from the Mediterranean and these are reviewed more comprehensively in Table 4 of Costa et al. (2005). Castro et al. (1988) suggested that there may be geographical variation in size at maturity for the chain dogfish *Scyliorhinus retifer*, and this was indeed supported by Sminkey and Tabit (1992) who documented smaller maturity in the northern part of the species' distribution.

There is a complete lack of age and growth estimates for deepwater scyliorhinids, and the vertebrae of many species may be to poorly calcified to yield age estimates (S. Irvine pers. comm.). Tursi et al. (1993) suggested, without quantitative data, that maturity is probably reached in *G. melastomus* at around 3–4 years, and that maximum size corresponds to at least 7–8 years. Attempts to age *Apristurus brunneus, A. kampae* and *Parmaturus xaniurus* by researchers at the Pacific Shark Research Center at Moss Landing Marine Laboratories have proved unsuccessful (B. Flammang, pers. comm.).

Table 2.11. Reproductive biology of deepwater oviparous scyliorhinid sharks.

Species	**Location**	**TL_{max} (mm)**	**Maturity (mm TL)**	**Maturity $\%TL_{max}$**	**Ovarian fecundity**	**Size at hatching (mm TL)**	**Reference**
Apristurus brunneus	California, Eastern Central Pacific	♀ 556 ♂ 625	425-475 450-500	76-85 72-80	29	--	Cross (1988)
	Western US, Eastern Central Pacific	♀ 660 ♂ 693	501 (L_{50}) 514 (L_{50})	76 74	1-16	--	Flammang et al. (in press)
Apristurus kampae	Western US, Eastern Central Pacific	♀ 590 ♂ 647	490 (L_{50}) 485 (L_{50})	83 75	4-8	--	Flammang et al. (in press)
Apristurus melanoasper	North Atlantic	♀ 732 ♂ 761	550-590 610-640	75-81 80-84	--	--	Iglésias et al. (2004)
Apristurus microps	Southern Africa, SE Atlantic	♀ 567 ♂ 610	483 (L_{50}) 508 (L_{50})	85 83	7-8	--	Ebert et al. (2006)
Apristurus saldanha	Southern Africa, SE Atlantic	♀ 773 ♂ 885	695 (L_{50}) 692 (L_{50})	90 78	16-20	--	Ebert et al. (2006)
Apristurus sp. [Compagno & Ebert]	Southern Africa, SE Atlantic	♀ 625 ♂ 685	475 (L_{50}) 479 (L_{50})	76 70	3-5	--	Ebert et al. (2006)
Bythaelurus dawsoni	New Zealand, SW Pacific	♀ 412 ♂ 418	~330-360 (L_{50}) ~340-350 (L_{50})	80-87 81-84	5-9	--	Francis (2006)
Galeus antillensis	Puerto Rico, Western Central Atlantic	♀ 460* ♂ --	<335	73	4-8	--	Parsons (1986); *Compagno et al. (2005)
	Caribbean, Western Central Atlantic	♀ 458 ♂ 362	339 327	74 90	--	--	Konstantinou et al. (2000)
Galeus arae	Western Central Atlantic	♀ 327 ♂ 325	272 279	83 86	--	--	Konstantinou et al. (2000)
Galeus cadenati	Caribbean, Western Central Atlantic	♀ 335 ♂ 270	289 >270	86 --	--	--	Konstantinou et al. (2000)
Galeus melastomus	Ionian Sea, Central Mediterranean	♀ 550 ♂ 500	490 (L_{50}) 450 (L_{50})	89 90	8-23 (~12)	70	Tursi et al. (1993)
	Adriatic Sea, Central Mediterranean	♀ -- ♂ --	508 (L_{50}) 448 (L_{50})	--	--	--	Ungaro et al. (1997)
	Alboran Sea, Western Mediterranean	♀ 620 ♂ 630	488 443	79 70	--	<100	Rey et al. (2004)

Table 2.11 (continued).

Species	Location	TL_{max} (mm)	Maturity (mm TL)	Maturity $\%TL_{max}$	Ovarian fecundity	Size at hatching (mm TL)	Reference
Galeus melastomus (continued)	Portugal, NE Atlantic	♀ 670 ♂ 643	>560 >490	84 76	--	<94	Costa et al. (2005)
Galeus murinus	NE Atlantic	♀ 530 ♂ 630	<460 <479	87 76	--	--	Muñoz-Chápuli & Perez Ortega (1985); Iglésias et al. (2002); Compagno et al. (2005)
Galeus piperatus	Gulf of California, Eastern Central Pacific	♀ 360 ♂ --	~180	50	2->10	<70	Mathews (1975)
Holohalaelurus regani	South Africa, SE Atlantic	♀ 520 ♂ 685	400-450 450-500	77-87 66-73	--	<110	Richardson et al. (2000)
Parmaturus xaniurus	California, Eastern Central Pacific	♀ 574 ♂ 516	425-475 375-425	74-83 73-82	23	--	Cross (1988)
	Western US, Eastern Central Pacific	♀ 579 ♂ 512	501 (L_{50}) 444 (L_{50})	87 87	1-11	--	Flammang et al. (in press)
Scyliorhinus capensis	Southern Africa, SE Atlantic	♀ 880 ♂ 1020	756 (L_{50}) 829 (L_{50})	86 81	9-12	--	Ebert et al. (2006)
Scyliorhinus retifer	US east coast, NW and Western Central Atlantic	♀ 590* ♂ 590*	~520 ~500	88 85	--	100-110 (106) (in captivity)	Castro et al. (1988); *Compagno et al. (2005)
	Mid-Atlantic Bight, NW Atlantic	♀ 437 ♂ 464	<380 <394	87 85	6-20	--	Sminkey & Tabit (1992)

Family Proscylliidae. Finback Catsharks.

The biology of the finback catsharks is very poorly-known. The deepwater species are yolk-sac viviparous with small litter sizes of 1–2 pups (Nair and Appukuttan 1974, Compagno in prep. b). These sharks are notable for the very large size of pups relative to maternal size and the small difference between size at birth, size at maturity and maximum size (Compagno in prep. b). In the pygmy ribbontail shark *Eridacnis radcliffei*, size at birth is ~110mm TL, female maturity at ~150–160mm TL and female maximum size is 240mm TL (Nair and Appukuttan 1974, Compagno in prep. b). Hence, size at birth represents $46\%TL_{max}$, and female size at maturity $63–67\%TL_{max}$. The small size of these species (*E. barbouri* grows to 340mm TL and *E. sinuans* to 370mm TL) together with apparent fast maturity after birth, suggests that finback catsharks may be fast growing. The large relative size at birth though suggests a long gestation period, and reproductive output is probably low in this family.

The undescribed Andaman Sea endemic *Proscyllium* sp. A is known only from five specimens (Compagno et al. 2005).

Family Pseudotriakidae. False Catsharks.

The false catsharks are the only carcharhinoid sharks, and indeed the only non-lamnoid sharks, to display oophagy (Yano 1992, 1993, Musick and Ellis 2005). Consequently, fecundity is low. Yano (1993) found the slender smoothhound *Gollum attenuatus* to generally possess two embryos, one in each uterus, although a small number of specimens contained only a single embryo (1.8% of gravid females examined) and two females contained three embryos (in both cases, one of these had failed to develop). In the false catshark *Pseudotriakis microdon*, only litter sizes of two have been observed (Saemundsson 1922, Taniuchi et al. 1984, Yano 1992, Stewart 2000). The gestation period of both species is unknown, but for *P. microdon* at least, it is likely extended, presumably >1 year and possibly two or three years (Yano unpublished data in Kyne et al. 2004). Both sexes of *G. attenuatus* mature at ~700mm TL, representing 64%TL_{max}, while maturity in *P. microdon* is at a very large size, from 2560mm TL in females, representing 86%TL_{max} (Forster et al. 1970, Kyne et al. 2005).

Family Triakidae. Houndsharks.

The biology of the deepwater houndsharks is poorly-known. There is no information on the darksnout sicklefin houndshark *Hemitriakis abdita* beyond that in its original description (Compagno and Stevens 1993). Triakids are mostly placental viviparous (Musick and Ellis 2005) and litter sizes of 4-5 have been reported for both the longnose houndshark *Iago garricki* (Last and Stevens 1994) and the bigeye houndshark *I. omanensis* (Fishelson and Baranes 1998). While there is a considerable amount of information on the biology of the shelf subspecies of the dusky smoothhound *Mustelus canis canis*, there is little specific to the island subspecies *M. c. insularis* which occurs on the outer shelf and slope. The shelf subspecies has been demonstrated to bear litters of 3–18 pups, reproduce annually with a gestation period of 11–12 months, reach maturity at 4–7 years for females and 2–3 years for males, and live to a maximum of 10 years for females and 6 years for males (Conrath and Musick 2002, Conrath et al. 2002). How these biological parameters relate to the island subspecies is unknown.

Family Carcharhinidae. Requiem Sharks.

Due to its scattered distribution and deep benthic habitat, the only ‘deepwater’ requiem shark, the bignose shark *Carcharhinus altimus*, is poorly-known relative to many other species in the family. It is a diurnal vertical migrator (Anderson and Stevens 1996) and this is discussed later in this Section (see page 104). Carcharhinids are placental viviparous, with the exception of the yolk-sac viviparous tiger shark *Galeocerdo cuvier* (Musick and Ellis 2005). Litter size in *C. altimus* is reported at 3–15 and although the gestation period of the species is unknown, it is usually 9–12 months in requiem sharks, and in this family the reproductive cycle may be either annual or biennial (Stevens and McLoughlin 1991, Compagno et al. 2005). This is a large shark, possibly reaching 3000mm TL with size at birth from 600mm TL, female maturity from 2050mm TL and male maturity from 2040mm TL (Stevens and McLoughlin 1991, Crow et al. 1996, Compagno et al. 2005).

PART 2. BATOIDS

Order Rajiformes. Batoids.

Family Rhinobatidae. Guitarfishes.

The sole deepwater rhinobatid, the stripenose guitarfish *Rhinobatos variegatus* is known only from the holotype collected at 366m depth in the Gulf of Mannar off India. Guitarfishes are yolk-sac viviparous species producing litters of 1–18 pups annually (Kyne and Bennett 2002), but there is no specific information available on *R. variegatus* other than that given in the original description (Nair and Lal Mohan 1973).

Family Narcinidae. Numbfishes.

Aspects of the general biology of the numbfishes are poorly-known. The family, like other electric rays is yolk-sac viviparous, but details on the reproductive cycle, fecundity and maturity, as well as age and growth information is generally lacking. A litter size of 1–2 with a size at birth of >96mm TL has been observed in the recently described Brazilian blind torpedo *Benthobatis kreffti* (Rincon et al. 2001) and a litter size of two in the western numbfish *Narcine lasti* with size at birth probably close to 80mm TL (Carvalho and Séret 2002). The Taiwanese blind numbfish *B. yangi* is known only from a limited number of specimens detailed in its original description while the dark blindray *B. moresbyi* is known only from five specimens (Carvalho et al. 2003). There remains numerous undescribed species within the family, including the deepwater *Narcine* sp. C [Last & Stevens, 1994] from Australia.

Family Narkidae. Sleeper Rays.

There is minimal information on the biology of the sleeper rays. The biology of the rare Natal sleeper ray *Heteronarce garmani* is 'virtually unknown' (Compagno et al. 1989). The two endemic New Zealand sleeper rays of the genus *Typhlonarke* are also rare and poorly-known, although they reportedly have up to 11 pups per litter with a size at birth of 90–100mm TL (Duffy 2003a).

Family Torpedinidae. Torpedo Rays.

As with other electric ray families, there is relatively little information on the biology of the torpedo rays. The biology of some shallower water species (i.e. *Torpedo californica, T. marmorata* and *T. torpedo*) is reasonably well known, but apart from some minimal data on the New Zealand torpedo ray *T. fairchildi* and the great torpedo *T. nobiliana*, there is little information on the deeper water torpedos. Most are poorly-known and one, the smalldisk torpedo *T. microdiscus*, is known only from two specimens collected from submarine ridges in the Southeast Pacific. A litter size of eight has been reported for *T. fairchildi* (see Duffy 2003b), while Trunov and Kukuev (2005) noted 35 large follicles in the ovaries of *T. nobiliana* from the Azores and Capapé (1974) estimated a gestation period of ~12 months for that species from Tunisia. Abdel-Aziz (1994) noted that ovarian fecundity in the shallower water *T. torpedo* and *T. marmorata* is higher than uterine fecundity, and as such, actual fecundity in *T. nobiliana* is likely lower than the ovarian fecundity of 35 reported by Trunov and Kukuev (2005). Reported litter sizes for shallower water species are generally small, for example Abdel-Aziz (1994) reports 2–12 (average 7.2) for *T. torpedo* and 3–16 (9.3) for *T. marmorata* from Egypt, Capapé (1974) 6–10 (8) for *T. marmorata* from Tunisia, and Neer and Cailliet (2001) 17 for a single *T. californica*. Gestation is variable between shallower water species, Abdel-Aziz (1994) noting an annual reproductive cycle with a gestation period of 5–6 months in *T. torpedo* and a probable biennial cycle with a gestation period of 10–12 months for *T. marmorata*. Ageing studies of the deepwater torpedos are lacking, but *T.*

californica was aged to 16 years by Neer and Cailliet (2001) with age at maturity estimated at nine years for females and six years for males. These biological parameters of the shallow water species suggest that productivity in the deeper water torpedos is low.

Family Arhynchobatidae. Softnose Skates.

Despite the high diversity of the softnose skates, there is very little detailed information on their biology. The softnose skates include some of the deepest occurring chondrichthyans, several *Bathyraja* spp reaching depths of over 2900m. The vast majority of species in the family are poorly-known due to scattered distributions, deep occurrence, taxonomic uncertainty and limited material, resulting in the biology of many species being virtually unknown. The systematics of the Indo-West Pacific fauna still requires considerable attention and 24% of the deepwater species in the family remain undescribed. Several species are known only from a handful of specimens, such as the slimtail skate *Bathyraja longicauda* and the Peruvian skate *B. peruana* of the Southeast Pacific. Others, such as the Aguja skate *B. aguja*, also from the Southeast Pacific, are known only from a single specimen. Published literature is often concerned with biogeography, systematics and taxonomy or reports on incidental captures. For example, Stehmann and Merrett (2001) reported on the first observations of embryos and egg cases of the deep slope Richardson's skate *B. richardsoni* and the pallid skate *B. pallida*, while Orlov and Biryukov (2005) provided details of two female Okhotsk skate *B. violacea* containing egg cases ready for deposition. Such accounts are slowly advancing our knowledge of this speciose group, and there is a gathering volume of information on the arhynchobatid skates of some regions as projects proceed in the North Pacific (Japanese, Russian and US research institutes) and in the Southwest Atlantic (collaborative projects between Argentina and Germany, and research by the Falkland Islands Fishery Department and other agencies). It is from these two regions that the more detailed biological information on a handful of species is available.

Reproductive and age and growth parameters for softnose skates are summarized in Tables 2.12 and 2.13, respectively.

Ebert (2005) provided a detailed account of the reproductive biology of the seven *Bathyraja* and one *Rhinoraja* skates from the eastern Bering Sea in the North Pacific. For all species, size at maturity (L_{50}) was >80%TL_{max}, with the exception of male *B. parmifera* (79%TL_{max}). Ebert (2005) noted that for these skates there is an extended juvenile stage, a brief adolescent stage with little growth after maturity. In *B. aleutica*, Ebert (2005) recognised that ovarian fecundity increased in females up to 1450mm TL, only to decline in the larger animals. In addition, he observed that some of the largest *B. aleutica*, *B. lindbergi* and *B. minispinosa* were reproductively inactive with atrophied ovaries, suggesting either a period of reproductive inactivity or senescence, whereby the older females have surpassed their reproductive life. This would further reduce the limited reproductive output of these skate species (see further discussion on reproductive output under the family Rajidae).

Many skate species have been shown to exhibit year-round egg-laying, although shallow inshore species may have more defined laying seasons (Ruocco et al. 2006). Henderson et al. (2004) observed year-round egg-laying in *B. albomaculata* from the Falkland/Malvinas Islands, although with peaks in deposition activity in autumn and winter. *Bathyraja albomaculata* from off continental South America (Uruguay, Argentina and southwest Chile) were observed carrying egg cases in April, September and October, also suggesting year-round laying (Ruocco et al. 2006). While ovarian fecundities are available for several species (see Table 2.12) there are no estimates of annual or lifetime fecundity for the softnose skates.

Age and growth data for the arhynchobatid skates is limited to a handful of species, mostly unpublished (Table 2.13). A maximum age for the group of 29 years has been estimated for female *B. griseocauda* (P. Brickle, pers. comm.). Age at maturity appears to be late, ≥10 years for females of all species aged to date. Further age and growth studies are currently underway for the Alaskan skate fauna (*B. aleutica*, *B. interrupta*, *B. minispinosa* and *B. taranetzi*) by researchers from the Pacific Shark Research Center at Moss Landing Marine Laboratories (D. Ebert, pers. comm.).

Table 2.12. Reproductive biology of the deepwater arhynchobatid skates.

Species	**Location**	**TL$_{max}$ (mm)**	**Maturity (mm TL)**	**Maturity %TL$_{max}$**	**Ovarian fecundity**	**Size at hatching (mm TL)^1**	**Reference**
Bathyraja abyssicola	North Pacific	♀ 1570 ♂ 1350	1450 1100	92 81	--	--	Matta et al. (2006) and references within
Bathyraja albomaculata	Falkland/ Malvinas Is., SW Atlantic	♀ --* ♂ --	-- --	--	4-32 (14)	♀ 98mm DW ♂ 105mm DW	Henderson et al. (2004)
	Uruguay, Argentina, Chile, SW Atlantic	♀ 762 ♂ 732	653 (L$_{50}$) 628 (L$_{50}$)	86 86	right (4.3) left (6.4)	--	Ruocco et al. (2006)
Bathyraja aleutica	Bering Sea, North Pacific	♀ 1540 ♂ 1330	1330 (L$_{50}$) 1210 (L$_{50}$)	86 91	7-20	<241	Ebert (2005)
Bathyraja interrupta	Bering Sea, North Pacific	♀ 820 ♂ 825	700 (L$_{50}$) 694 (L$_{50}$)	85 84	5-11	<162	Ebert (2005)
Bathyraja lindbergi	Bering Sea, North Pacific	♀ 965 ♂ 964	846 (L$_{50}$) 784 (L$_{50}$)	88 81	5-13	<170	Ebert (2005)
Bathyraja maculata	Bering Sea, North Pacific	♀ 1084 ♂ 1083	990 (L$_{50}$) 937 (L$_{50}$)	91 87	8-16	<191	Ebert (2005)
Bathyraja minispinosa	Bering Sea, North Pacific	♀ 795 ♂ 801	661 (L$_{50}$) 695 (L$_{50}$)	83 87	4-12	<151	Ebert (2005)
Bathyraja parmifera	Bering Sea, North Pacific	♀ 1095 ♂ 1110	920 (L$_{50}$) 879 (L$_{50}$)	84 79	6-16	<220	Ebert (2005)
	Bering Sea, North Pacific	♀ 1190 ♂ 1180	933 (L$_{50}$) 918 (L$_{50}$)	78 78	21-37	210-220	Matta (2006)
Bathyraja trachura	Bering Sea, North Pacific	♀ 885 ♂ 825	735 (L$_{50}$) 755 (L$_{50}$)	83 92	3-12	<196	Ebert (2005)
Rhinoraja taranetzi	Bering Sea, North Pacific	♀ 770 ♂ 670	630 (L$_{50}$) 560 (L$_{50}$)	82 84	4-13	<185	Ebert (2005)

---

[1] Unless specified as disc width (DW). *Maturity estimates and maximum sizes for *B. albomaculata* from Henderson et al. (2004) are not included here, due to the most probable inclusion of other misidentified species representing their largest samples. These errors are detailed in Henderson et al. (2004).

Table 2.13. Age and growth of arhynchobatid skates. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL or DW), k ($year^{-1}$), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years).

Species	Location	VBGM parameters			t_{max}	A_{mat}	Reference
		L_∞	k	t_0			
Bathyraja albomaculata	Falkland/Malvinas Is., SW Atlantic	♀ 649mm DW	0.09	-1.94	17	10	Henderson et al. (2004)
		♂ 706mm DW	0.07	-2.39	17	11	
	Falkland/Malvinas Is., SW Atlantic	♀ 1112mm TL	0.048	-3.9	--	14.4	M. Gallagher (pers. comm.)
		♂ 953mm TL	0.060	-3.8	--	12.5	
Bathyraja brachyurops	Falkland/Malvinas Is., SW Atlantic	♀ 1204mm TL	0.07	-1.95	16	11.12	P. Brickle (pers. comm.)
		♂ 1311mm TL	0.05	-2.55	18	11.55	
	Falkland/Malvinas Is., SW Atlantic	♀ 1301mm TL	0.060	-2.2	--	11.7	M. Gallagher (pers. comm.)
		♂ 1296mm TL	0.058	-2.1	--	10.1	
Bathyraja griseocauda	Falkland/Malvinas Is., SW Atlantic	♀ 3652mm TL*	0.02	-3.46	29	18.10	P. Brickle (pers. comm.)
		♂ 3589mm TL*	0.02	-3.04	20	15.26	
	Falkland/Malvinas Is., SW Atlantic	♀ 3029mm TL	0.022	-2.6	--	23.7	M. Gallagher (pers. comm.)
		♂ 2197mm TL	0.034	-2.2	--	18.3	
Bathyraja parmifera	Eastern Bering Sea, North Pacific	♀ 1446mm TL	0.09	-1.75	17	10	Matta & Gunderson (in press)
		♂ 1263mm TL	0.12	-1.39	15	9	
Bathyraja scaphiops	Falkland/Malvinas Is., SW Atlantic	♀ 1196mm TL	0.063	-1.9	--	13.5	M. Gallagher (pers. comm.)
		♂ 1296mm TL	0.058	-2.1	--	9.0	

*The estimates of L_∞ for *B. griseocauda* are inflated (max size of species ~2000mm TL).

Family Rajidae. Hardnose Skates.

There is considerably more information available in the biology of the hardnose skates than most other batoid families, particularly for shelf species. Overall though, the knowledge of this family, the most speciose of all the deepwater chondrichthyan families, remains poor. As with the arhynchobatids, the systematics of the family are not yet resolved, and there remains many undescribed species (19% of deepwater species). The family contains the deepest recorded chondrichthyan fish, Bigelow's skate *Rajella bigelowi* which has been recorded to 4156m depth (Stehmann 1990) (*Amblyraja* are also amongst the deepest, reaching ~2600m depth). The majority of available information on hardnose skates is derived from the North Atlantic and North Pacific, but there is also a growing body of work from southern regions including New Zealand, South America and the Antarctic.

Reproductive and age and growth parameters for hardnose skates are summarized in Tables 2.14 and 2.15, respectively.

Like the softnose skates, reproductive activity appears to occur year-round and this has been demonstrated for such species as the smooth skate *Malacoraja senta* and the thorny skate *Amblyraja radiata* (Sulikowski et al. 2005b, 2007). Again, as with other oviparous families, fecundity estimates are difficult and there is little ovarian fecundity information for the deepwater hardnose skates. Two species of rajid are known to carry multiple embryos per egg case, the mottled skate *Raja pulchra*, an inshore coastal species from the Northwest Pacific, and the big skate *R. binoculata* from the eastern North Pacific (Ishiyama 1958, Hitz 1964, Ebert and Davis 2007). These are the only skates for which this has been observed. The big skate can carry 2–7 embryos per egg case, with an average of 3–4 (Hitz 1964).

There have been several ageing studies of rajid species, and while some are unvalidated and others preliminary, late maturity has again been demonstrated for the skates. Du Buit (1977) estimated a maximum age of 50 years for *Dipturus batis* while longevity of at least 20 years has been confirmed for *A. radiata* from skates tagged off Newfoundland (Templeman 1984). Ageing and growth estimates follow the general trend that larger species are slower growing and longer-lived than the smaller, faster-growing species (Sulikowski et al. 2005b).

Ebert (2005) estimated the number of reproductive years for several skate species by considering age at first maturity and maximum observed age. Estimates for deepwater rajid skates ranged from 13 reproductive years for *D. batis* and *D. innominatus* (from Du Buit 1977 and Francis et al. 2001, respectively), through 9 years for *Leucoraja wallacei* (from Walmsley-Hart et al. 1999), 6 years for *L. naevus* and *D. pullopunctata* (from Du Buit 1977 and Walmsley-Hart et al. 1999, respectively), to 4 years for *Raja rhina* and *D. nasutus* (from Zeiner and Wolf 1993 and Francis et al. 2001, respectively) and 1–3 years for *R. binoculata* (from Zeiner and Wolf 1993) (Ebert 2005). Considering some more recent publications (see Table 2.15) similar estimations would give 3–6 reproductive years for female *Amblyraja georgiana* (from Francis and Ó Maolagáin 2005), 7 years for *D. chilensis* (from Licandeo et al. 2006) and 4 years for *L. naevus* (from Gallagher et al. 2004). The age estimations of McFarlane and King (2006) give considerably more reproductive years for both *R. binoculata* (17 years) and *R. rhina* (19 years) than those calculated from Zeiner and Wolf (1993).

Estimates of annual and lifetime fecundity of rajid skates are highly variable between species. Annual fecundity has been estimated as 140 egg cases for *R. clavata* (shelf species; Holden 1975), 90 for *R. brachyura* (shelf species; Holden et al. 1971) and *L. naevus* (Du Buit 1976), 60 for *R. montagui* (shelf species; Holden et al. 1971), and 10–20 for *A. radiata* (Berestovskii 1994). Ebert and Davis (2007) calculated that annual fecundity in *R. binoculata* may reach 1260 based on assuming an average of 3.5 embryos per egg case, and egg-laying rates of 360 egg cases per year in captivity (K. Lewand, pers. comm. in Ebert and Davis 2007). Ebert (2005) extrapolated the annual fecundity of *R. clavata* to calculate a lifetime fecundity of ~980 egg cases based on the ageing estimates of Ryland and Ajayi (1984). For *R. montagui*, Ebert (2005) estimated annual production to be <200 egg cases per lifetime. Fecundity in *A. radiata* may be similarly low if one applies the upper annual egg case production of 20 from Berestovskii (1994), together with maximum ages of 16–20 (Templeton 1984, Sulikowski et al. 2005a) and a female age at maturity of 11 years (Sulikowski et al. 2006) which results in an estimated lifetime fecundity of 120–200 egg cases. At the other end of the scale, if the annual fecundity estimate of *R. binoculata* from Ebert and Davis (2007) (1260 young per year) is combined with the ageing results of King and McFarlane (2006) (17 reproductive years), the big skate in the eastern North Pacific may have a lifetime fecundity of 21420 young. This calculation assumes no senescence and continuous breeding throughout the adult life of the species. It should also be noted that temperature affects egg-laying rates (Holden et al. 1971) and will alter estimates of fecundity.

Table 2.14. Reproductive biology of the deepwater rajid skates.

Species	**Location**	L_{max}	**Maturity** (L_{50})	**Maturity** %L_{max}	**Ovarian fecundity**	**Size at hatching (mm TL)**	**Reference**
Amblyraja radiata	Gulf of Maine, NW Atlantic	♀ 1005mm TL ♂ 1003mm TL	875mm TL 865mm TL	87 86	--	--	Sulikowski et al. (2006)
Dipturus chilensis	Chile, SE Pacific	♀ 1170mm TL ♂ 930mm TL	1060mm TL 860mm TL	91 92	--	--	Licandeo et al. (2006)
Dipturus innominatus	New Zealand, SW Pacific	♀ 1380mm PL ♂ 1180mm PL	1122mm PL 933mm PL	81 79	--	--	Francis et al. (2001)
Dipturus laevis	Georges Bank, NW Atlantic	♀ 1335mm TL ♂ 1320mm TL	1163mm TL 1079mm TL	87 82	--	180-190*	Gedamke et al. (2005); *Bigelow & Schroeder (1953)
Dipturus nasutus	New Zealand, SW Pacific	♀ 740mm PL ♂ 680mm PL	591mm PL 517mm PL	80 76	--	--	Francis et al. (2001)
Dipturus polyommata	Queensland, Australia, Western Central Pacific	♀ 366mm TL ♂ 343mm TL	321mm TL 300mm TL	88 88	9-34 (20)	~100-110	Kyne et al. (in prep.)
Dipturus pullopunctata	South Africa, SE Atlantic	♀ 747mm DW ♂ 696mm DW	681-700mm DW 641-660mm DW	91-94 92-95	--	--	Walmsley-Hart et al. (1999)
Leucoraja naevus	Irish Sea, NE Atlantic	♀ 700mm TL ♂ 710mm TL	562mm TL 569mm TL	80 80	--	--	Gallagher et al. (2004)
Leucoraja wallacei	South Africa, SE Atlantic	♀ 571mm DW ♂ 512mm DW	400mm DW 395mm DW	70 77	--	--	Walmsley-Hart et al. (1999)
Raja binoculata	British Columbia, Canada, NE Pacific	♀ 1246mm TL ♂ 1220mm TL	830mm TL 650mm TL	67 53	--	--	McFarlane & King (2006)
Raja rhina	British Columbia, Canada, NE Pacific	♀ 2039mm TL ♂ 1836mm TL	900mm TL 720mm TL	44 39	--	--	McFarlane & King (2006)

Table 2.15. Age and growth of rajid skates. von Bertalanffy growth model (VBGM) parameters: L_∞ (mm TL, PL or DW), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years).

Species	**Location**	**VBGM parameters**			**t_{max}**	**A_{mat}**	**Reference**
		L_∞	**k**	**t_0**			
Amblyraja georgiana	Ross Sea, Antarctica	♀ 692mm PL ♂ 799mm PL	0.402 0.163	-0.73 -2.41	14 12	8-11 6-7	Francis & Ó Maolagáin (2005)[1]
Amblyraja radiata	Gulf of Maine, NW Atlantic	♀ 1270mm TL ♂ 1200mm TL	0.12 0.11	-0.4 -0.37	16 16	11 10.9	Sulikowski et al. (2005a, 2006)
Dipturus batis	Celtic Sea, NE Atlantic	♀+♂ 2537mm TL	0.057	-1.629	50	11	Du Buit (1977)
Dipturus chilensis	Chile, SE Pacific	♀ 1283mm PL ♂ 1078mm PL	0.112 0.134	-0.514 -0.862	21 18	14 11	Licandeo et al. (2006)
Dipturus innominatus	New Zealand, SW Pacific	♀+♂ 1505mm PL	0.095	-1.06	♀ 24 ♂ 15	13.0 8.2	Francis et al. (2001)
Dipturus laevis	Georges Bank, NW Atlantic	♀+♂ 1663mm TL	0.141	-1.291	-- --	♀ 6.5-7.2 ♂ 5.8-6.1	Gedamke et al (2005)
Dipturus nasutus	New Zealand, SW Pacific	♀+♂ 913mm PL	0.16	-1.20	♀ 9 ♂ 7	5.7 4.3	Francis et al. (2001)
Dipturus pullopunctata	South Africa, SE Atlantic	♀ 1327 ♂ 771mm DW	0.05 0.10	-2.20 -2.37	14 18	--	Walmsley-Hart et al. (1999)
Leucoraja naevus	Celtic Sea, NE Atlantic	♀+♂ 916mm TL	0.1085	-0.465	14	9	Du Buit (1977)
	Irish Sea, NE Atlantic	♀ 839mm TL ♂ 746mm TL	0.197 0.294	-0.151 -0.997	8 6	4.25 4.17	Gallagher et al. (2004)
Leucoraja wallacei	South Africa, SE Atlantic	♀ 435mm DW ♂ 405mm DW	0.26 0.27	-0.21 -0.08	15 12	--	Walmsley-Hart et al. (1999)
Raja binoculata	Canada, NE Pacific	♀ 1372mm TL ♂ 1315mm TL	0.06 0.07	-1.80 -2.17	26 23	10 7	McFarlane & King (2006)
	California, Eastern Central Pacific	♀ -- ♂	--	--	12 11	12 10	Zeiner & Wolf (1993)
	Gulf of Alaska, NE Pacific	♀ 2475mm TL ♂ 1533mm TL	0.0796 0.1524	-1.075 -0.632	14 15	--	Gburski et al. (in press)
Raja rhina	Canada, NE Pacific	♀ 2935mm TL ♂ 2330mm TL	0.04 0.05	-1.60 -2.10	26 25	8 6	McFarlane & King (2006)
	California, Eastern Central Pacific	♀ 1067mm TL ♂ 967mm TL	0.16 0.25	-0.3 0.73	13 12	10 10-11	Zeiner & Wolf (1993)
	Gulf of Alaska, NE Pacific	♀ 2341mm TL ♂ 1688mm TL	0.0368 0.0561	-1.993 -1.671	24 25	--	Gburski et al. (in press)

---

[1] Francis and Ó Maolagáin (2005) advise that there ageing estimates are preliminary and should be utilised with caution.

Family Anacanthobatidae. Legskates.

The biology of the entirely deepwater family Anacanthobatidae is very poorly-known. Many species have scattered or narrow distributions and there remains several undescribed species amongst the genus *Anacanthobatis*, some known only from a limited number of specimens. For several species there is little to no information available other than that included in their original descriptions. The family, like the hardnose and softnose skates is oviparous (Last and Compagno 1999), but details of reproductive biology are overall, lacking. Male *Anacanthobatis americanus* mature at ~320mm TL, representing 84%TL_{max}, male *A. borneensis* at ~260mm TL (81%TL_{max}), male *A.* sp. A [Last & Stevens, 1994] at ~430mm TL (80%TL_{max}), male *Cruriraja atlantis* at ~300mm TL (88%TL_{max}), male *C. poeyi* at ~320mm TL (94%TL_{max}) and *C. rugosa* at ~400mm TL (82%TL_{max}) (Bigelow and Schroeder 1953, Last and Stevens 1994, Last and Compagno 1999, McEachran and Carvalho 2002). It should be noted that some of these %TL at maturity estimates may be inaccurate due to a lack of specimens.

Family Plesiobatidae. Giant Stingarees.

The giant stingaree *Plesiobatis daviesi* is very poorly-known with virtually no information available on its biology due to scattered records and general scarcity. There is apparent regional variation in size, with maximum sizes in Australia reported to 2000mm TL, but to 2700mm TL elsewhere (Last and Stevens 1994). Reproductive mode is likely lipid histotroph viviparous given its relationship to the Urolophidae, but specific details are unavailable.

Family Urolophidae. Stingarees.

The urolophids are primarily shallow water coastal and inshore species with the exception of the outer shelf and upper slope wide stingaree *Urolophus expansus* and the deepwater Coral Sea stingaree *U. piperatus*. Stingarees are lipid histotrophs (viviparous) (Musick and Ellis 2005), and studies of coastal species has shown that they have small litter sizes of 1–2 pups, gestation periods of 10–12 months, reach maturity at 3–5 years for females and 2–4 years for males, and have longevities of 10–17 years for females and 8–14 years for males (White et al. 2005). There is no information on the biology of the Coral Sea endemic *U. piperatus*, while there is very limited information on the biology of *U. expansus* (Trinnie 2003, Treloar and Laurenson 2005). Treloar and Laurenson (2005) determined the onset of maturity in males at 360mm TL, or seven years of age (preliminary ageing, not validated) while Trinnie (2003) estimated L_{50} for males of 375mm TL (74%TL_{max}). There were insufficient females in both studies to provide any details of maturity in that sex.

Family Hexatrygonidae. Sixgill Stingrays.

The single species within the family Hexatrygonidae, the sixgill stingray *Hexatrygon bickelli* is poorly-known due to its rarity and scattered records. Reportedly reaches at least 1680mm TL with male maturity estimated at 1100mm TL (Compagno and Last 1999). A specimen from southern Africa possessed three full-term embryos of 480mm TL (Compagno and Last 1999). These are the only biological details available on the sixgill stingray.

Family Dasyatidae. Whiptail Stingrays.

While the shorttail or smooth stingray *Dasyatis brevicaudata* occurs inshore and on the shelf in Australia and New Zealand it is primarily a deepwater species off southern Africa, occurring there on the outermost shelf and upper slope (180–480m). This is a large stingray species, reaching 2100mm DW (Compagno et al. 1989), and although the shorttail stingray is currently under investigation in New Zealand (A. Le Port, pers. comm.), there is presently no information available on its biology, including where it occurs in deep water off Africa.

PART 3. HOLOCEPHALANS

Order Chimaeriformes. Modern Chimaeras.

The life history of the deepwater chimaroid fishes, both of the families Rhinochimaeridae and Chimaeridae is poorly-known. Substantially more information is available on the *Callorhinchus* species of the shelf (family Callorhinchidae) than other genera within this primarily deepwater order (in fact the three *Callorhinchus* spp are the only members of the order not to be considered deepwater, although these three species can all occur marginally on the upper slope).

Family Rhinochimaeridae. Longnose Chimaeras.

Holocephalans are oviparous, but the biology of all rhinochimaerids is virtually unknown, due to their deep occurrence, lack of specimens and historically poor taxonomic resolution. The longnose chimaeras are amongst the deepest recorded chondrichthyans with both the smallspine spookfish *Harriotta haeckeli* and the narrownose chimaera *H. raleighana* occurring to 2600m depth.

Family Chimaeridae. Shortnose Chimaeras.

The biology of the chimaerids is poorly-known with life history information available on only a handful of species. As with the rhinochimaerids, this is due in part to their deep occurrence, a lack of available material in many species and unresolved taxonomic issues. There remains several undescribed species and it is likely several more forms still await discovery. This is highlighted by recent finds of new *Hydrolagus* species from Indonesia (White et al. 2006) and from recent descriptions of endemic Galapagos Island species (Barnett et al. 2006, Quaranta et al. 2006). These latter species were observed and sampled utilising deepsea submersibles on the rocky upper to mid slopes around the islands, a method allowing access to habitats not easily sampled with traditional gear (i.e. trawling) (Quaranta et al. 2006). As such exploratory research ensues around the world more fauna is likely to be discovered. As with these Galapagos species, the distribution of many chimaeras is restricted and endemism appears to be high.

Reproductive parameters for chimaerid fishes are summarized in Table 2.16 and age and growth parameters for the silver chimaera *Chimaera monstrosa* are summarized in Table 2.17.

Chimaeras may be reproductively active throughout the year, without an apparent well-defined egg-laying season (ninespot chimaera *Hydrolagus barbouri*; Kokuho et al. 2003) or with a seasonal peak in activity (spotted ratfish *H. colliei*; see Sathyanesan 1966). In contrast, Malagrino et al. (1981) suggested that *C. monstrosa* has a reproductive season lasting 6–7 months with a peak in activity in the northern winter. In captive *H. colliei* egg cases have been observed to be laid in pairs every 10–14 days over a period of several months (Didier and Rosenberger 2002).

Preliminary age and growth estimates have been conducted for *C. monstrosa* from the Northeast Atlantic (Moura et al. 2004, Calis et al. 2005) with males aged to 30 years and females to 26 years off the west of Ireland. Age estimates off Portugal were considerable lower, up to 17 years for females and 15 years for males (Table 2.17). Variation in these estimates is likely due to the size range of fish sampled, with Calis et al. (2005) sampling individuals to a far greater maximum size than Moura et al. (2004) (i.e. 740mm vs. 571mm PSCFL). Johnson and Horton (1972) attempted several methods to age *H. colliei*, however none proved successful.

Table 2.16. Reproductive biology of the deepwater chimaerid fishes.

Species	**Location**	**L_{max}**	**Size at maturity**	**Maturity %L_{max}**	**Ovarian fecundity**	**Size at hatching**	**Reference**
Chimaera monstrosa	Portugal, NE Atlantic	♀ 571mm PSCFL ♂ 503mm PSCFL	459mm PSCFL 402mm PSCFL	80%PSCFL 80%PSCFL	(6.46)	--	Moura et al. (2004)
Hydrolagus barbouri	Japan, NW Pacific	♀ 680mm PCL ♂ 600mm PCL	550mm PCL 480mm PCL	81%PCL 80%PCL	--	~80mm PCL	Kokuho et al. (2003)
Hydrolagus colliei	Eastern Central and NE Pacific	♀ 360mm BDL ♂ 313mm BDL	240-250mm BDL 185-200mm BDL	67-69%BDL 59-64%BDL	--	140mm TL	Didier & Rosenberger (2002); Dider (2005)

Table 2.17. Age and growth parameters for *Chimaera monstrosa* from the Northeast Atlantic. von Bertalanffy growth model (VBGM) parameters for combined sexes: L_∞ (mm PSCFL), k (year^{-1}), t_0 (years); t_{max} oldest fish (years), A_{mat} age at maturity (years).

Location	**Sex**	**VBGM parameters**			**t_{max}**	**A_{mat}**	**Reference**
		L_∞	**k**	**t_0**			
Portugal	♀ ♂	636 533	0.10 0.14	-1.08 -0.50	17 15	-- --	Moura et al. (2004)
Rockall Trough and Faroe-Shetland Channel	♀ + ♂	789	0.0673	-2.513	♀ 26 ♂ 30	11.2 13.4	Calis et al. (2005)

SEGREGATION, MOVEMENT AND MIGRATION PATTERNS OF DEEPWATER CHONDRICHTHYANS

Deepwater chondrichthyans are often segregated bathymetrically by size, sex or maturity stage. Segregation has been demonstrated by changes in the catch composition with depth, including for such species as the New Zealand lanternshark *Etmopterus baxteri*, the black dogfish *Centroscyllium fabricii*, the great lanternshark *E. princeps*, the roughskin dogfish *Centroscymnus owstoni*, the Portuguese dogfish *C. coelolepis* and the spotted ratfish *Hydrolagus colliei* (Yano and Tanaka 1988, Wetherbee 1996, Jakobsdóttir 2001, Didier and Rosenberger 2002). Several studies have noted a lack of gravid females, and it has been suggested that these may make movements into, or occur in, deeper water (possibly occupying nursery areas) or that they may be bathypelagic (and thus less susceptible to capture in benthic fishing gear) (Yano and Tanaka 1988, Wetherbee 1996, Jakobsdóttir 2001). Nursery areas have not been identified for deepwater shark species.

The short and long-term (including seasonal) movement and migration patterns of deepwater chondrichthyans are poorly-known. The problems associated with tagging animals caught from depth and ensuring their survival once returned to the water, along with logistical constraints, has limited the tagging and tracking of deepwater species. As such tracking studies of 'deepwater' species has largely been restricted to species which also regularly occur in the epipelagic zone, at or close to the surface, such as the basking shark *Cetorhinus maximus* (discussed briefly under that species' account in the main body of this Section), sleeper sharks (*Somniosus microcephalus* and *S. pacificus*) and the bigeye thresher shark (*Alopias superciliosus*). Preliminary tracking of deeper water species has been trialled on the bluntnose sixgill shark *Hexanchus griseus* (Carey and Clark 1995), the needle dogfish *Centrophorus acus* (Yano and Tanaka 1986) and the Portuguese dogfish *Centroscymnus coelolepis* (Bagley et al. 1994).

A number of deepwater squaloid sharks, particularly small pelagic species in the family Dalatiidae, are vertical migrators. These sharks undertake daily migrations from deep water towards to the surface at night, returning to depth during the day. Daily vertical movements may be in excess of 3000m (Compagno in prep. a) and these appear to be linked to the diel migrations of their prey. Hulbert et al. (2006) showed that diel vertical migrations in *S. pacificus* occurred only 25% of the time (i.e. 177 out of 726 days) and as such movement patterns are more complex than daily repeated vertical movements. Sharks were seen to also undertake 'systematic vertical oscillations' ('methodical ascents and descents with little pause in transition') and 'irregular vertical movements' ('small-amplitude movements with random frequency') with the most time spent at depths of 150-450m (Hulbert et al. 2006).

Diel vertical migration also occurs in the bignose shark *Carcharhinus altimus*. Anderson and Stevens (1996) reviewed catch records of the poorly-known species determining that the sharks occupy epibenthic waters at depths of 90–500m during the day, moving either into shallower water or upwards into the epipelagic zone at night. Telemetry studies employing acoustic tags (short-term) and pop-up satellite archival tags (long-term) of another vertical migrator, *A. superciliosus*, has revealed consistent diel movement patterns with the species occurring at depth during the day (generally 200–500m, but with dives to 732m) and moving up in the water column to occupy depths of 10–130m by night (Nakano et al. 2003, Weng and Block 2004).

Bagley et al. (1994) used acoustic transmitters imbedded in baits employed at 1517–1650m to briefly track three *C. coelolepis*, the deepest tracked chondrichthyans. All sharks moved outside the range of the recording equipment (500m) within 6 hours of bait deployment and Bagley et al. (1994) suggested that this indicated no site fidelity. A single *C. acus* acoustically tracked for nearly 21 hours in Japan generally swam parallel to the 500m depth contour, mostly remaining close to the seafloor although making some vertical movements to between

10 and 50m into the water column (Yano and Tanaka 1986). Short-term acoustic tracking of two *H. griseus* (2-4 days) revealed that the sharks generally remained between depths of 600–1100m, swimming back and forth within limited areas, although one took a deep excursion to 1500m (Carey and Clark 1995). These three studies show that results from tracking deepwater sharks are preliminary at best and little remains known about their movement and migration patterns.

PRODUCTIVITY OF DEEPWATER CHONDRICHTHYANS

The chondrichthyans are generally considered to be K-selected because they are relatively slow growing, mature late, and have a low reproductive output (Musick 1999). However, within the group there are a wide range of life histories along a continuum from very low productivity to relatively high productivity. For example, the Australian sharpnose shark *Rhizoprionodon taylori* matures after only one year, lives to seven years, and has litters of up to ten young every year after maturing (Simpfendorfer 1999). This species has a high intrinsic rate of population increase, and the population can double in size in a period of 2.55 years if it is substantially below carrying capacity. In contrast, the spiny dogfish *Squalus acanthias* in the eastern North Pacific matures after 25 years, lives to 70 years, and has litters of approximately 22 young every three years after maturity (Jones and Geen 1977, McFarlane and Beamish 1987, Saunders and McFarlane 1993). As a result, its intrinsic rate of increase is much lower, and it has a population doubling time of around 42 years. Most sharks fit on the continuum between these two species.

Work on the productivity (i.e. their ability to sustain fishing pressure or recover from overfishing) of chondrichthyan species has been largely restricted to those inhabiting the continental shelf or pelagic areas (e.g. Smith et al. 1998, Cortés 2002). Deepwater species have rarely been investigated, largely due to the lack of appropriate life history data. However, over recent years there has been an increase in available data, making a preliminary comparative analysis of productivities of deepwater chondrichthyans possible. Even with this increase in available data, there is still a dearth of information. In this study we were able to gather sufficient data for a simple analysis of productivity for 13 (2.2%) of the 581 identified species of deepwater elasmobranchs. The purpose of this analysis was to determine the productivity of deepwater elasmobranchs using the intrinsic rebound potential method of Au and Smith (1997), and compare these values to those of other chondrichthyans. The application of a constant method facilitated the comparative approach both between deepwater species and between all chondrichthyans.

Methods

The productivity of a species was determined using the intrinsic rebound potential method described by Au and Smith (1997) and Smith et al. (1998). Detailed information on the method, including assumptions, can be found in Smith et al. (1998). Data required to determine the intrinsic rebound potential (r_{2M}) were age at maturity (α), maximum reproductive age (w), annual female litter size (b) (total litter size divided by the sex ratio and the periodicity of breeding), natural mortality (M) and the proportion of the population surviving to maturity (l_α). Data were taken from the primary and unpublished literature, which is presented in the life history family accounts earlier in this Section of the report. Maximum ages were taken as the maximum observed age. Reproductive periodicity was assumed to be 2 years for viviparous species (see discussion earlier in the Introduction to this Section of the report). Natural mortality was estimated using a method described by Jensen (1996) that determined M as a function of the von Bertalanffy parameter k ($M = 1.6k$). When k was not available, the method described by Hoenig (1983) that calculates M from maximum age ($M = 1.44 - 0.982\ln w$) was used. Jensen's method was preferred as most of the data was collected from populations that were being fished and to use the Hoeing method to calculate M it is necessary to assume that there is no fishing. The proportion of individuals reaching maturity was calculated using the function $l_\alpha = e^{-\alpha M}$. Data used in the analysis is given in Table 2.18. Annual egg production of skates is difficult to determine due to a continuous production of eggs over an extended season. This limited the number of species from these groups for which data was available.

The Au and Smith (1997) method assumes that maximum productivity of a population is reached when total mortality is equal to twice the level of natural mortality (i.e. r_{2M}).

However, for some shark species it has been suggested that maximum productivity occurs at levels below twice natural mortality. For this reason we also calculated $r_{1.5M}$. Density-dependence was incorporated by calculating r_{2M} assuming that reproductive output was increased by a factor of 25% (i.e. 1.25*b*).

Data for comparison to those of the deepwater chondrichthyans was taken from Smith et al. (1998) who used the same method of determining intrinsic rebound potentials.

Table 2.18. Life history data used to calculate intrinsic rebound potentials of deepwater elasmobranchs. Reprod per., reproductive periodicity; *b*, annual female litter size; α, age at maturity; *w,* maximum reproductive age; *M,* natural mortality; l_α, proportion of the population surviving to maturity.

Species	Litter size	Reprod per.	b	α	w	M	l_α
Squalidae							
Squalus blainvillei	4	2	1	5	8	0.1632	0.442
Squalus megalops	3	2	0.75	15	32	0.0480	0.487
Squalus mitsukurii[1]	4.5	2	1.125	16	27	0.0816	0.271
Squalus mitsukurii[2]	3.5	2	0.875	15	27	0.0656	0.374
Centrophoridae							
Centrophorus granulosus	1	2	0.25	16.5	39	0.1600	0.071
Centrophorus squamosus	8.1	2	2.025	35	70	0.0651[a]	0.102
Deania calcea[3]	8	2	2	21.5	37	0.0816	0.173
Deania calcea[4]	11	2	2.75	25	35	0.1232	0.046
Etmopteridae							
Etmopterus baxteri	9	2	2.25	30	57	0.0640	0.147
Somniosidae							
Centroselachus crepidater	6	2	1.5	20	54	0.1152	0.100
Proscymnodon plunketi	17	2	4.25	29	39	0.1156[a]	0.035
Rajidae							
Amblyraja radiata	15	1	7.5	11	16	0.1920	0.133
Leucoraja naevus	90	1	45	4	8	0.3152	0.283
Raja binoculata	1260	1	630	10	26	0.0960	0.383
Chimaeridae							
Chimaera monstrosa	6.5	1	3.25	11	26	0.1600	0.172

[a]Calculated using Hoeing (1983) method; [1]Ogasawara Islands, Japan, NW Pacific; [2]Hancock Seamount, NW Pacific; [3]Southeastern Australia; [4]Rockall Trough and Porcupine Bank, NE Atlantic.

Results and Discussion

Intrinsic rebound potentials for deepwater sharks ranged from 0.0064 yr^{-1} for *Proscymnodon plunketi* to 0.11 yr^{-1} for *Leucoraja naevus* (Table 2.19). The most conservative values of rebound potentials ($r_{1.5M}$) were mostly below 0.0086 yr^{-1}, but reached as high as 0.03 yr^{-1}. Optimistic values (r_{2M} 1.25*b*) were mostly less than 0.025 yr^{-1}. Population doubling times for conservative values were between 19 and 109 yr, while those of the optimistic scenarios ranged from 6 to 40 yr. All but a few of the intrinsic rebound potentials calculated, irrespective of whether they were conservative or optimistic, fall in the range considered by Musick et al. (2001) to be very low (<0.05 yr^{-1}). The few remaining values all fell within the low category (0.05-0.15). All deepwater species should therefore be considered to have limited productivity and so have limited ability to sustain high levels of fishing pressure and be slow to recover from overfishing. The population doubling times indicate that once a stock has been depleted, it will be decades, and potentially centuries, before it will recover. Fisheries that take deepwater chondrichthyans, both as targeted species or as bycatch, need to be carefully managed and should take a precautionary approach.

Table 2.19. Intrinsic rebound potentials ($r_{1.5M}$, r_{2M}) and population doubling times (T_{x2}) for deepwater chondrichthyans with no increase in reproductive output (*b*) and with a 25% increase (1.25*b*).

	b		***b***		**1.25*b***	
Species	$r_{1.5M}$	T_{x2}	r_{2M}	T_{x2}	r_{2M}	T_{x2}
Squalidae						
Squalus blainvillei	0.0162	42.79	0.0312	22.23	0.0670	10.35
Squalus megalops	0.0075	92.40	0.0144	48.07	0.0247	28.07
Squalus mitsukurii[1]	0.0086	80.69	0.0163	42.40	0.0273	25.35
Squalus mitsukurii[2]	0.0080	86.89	0.0153	45.30	0.0266	26.09
Centrophoridae						
Centrophorus granulosus	0.0161	42.98	0.0278	24.96	0.0384	18.04
Centrophorus squamosus	0.0070	99.53	0.0125	55.43	0.0175	39.66
Deania calcea[3]	0.0083	83.79	0.0155	44.85	0.0237	29.25
Deania calcea[4]	0.0076	91.66	0.0141	49.31	0.0218	31.73
Etmopteridae						
Etmopterus baxteri	0.0071	98.13	0.0130	53.50	0.0187	37.02
Somniosidae						
Centroselachus crepidater	0.0133	52.15	0.0230	30.20	0.0314	22.05
Proscymnodon plunketi	0.0064	108.96	0.0119	58.35	0.0187	37.07
Rajidae						
Amblyraja radiata	0.0149	46.39	0.0278	24.92	0.0457	15.18
Leucoraja naevus	0.0371	18.69	0.0674	10.28	0.1100	6.30
Raja binoculata	0.0163	42.50	0.0302	22.94	0.0450	15.39
Chimaeridae						
Chimaera monstrosa	0.0202	34.35	0.0358	19.38	0.0508	13.63

[1] Ogasawara Islands, Japan, NW Pacific; [2] Hancock Seamount, NW Pacific; [3] Southeastern Australia; [4] Rockall Trough and Porcupine Bank, NE Atlantic.

The skates (families Arhynchobatidae and Rajidae) probably have the highest reproductive rates of any elasmobranch, with some species potentially producing hundreds of eggs per year. In the case of some species of *Raja* individual egg cases contain multiple eggs (Ebert and Davis 2007), increasing their fecundity. Despite these high reproductive rates, these species appear to be only reproductively active for a relatively short period of their life. Ebert (2005) reported that large (and hence older) female *Bathyraja* were senescent and so may only reproduce for a few years. This limitation on reproduction is likely to translate into low intrinsic rebound potentials as demonstrated by *Leucoraja naevus* which despite having an annual fecundity of 90, had a intrinsic rebound potential of 0.0371 yr^{-1}, due to a short reproductive life (Table 2.19).

The intrinsic rebound potential values of deepwater chondrichthyan fishes fall at the lower end of the productivity scale of elasmobranchs, and include the lowest levels observed to date (Figure 2.1). Where the values of deepwater sharks fell within the range of continental shelf species they often had lower productivities for the same age at maturity. The values used in the comparison were the moderate levels (r_{2M} 1.0b), and so actual values may be even lower. These low levels of productivity are in part a function of the life history of deepwater species, where low temperatures and limited food result in slow rates of growth and late maturity. Interestingly, some of the elasmobranch groups that live the deepest (e.g. scyliorhinid sharks of the genus *Apristurus*) were not represented in this analysis due to the lack of available age data. Research to age these types of animals is imperative if the productivity, and hence their ability to sustain fishing pressure, of these very deep water species is to be determined. Traditional ageing methods that rely on seasonal changes in calcification rates of the vertebrae or caudal thorns to produce banding patterns are of limited use for species from the stable and uniform habitats of the deep sea.

There was a significant decline in the intrinsic rebound potential of species with increasing maximum depth (Figure 2.2). This indicates that deeper living species are likely to have decreased abilities to sustain fishing or rebound from population declines. While such an observation is not a surprise, it does provide the ability to predict, within the bounds of confidence intervals, the rebound potentials of species for which only the maximum depth of occurrence is known.

This analysis, carried out using a simple approach, allowed comparison between taxa and the ability to include species with limited data. The simple method required a number of assumptions about the populations, including age-independent levels of natural and fishing mortality, no maternal size – litter size relationship (which has been observed in some species such as *E. baxteri*; Irvine 2004), and no fishing of juveniles. More detailed methods will be required to develop management strategies for individual species, or groups of species. However, such analyses were beyond the scope of this study, and their data requirements mean they could be undertaken for only a handful of species.

Conclusion

The analysis of intrinsic rebound potential of deepwater chondrichthyans shows that they have low to very low values. These fall at the lower end of the productivity values of all chondrichthyans and indicates that as a group they have a limited ability to sustain fishing pressure or recover from overfishing. As such, management of fisheries that take deepwater chondrichthyan species need to be carefully managed. The collection of more data on the life history of all groups of deepwater chondrichthyans needs to be a high priority to provide a more comprehensive understanding of their productivity.

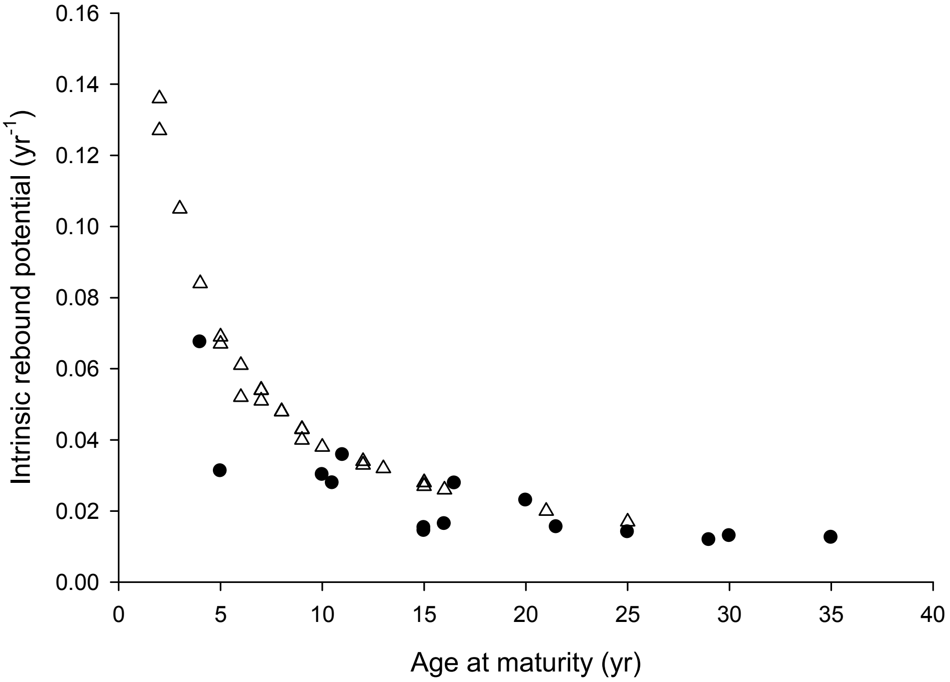


Figure 2.1. Comparison of intrinsic rebound potentials (r_{2M} 1.0*b*) of deepwater (closed circles) and coastal and pelagic (open triangles) chondrichthyan species. Data for coastal and pelagic species from Smith et al. (1998).

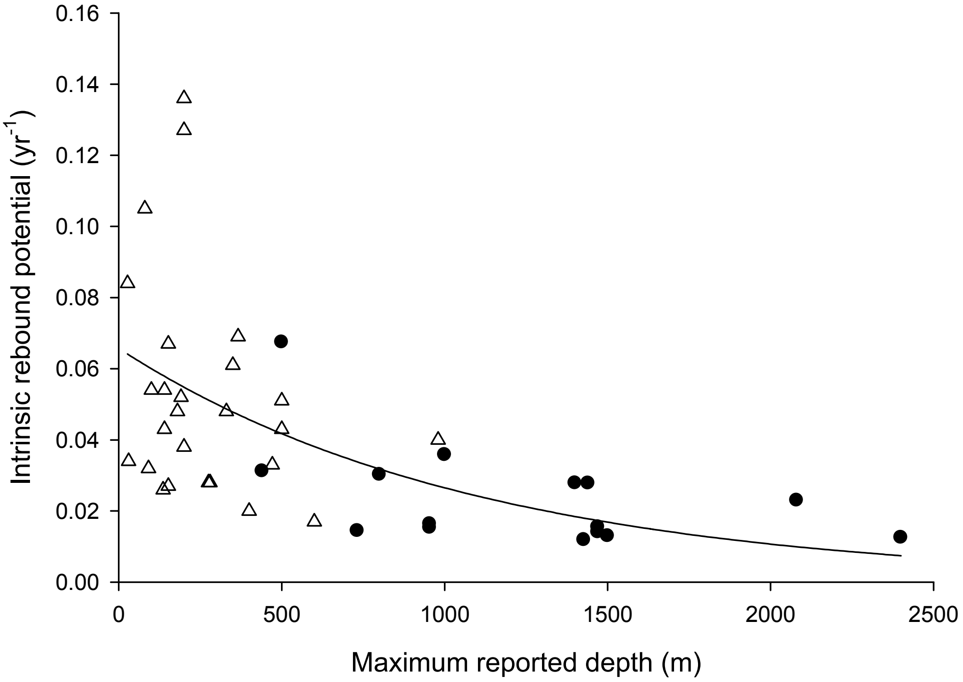


Figure 2.2. Intrinsic rebound potential as a function of maximum observed depth for deepwater (closed circles) and coastal and pelagic (open triangles) chondrichthyan species. The relationship between rebound potential and maximum depth is $r_{2M} = 0.0657e^{-0.0009Depth}$ ($r^2 = 0.31$). Rebound potential data for coastal and pelagic species from Smith et al. (1998), depth data from Section I of this report and Compagno et al. (2005).

SECTION II LITERATURE

Abdel-Aziz, S.H. 1994. Observations on the biology of the common torpedo (*Torpedo torpedo*, Linnaeus, 1758) and marbled electric ray (*Torpedo marmorata*, Risso, 1810) from Egyptian Mediterranean waters. Australian Journal of Marine and Freshwater Research 45(4):693-704.

Acuña, E., Villarroel, J.C., Catalán, R. and Herrera, P. 2003. Reproduction and feeding habits of two deep-Sea sharks from Central-Northern Chile: the etmopterid *Aculeola nigra* De Buen, 1959 and the scylliorinid *Bythalaelurus canescens* (Günther, 1878). Abstract. Conservation and management of deepsea chondrichthyan fishes. Joint FAO and IUCN Shark Specialist Group Pre-conference Meeting in conjunction with Deepsea 2003. University of Otago, Portobello Marine Laboratory, Portobello, New Zealand, 27-29 November 2003.

Anderson, R.C. and Stevens, J.D. 1996. Review of information on diurnal vertical migration in the bignose shark (*Carcharhinus altimus*). Marine and Freshwater Research 47(4):605-608.

Au, D.W. and Smith, S.E. 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). Canadian Journal of Fisheries and Aquatic Sciences 54:415-420.

Bagley, P.M., Smith, A. and Priede, I.G. 1994. Tracking movements of deep demersal fishes in the Porcupine Seabight, North-east Atlantic Ocean. Journal of the Marine Biological Association of the United Kingdom 74:473-480.

Balart, E.F., Gonzalez-Garcia, J. and Villavicencio-Garayzar, C. 2000. Notes on the biology of *Cephalurus cephalus* and *Parmaturus xaniurus* (Chondrichthyes: Scyliorhinidae) from the west coast of Baja California Sur, Mexico. Fishery Bulletin 98(1):219-221.

Bañón, R., Piñeiro, C. and Casas, M. 2006. Biological aspects of deep-water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* in Galician waters (north-western Spain). Journal of the Marine Biological Association of the United Kingdom 86(4):843-846.

Barnett, L.A.K., Didier, D.A., Long, D.J. and Ebert, D.A. 2006. *Hydrolagus mccoskeri* sp. nov., a new species of chimaeroid fish from the Galapagos Islands (Holocephali: Chimaeriformes: Chimaeridae). Zootaxa 1328:27-38.

Barrull, J. and Mate, I. 2001. First record of a pregnant female little sleeper shark *Somniosus rostratus* (Risso, 1826) on the Spanish Mediterranean coast. Boletin Instituto Espanol de Oceanografia 17(3-4):323-325.

Bass, A.J., D'Aubrey, J.D. and Kistmasamy, N. 1975. Sharks of the east coast of southern Africa. V. The families Hexanchidae, Chlamydoselachidae, Heterodontidae, Pristiophoridae and Squatinidae. Investigational Report Oceanographic Research Institute 43:1-50.

Baumgartner, N., Arkhipkin, A.I., Shcherbich, Z.N. and Brickle, P. 2005. Age, growth and maturity of the broad nose skate, *Bathyraja brachyurops* (Fowler, 1910) and the gray tail skate, *Bathyraja griseocauda* (Norman, 1937) around the Falkland Islands. ICES CM 2005/N:02.

Berestovskii, E.G. 1994. Reproductive biology of skates of the family Rajidae in the seas of the far north. Journal of Ichthyology 34(6):26-37.

Bigelow, H.B. and Schroeder, W.C. 1948. Sharks. In: Fishes of the Western North Atlantic. Memoirs of the Sears Foundation for Marine Research 1(1):59-546.

Bigelow, H.B. and Schroeder, W.C. 1953. Sawfishes, guitarfishes, skates and rays. In: Fishes of the Western North Atlantic. Memoirs of the Sears Foundation for Marine Research 1(2):1-514.

Braccini, J.M., Gillanders, B.M. and Walker, T.I. 2006. Determining reproductive parameters for population assessments of chondrichthyan species with asynchronous ovulation and parturition: piked spurdog (*Squalus megalops*) as a case study. Marine and Freshwater Research 57(1):105-119.

Bridge, N.F., Mackay, D. and Newton, G. 1998. Biology of the ornate angel shark (*Squatina tergocellata*) from the Great Australian Bight. Marine and Freshwater Research 49(7):679-686.

Cadenat, J. and Blache, J. 1981. Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). Faune tropicale, OSTROM 21:1-330.

Calis, E., Jackson, E.H., Nolan, C.P. and Jeal, F. 2005. Preliminary age and growth estimates of the rabbitfish, *Chimaera monstrosa*, with implications for future resource management. e-Journal of Northwest Atlantic Fishery Science 35, art. 21.

Camhi, M., Fowler, S., Musick, J, Bräutigam, A. and Fordham, S. 1998. Sharks and their relatives – ecology and conservation. Occasional Paper of the IUCN Species Survival Commission No. 20.

Cannizzaro, L., Rizzo, P., Levi, D. and Gancitano, S. 1995. Age determination and growth of *Squalus blainvillei* (Risso, 1826). Fisheries Research 23(1-2):113-125.

Capapé, C. 1974. Note préliminaire sur la biologie de *Torpedo* (*Torpedo*) *marmorata* Risso 1810 et de *Torpedo* (*Tetronarce*) *nobiliana* Bonaparte, 1835 des côtes tunisiennes. Archives de L'Institut Pasteur de Tunis 51(3):257-267.

Capapé, C., Seck, A.A. and Quignard, J.-P. 1999. Observations on the reproductive biology of the angular rough shark, *Oxynotus centrina* (Oxynotidae). Cybium 23(3):259-271.

Capapé, C. Hemida, F., Guélorget, O., Barrull, J., Mate, I., Ben Souissi, J. and Bradaï, M.N. 2004. Reproductive biology of the bluntnose sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) (Chondrichthyes: Hexanchidae) from the Mediterranean Sea: a review. Acta Adriatica 45(1):95-106.

Capapé, C., Diatta, Y., Seck, A.A., Guélorget, O., Ben Souissi, J. and Zaouali, J. 2005. Reproduction of the sawback angelshark *Squatina aculeata* (Chondrichthyes: Squatinidae) off Senegal and Tunisia. Cybium 29(2):147-157.

Carey, F.G. and Clark, E. 1995. Depth telemetry from the sixgill shark, *Hexanchus griseus*, at Bermuda. Environmental Biology of Fishes 42:7-14.

Carvalho, M.R. de and Séret, B. 2002. *Narcine lasti*, a new species of numbfish from Western Australia and Indonesia (Chondrichthyes: Torpediniformes: Narcinidae). Records of the Western Australian Museum 20:393-408.

Carvalho, M.R. de, Compagno L.J.V. and Ebert, D.A. 2003. *Benthobatis yangi*, a new species of blind electric ray from Taiwan (Chondrichthyes: Torpediniformes: Narcinidae). Bulletin and Marine Science 72(3):923-939.

Castro, J.I., Bubucis, P.M. and Overstrom, N.A. 1988. The reproductive biology of the chain dogfish, *Scyliorhinus retifer*. Copeia 1988(3):740-746.

Chen, C., Taniuchi, T. and Nose, Y. 1981. Some aspects of reproduction in the pointed-snout dogfish *Squalus japonicus* taken off Nagasaki and Choshi. Bulletin of the Japanese Society of Scientific Fisheries 47(9):1157-1164.

Chen, C.-T., Liu, K.-M. and Chang, Y.-C. 1997. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. Ichthyological Research 44(3):227-235.

Clarke, M.W., Connolly, P.L. and Bracken, J.J. 2001. Aspects of reproduction of the deep water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. Journal of the Marine Biological Association of the United Kingdom 81(6):1019-1029.

Clarke, M.W.; Connolly, P.L. and Bracken, J.J. 2002a. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. Journal of Fish Biology 60(3):501-514.

Clarke, M.W., Connolly, P.L. and Bracken, J.J. 2002b. Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* west and north of Ireland. Fisheries Research 56(2):139-153.

Coelho, R. and Erzini, K. 2005. Length at first maturity of two species of lantern sharks (*Etmopterus spinax* and *Etmopterus pusillus*) off southern Portugal. Journal of the Marine Biological Association of the United Kingdom 85(5):1163-1165.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes. No. 1, Vol. 2. FAO, Rome.

Compagno, L.J.V. In prep. a. Sharks of the World. An annotated and illustrated catalogue of the shark species known to date. Volume 1. (Hexanchiformes, Squaliformes, Squatiniformes and Pristiophoriformes). FAO Species Catalogue for Fisheries Purposes No. 1, Vol.3. FAO, Rome.

Compagno, L.J.V. and Last, P.R. 1999. Hexatrygonidae. Sixgill stingrays. Pp. 1477-1478. In: Carpenter, K.E. and Niem, V.H. (eds.). FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophyrnidae). FAO, Rome.

Compagno, L.J.V. and Stevens, J.D. 1993. *Hemitriakis falcata* n.sp. and *H. abdita* n.sp., two new houndsharks (Carcharhiniformes: Triakidae) from Australia. Records of the Australian Muesum 45:195-220.

Compagno, L.J.V., Ebert, D.A. and Smale, M.J. 1989. Guide to the sharks and rays of southern Africa. New Holland Publishers Ltd., London.

Compagno, L., Dando, M. and Fowler, S. 2005. A field guide to sharks of the world. Collins, London.

Conrath, C.L. and Musick, J.A. 2002. Reproductive biology of the smooth dogfish, *Mustelus canis*, in the northwest Atlantic Ocean. Environmental Biology of Fishes 64(4):367-377.

Conrath, C.L., Gelsleichter, J. and Musick, J.A. 2002. Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. Fishery Bulletin 100(4):674-682.

Cortés, E. 2000. Life history patterns and correlations in sharks. Reviews in Fisheries Science 8(4):299-344.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: applications to shark populations and their conservation. Conservation Biology 16:1048-1062.

Costa, M.E., Erzini, K. and Borges, T.C. 2005. Reproductive biology of the blackmouth catshark, *Galeus melastomus* (Chondrichthyes: Scyliorhinidae) off the south coast of Portugal. Journal of the Marine Biological Association of the United Kingdom 85(5):1173-1183.

Cross, J.N. 1988. Aspects of the biology of two scyliorhinid sharks, *Apristurus brunneus* and *Parmaturus xaniurus*, from the upper continental slope off southern California. Fishery Bulletin 86(4):691-702.

Crow, G.L., Lowe, C.G. and Wetherbee, B.M. 1996. Shark records from longline fishing programs in Hawai'i with comments on Pacific Ocean distributions. Pacific Science 50(4):382-392.

Cunha, C.M. and Gonzalez, M.B. 2006. Pregnancy in *Squaliolus laticaudus* (Elasmobranch: Dalatiidae) from Brazil. Environmental Biology of Fishes 75(4):465-469.

Daley, R., Stevens, J. and Graham, K. 2002. Catch analysis and productivity of the deepwater dogfish resource in southern Australia. FRDC Final Report, 1998/108. Fisheries Research and Development Corporation, Canberra.

Davis, C.D., Cailliet, G.M. and Ebert, D.A. 2006. Age and growth of the roughtail skate, *Bathyraja trachura*, (Gilbert, 1892) from the eastern North Pacific. Abstract. 2006 Joint Meeting of Ichthyologists and Herpetologists, New Orleans, USA, 12-17 July 2006.

Desbrosses, P. 1938. Croissances émigration du requin griset, *Hexanchus griseus* (Bonnaterre 1788) Rafinesque 1810. Revue des travaux de l'Institut des pêches maritimes 11(1):53-57.

Didier-Dagit, D.A. 2005. *Hydrolagus colliei*. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 06 February 2007.

Didier, D.A. and Rosenberger, L.J. 2002. The spotted ratfish, *Hydrolagus colliei*: Notes on its biology with a redescription of the species (Holocephali: Chimaeridae). California Fish and Game 88(3):112-125.

Du Buit, M.H. 1976. The ovarian cycle of the cuckoo ray, *Raja naevus* (Müller and Henle), in the Celtic Sea. Journal of Fish Biology 8:199-207.

Du Buit, M.H. 1977. Age et croissance de *Raja batis* et de *Raja naevus* en Mer Celtique. Journal du Conseil International pour l'Exploration de la Mer 37:261-265.

Duffy, C.A.J. 1997. Further records of the goblin shark, *Mitsukurina owstoni* (Lamniformes: Mitsukurinidae), from New Zealand. New Zealand Journal of Zoology 24(2):167-171.

Duffy, C.A.J. 2003a. Blind electric ray *Typhlonarke aysoni* (Hamilton, 1902) and oval electric ray *Typhlonarke tarakea* Phillipps, 1929. Pg. 138. In: Cavanagh, R.D., Kyne, P.M., Fowler, S.L., Musick, J.A. and Bennett, M.B. (2003). The Conservation Status of Australasian Chondrichthyans: Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop, Queensland, Australia, 7-9 March 2003. School of Biomedical Sciences, University of Queensland: Brisbane.

Duffy, C.A.J. 2003b. New Zealand torpedo ray *Torpedo fairchildi* Hutton, 1872. Pp. 139-140. In: Cavanagh, R.D., Kyne, P.M., Fowler, S.L., Musick, J.A. and Bennett, M.B. (2003). The Conservation Status of Australasian Chondrichthyans: Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop, Queensland, Australia, 7-9 March 2003. School of Biomedical Sciences, University of Queensland: Brisbane.

Duffy, C., Bishop, S. and Yopak, K. 2003. Distribution and biology of *Cirrhigaleus barbifer* (Squalidae) in New Zealand waters. Abstract. Conservation and management of deepsea chondrichthyan fishes. Joint FAO and IUCN Shark Specialist Group Pre-conference Meeting in conjunction with Deepsea 2003. University of Otago, Portobello Marine Laboratory, Portobello, New Zealand, 27-29 November 2003.

Duffy, C.A.J., Ebert, D.A. and Stenberg , C. 2004. *Mitsukurina owstoni*. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. www.iucnredlist.org. Downloaded on 19 January 2007.

Ebert, D.A. 1986. Biological aspects of the sixgill shark, *Hexanchus griseus*. Copeia 1986(1):131-135.

Ebert, D.A. 2002. Some observations on the reproductive biology of the sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) from southern African waters. South African Journal of Marine Science 24:359-363.

Ebert, D.A. 2005. Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. Journal of Fish Biology 66(3):618-649.

Ebert, D.A. and Davis, C.D. 2007. Descriptions of skate egg cases (Chondrichthyes: Rajiformes: Rajoidei) from the eastern North Pacific. Zootaxa 1393:1-18.

Ebert, D.A., Compagno, L.J.V. and Natanson, L.J. 1987. Biological notes on the Pacific sleeper shark, *Somniosus pacificus* (Chondrichthyes: Squalidae). California Fish and Game 73 (2):117-123.

Ebert, D.A., Compagno, L.J.V. and Cowley, P.D. 2006. Reproductive biology of catsharks (Chondrichthyes: Scyliorhinidae) off the west coast of southern Africa. ICES Journal of Marine Science 63:1053-1065.

Fenton, G.E. 2001. Radiometric ageing of sharks. FRDC Final Report, 1994/021. Fisheries Research and Development Corporation, Canberra.

Fergusson, I.K., Graham, K.J. and Compagno, L.J.V. In press. Distribution, abundance and biology of the smalltooth sandtiger shark *Odontaspis ferox* (Risso, 1810) (Lamniformes: Odontaspididae). Environmental Biology of Fishes.

Fishelson, L. and Baranes, A. 1998. Observations on the Oman shark, *Iago omanensis* (Triakidae), with emphasis on the morphological and cytological changes of the oviduct and yolk-sac during gestation. Journal of Morphology 236:151-165.

Fischer, A.F., Veras, D.P., Hazin, F.H.V., Broadhurst, M.K., Burgess, G.H. and Oliveira, P.G.V. 2006. Maturation of *Squalus mitsukurii* and *Cirrhigaleus asper* (Squalidae, Squaliformes) in the southwestern equatorial Atlantic Ocean. Journal of Applied Ichthyology 22:495-501.

Flammang, B.E., Ebert, D.A. and Cailliet, G.M. In press. Reproductive biology of deep-sea catsharks (Chondrichthyes: Scyliorhinidae) in the eastern North Pacific. Environmental Biology of Fishes.

Forster, G.R., Badcock, J.R., Longbottom, M.R., Merrett, N.R. and Thomson, K.S. 1970. Results of the Royal Society Indian Ocean Deep Slope Fishing Expedition, 1969. Proceedings of the Royal Society of London Series B 175:367-404.

Francis, M.P. 2006. Distribution and biology of the New Zealand endemic catshark, *Halaelurus dawsoni*. Environmental Biology of Fishes 75(3):295-306.

Francis, M.P. and Duffy, C. 2002. Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. Marine Biology 140(4):831-842.

Francis, M.P. and Ó Maolagáin, C. 2005. Age and growth of the Antarctic skate (*Amblyraja georgiana*) in the Ross Sea. CCAMLR Science 12:183-194.

Francis, M.P., Ó Maolagáin, C. and Stevens, D. 2001. Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*. New Zealand Journal of Marine and Freshwater Research 35(4):831-842.

Fujita, K. Oviphagous embryos of the pseudochariid shark, *Pseudocarcharias kamoharai*, from the central Pacific. Japanese Journal of Ichthyology 28(1):37-44.

Gadig, O.B.F. and Gomes, U.L. 2002. First report on embryos of *Isistius brasiliensis*. Journal of Fish Biology 60(5):1322-1325.

Gallagher, M.J. and Nolan, C.P. 1999. A novel method for the estimation of age and growth in rajids using caudal thorns. Canadian Journal of Fisheries and Aquatic Sciences 56(9):1590-1599.

Gallagher, M.J., Nolan, C.P. and Jeal, F. 2004. Age, growth and maturity of the commercial ray species from the Irish Sea. Journal of Northwest Atlantic Fishery Science 35:47-66.

Gburski, C.M., Gaichas, S.K. and Kimura, D.K. In press. Age and growth of the big skate (*Raja binoculata*) and longnose skate (*R. rhina*) in the Gulf of Alaska. Environmental Biology of Fishes.

Gedamke, T., DuPaul, W.D. and Musick, J.A. 2005. Observations on the life history of the barndoor skate, *Dipturus laevis*, on Georges Bank (Western North Atlantic). Journal of Northwest Atlantic Fishery Science 35:67-78.

Gennari, E., Scacco, U. and Vacchi, M. 2002. A simple technique for a preliminary vertebral ageing study in the velvet belly, *Etmopterus spinax* (Squalidae) in central Mediterranean Sea. Poster. 6th European Elasmobranch Association Meeting, 6-8 September 2002, National Museum and Galleries of Wales, Cardiff, Wales, UK.

Gilmore, R.G. 1983. Observations on the embryos of the longfin mako, *Isurus paucus*, and the bigeye thresher, *Alopias superciliosus*. Copeia 1983(2):375-382.

Gilmore, R.G. 1993. Reproductive biology of lamnoid sharks. Environmental Biology of Fishes 38(1-3):95-114.

Girard, M. and Du Buit, M.-H. 1999. Reproductive biology of two deep-water sharks from the British Isles, *Centroscymnus coelolepis* and *Centrophorus squamosus* (Chondrichthyes: Squalidae). Journal of the Marine Biological Association of the United Kingdom 79(5):923-931.

Golani, D. and Pisanty, S. 2000. Biological aspects of the gulper shark, *Centrophorus granulosus* (Bloch & Schneider, 1801), from the Mediterranean coast of Israel. Acta Adriatica 41(2):71-77.

Goldman, K.J. 2004. Age and growth of elasmobranch fishes. Pp. 97-132. In: Musick, J.A. and Bonfil, R. (eds.). Elasmobranch fisheries management techniques. APEC Fisheries Working Group, Singapore.

Goto, T. and Last, P.R. 2002. A new parascylliid species, *Parascyllium sparsimaculatum*, from Western Australia (Elasmobranchii: Orectolobiformes). Ichthyological Research 49:15-20.

Graham, K.J. 2005. Distribution, population structure and biological aspects of *Squalus* spp. (Chondrichthyes: Squaliformes) from New South Wales and adjacent Australian waters. Marine and Freshwater Research 56(4):405-416.

Guallart, J. 1998. Contribución al conocimientto de la taxonomía y la biología del tiburón batial *Centrophorus granulosus* (Bloch & Schneider, 1801) (Elasmobranchii, Squalidae) en el Mar Balear (Mediterráneo occidental). PhD Thesis, Universitat de Valencia, Valencia.

Guallart, J. and Vicent, J.J. 2001. Changes in composition during embryo development of the gulper shark, *Centrophorus granulosus* (Elasmobranchii, Centrophoridae): an assessment of maternal-embryonic nutritional relationships. Environemental Biology of Fishes 61:135-150.

Gubanov, E.P. 1978. Reproduction of some species of the pelagic sharks from the equatorial zone of the Indian Ocean. Voprosy Ikhtiologii 18(5):879-891.

Gudger, E.W. and Smith, B.G. 1933. The natural history of the frilled shark *Chlamydoselachus anguineus*. Article 5. Pp. 243-330. In: Gudger, E.W. (ed.). The Bashford Dean Memorial Volume Archaic Fishes. American Museum of Natural History, New York.

Hazin, F.H.V., Fischer, A.F., Broadhurst, M.K., Veras, D., Oliveira, P.G. and Burgess, G.H. 2006. Notes on the reproduction of *Squalus megalops* off northeastern Brazil. Fisheries Research 79:251-257.

Henderson, A.C., Flannery, K. and Dunne, J. 2003. Biological observations on shark species taken in commercial fisheries to the west of Ireland. Biology and Environment: Proceedings of the Royal Irish Academy 103B(1):1-7.

Henderson, A.C., Arkhipkin, A.I. and Chtcherbich, J.N. 2004. Distribution, growth and reproduction of the white-spotted skate *Bathyraja albomaculata* (Norman, 1937) around the Falkland Islands. e-Journal of Northwest Atlantic Fishery Science 35:art. 1.

Hitz, C.R. 1964. Observations on egg cases of the big skate (*Raja binoculata* Girard) found in Oregon coastal waters. Journal of the Fisheries Research Board of Canada 21(4):851-854.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 81:898-903.

Hoenig, J.M. and Gruber, S.H. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Technical Reports NMFS 90:1-16.

Holden, M.J. 1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. Pp. 117-137. In: Jones, F.R.H. (ed.). Sea fisheries research. Elk Science, London.

Holden, M.J. 1975. The fecundity of *Raja clavata* in British waters. Journal du Conseil International pour l'Exploration de la Mer 36:110-118.

Holden, M.J., Rout, D.W. and Humphreys, C.N. 1971. The rate of egg laying by three species of ray. Journal du Conseil International pour l'Exploration de la Mer 33(3):335-339.

Horie, T. and Tanaka, S. 2000. Reproduction and food habits of two species of sawtail catsharks, *Galeus eastmani* and *G. nipponensis*, in Suruga Bay, Japan. Fisheries Science 66(5):812-825.

Hulbert, L.B., Sigler, M.F. and Lunsford, C.R. 2006. Depth and movement behaviour of the Pacific sleeper shark in the north-east Pacific Ocean. Journal of Fish Biology 69:406-425.

Iglesias, S.P., Du Buit, M.-H. and Nakaya, K. 2002. Egg capsules of deep-sea catsharks from eastern North Atlantic, with first descriptions of the capsule of *Galeus murinus* and *Apristurus aphyodes* (Chondrichthyes: Scyliorhinidae). Cybium 26(1):59-63.

Iglésias, S.P., Nakaya, K. and Stehmann, M. 2004. *Apristurus melanoasper*, a new species of deep-water catshark from the north Atlantic (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). Cybium 28(4): 345-356.

Irvine, S.B. 2004. Age, growth and reproduction of deepwater dogfishes from southeastern Australia. PhD Thesis, Deakin University, Australia.

Irvine, S.B., Stevens, J.D. and Laurenson, L.J.B. 2006a. Comparing external and internal dorsal-spine bands to interpret the age and growth of the giant lantern shark, *Etmopterus baxteri* (Squaliformes: Etmopteridae). Environmental Biology of Fishes 77:253-264.

Irvine, S.B., Stevens, J.D. and Laurenson, L.J.B. 2006b. Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*. Canadian Journal of Fisheries and Aquatic Sciences 63(3):617-627.

Ishiyama, R. 1958. Studies on the Rajid fishes (Rajidae) found in the waters around Japan. Journal of Shimonoseki College of Fisheries 7(2-3):193-394.

Jabobsdóttir, K.B. 2001. Biological aspects of two deep-water squalid sharks: *Centroscyllium fabricii* (Reinhardt, 1825) and Etmopterus princeps (Collett, 1904) in Icelandic waters. Fisheries Research 51(2-3):247-265.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Journal of Fisheries and Aquatic Sciences 53:820-822.

Johnson, A.G. and Horton, H.F. 1972. Length-weight relationship, food habits, parasites, and sex and age determination of the ratfish, *Hydrolagus colliei* (Lay and Bennett). Fishery Bulletin 70(2):421-429.

Jones, B.C. and Geen, G.H. 1977. Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia. Journal of the Fisheries Research Board of Canada 34:1286-1292.

Kabasakal, H. 2004. Preliminary observations on the reproductive biology and diet of the bluntnose sixgill shark, *Hexanchus griseus* (Bonnaterre, 1788) (Chondrichthyes: Hexanchidae), in Turkish seas. Acta Adriatica 45(2):187-196.

Kokuho, T., Nakaya, K. and Kitagawa, D. 2003. Distribution and reproductive biology of the nine-spot ratfish *Hydrolagus barbouri* (Holocephali; Chimaeridae). Memoirs of the Graduate School of Fisheries Sciences Hokkaido University 50(2):63-87.

Konstantinou, H., McEachran, J.D. and Woolley, J.B. 2000. The systematics and reproductive biology of the *Galeus arae* subspecific complex (Chondrichthyes: Scyliorhinidae). Environmental Biology of Fishes 57(2):117-129.

Kyne, P.M. and Bennett, M.B. 2002. Reproductive biology of the eastern shovelnose ray, *Aptychotrema rostrata* (Shaw & Nodder, 1794) from Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* 53:583-589.

Kyne, P.M., Yano, K. and White, W.T. 2004. *Pseudotriakis microdon*. *In:* IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 22 January 2007.

Kyne, P.M., Johnson, J.W., White, W.T. and Bennett, M.B. 2005. First records of the false catshark, *Pseudotriakis microdon* Capello, 1868, from the waters of eastern Australia and Indonesia. Memoirs of the Queensland Museum 51(2):525-530.

Kyne, P.M., Courtney, A.J. and Bennett, M.B. In prep. Aspects of the reproductive biology and diet of *Dipturus polyommata* (Ogilby, 1910) (Elasmobranchii: Rajidae) from southern Queensland, Australia.

Last, P.R. and Compagno, L.J.V. 1999. Anacanthobatidae. Legskates. Pp. 1462-1466. In: Carpenter, K.E. and Niem, V.H. (eds.). FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophyrnidae). FAO, Rome.

Last, P.R. and Stevens, J.D. 1994. Sharks and rays of Australia. CSIRO Publishing, Melbourne.

Last, P.R., Burgess G.H. and Séret, B. 2002. Description of six new species of lantern-sharks of the genus *Etmopterus* (Squaloidea: Etmopteridae) from the Australasian region. Cybium 26(3): 203–223.

Licandeo, R.R., Lamilla, J.G., Rubilar, P.G. and Vega, R.M. 2006. Age, growth, and sexual maturity of the yellownose skate *Dipturus chilensis* in the south-eastern Pacific. Journal of Fish Biology 68(2):488-506.

Litvinov, F.F. 1990. Ecological characteristics of the spiny dogfish, *Squalus mitsukurii* from the Nazca and Sala-y-Gomez submarine ridges. Journal of Ichthyology 30:104-115.

Liu, K.-M., Chiang, P.-J. and Chen, C.-T. 1998. Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. Fishery Bulletin 96(3):482-491.

Lucifora, L.O., Valero, J.L. and Garcia, V.B. 1999. Length at maturity of the greeneye spurdog shark, *Squalus mitsukurii* (Elasmobranchii: Squalidae), from the SW Atlantic, with comparisons with other regions. Marine and Freshwater Research 50(7):629-632.

Lucifora, L.O., Menni, R.C. and Escalante, A.H. 2002. Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. ICES Journal of Marine Science 59:553-561.

Mathews, C.P. 1975. Some observations on the ecology of *Galeus plperatus* Springer and Wagner, a little known shark endemic to the northern Gulf of California. Journal of Fish Biology 7(1):77-82.

McEachran, J.D. and de Carvalho, M.R. 2002. Batoid fishes. Pp. 507-589. In: Carpenter, K.E. (ed.). The Living Marine Resources of the Western Central Atlantic. Volume 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras. FAO Species Identification Guides for Fishery Purposes. FAO, Rome.

McFarlane, G.A. and Beamish, R.J. 1987. Validation of the dorsal spine method of age determination for spiny dogfish. Pp. 287-300. In: Summerfelt, R.C and Hall, G.E. (eds.). Age and growth of fish. The Iowa State University Press, Ames, USA.

McFarlane, G.A. and King, J.R. 2006. Age and growth of big skate (*Raja binoculata*) and longnose skate (*Raja rhina*) in British Columbia waters. Fisheries Research 78(2-3):169-178.

McFarlane, G.A., King, J.R. and Saunders, M.W. 2002. Preliminary study on the use of neural arches in the age determination of bluntnose sixgill sharks (*Hexanchus griseus*). Fishery Bulletin 100(4):861-864.

McLaughlin, D.M. and Morrissey, J.F. 2005. Reproductive biology of *Centrophorus* cf. *uyato* from the Cayman Trench, Jamaica. Journal of the Marine Biological Association of the United Kingdom 85(5):1185-1192.

Malagrino, G., Takemura, A. and Mizue, K. 1981. Studies on Holocephali. 2. On the reproduction of *Chimaera phantasma* Jordan et Snyder caught in the coastal waters of Nagasaki. Bulletin of the Faculty of Fisheries Nagasaki University 51:1-7.

Matta, M.E. 2006. Aspects of the life history of the Alaska skate, *Bathyraja parmifera*, in the eastern Bering Sea. MS Thesis, University of Washington, Seattle, WA. 92 pp.

Matta, M.E. and Gunderson, D.R. In press. Age, growth, maturity, and mortality of the Alaska skate, *Bathyraja parmifera*, in the eastern Bering Sea. Environmental Biology of Fishes.

Matta, B., Gaichas, S., Lowe, S., Stevenson, D., Hoff, G. and Ebert, D. 2006. Section 16.3. Bering Sea and Aleutian Islands skates. Pp. 1017-1062. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fisheries Management Council, Anchorage, AK.

Megalofonou, P. and Damalas, D. 2004. Morphological and biological characteristics of a gravid angular rough shark (*Oxynotus centrina*) and its embryos from the Eastern Mediterranean Sea. Cybium 28(2):105-110.

Moreno, J.A. and Moron, J. 1992. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839). Australian Journal of Marine and Freshwater Research 43(1):77-86.

Moura, T., Figueiredo, I., Bordalo Machado, P. and Serrano Gordo, L. 2004. Growth pattern and reproductive strategy of the holocephalan *Chimaera monstrosa* along the Portuguese continental slope. Journal of the Marine Biological Association of the United Kingdom 84(4):801-804.

Muñoz-Chápuli, R. and Perez Ortega, A. 1985. Resurrection of *Galeus atlanticus* (Vaillant, 1888), as a valid species from the NE-Atlantic Ocean and the Mediterranean Sea. Bulletin du Muséum national d'histoire naturelle, Paris, 4e série, 7, section A, 1:219-233.

Musick, J.A. 1999. Ecology and conservation of long-lived marine animals. Pp. 1-10 In: Musick, J.A. (ed.). Life in the slow lane, ecology and conservation of long-lived marine animals. American Fisheries Society Symposium 23.

Musick, J.A. and Ellis, J.K. 2005. Reproductive evolution of chondrichthyans. Pp. 45-79. Hamlett, W.C. (ed.). Reproductive biology and phylogeny of Chondrichthyes. Sharks, batoids and chimaeras. Science Publishers, Inc., Enfield, USA.

Musick, J.A., Harbin, M.M., Berkeley, S.A., Burgess, G.H., Eklund, A.M., Findley, L., Gilmore , R.G., Golden, J.T., Ha, D.S., Huntsman, G.R., McGovern, J.C., Parker, S.J., Poss, S.G., Sala, E., Schmidt, T.W., Sedberry, G.R., Weeks, H. and Wright, S.G. 2001. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25(11):6-30.

Myagkov, N.A. and Kondyurin, V.V. 1978. Reproduction of the cat shark *Apristurus saldancha* (Barnard, 1925) (Scyliorhinidae, Lamniformes). Biologiya Morya 1978(2):86-87.

Nair, R.V. and Lal Mohan, R.S. 1973. On a new deep sea skate, *Rhinobatos variegatus*, with notes on the deep sea sharks *Halaelurus hispidus*, *Eridacnis radcliffei* and *Eugaleus omanensis* from the Gulf of Mannar. Senckenbergiana biologica 54(1-3):71-80.

Nair, R.V. and Appukuttan, K.K. 1974. Observations on the developmental stages of the smooth dogfish, *Eridacnis radcliffei* Smith from Gulf of Mannar. Indian Journal of Fisheries 21(1):141-151.

Nakano, H., Matsunaga, H., Okamoto, H. and Okazaki, M. 2003. Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. Marine Ecology Progress Series 265:255-261.

Nakaya, K. and Nakano, H. 1995. *Scymnodalatias albicauda* (Elasmobranchii, Squalidae) is a prolific shark. Japanese Journal of Ichthyology 42(3-4):325-328.

Neer, J.A. and Cailliet, G.M. 2001. Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia 2001(3)842-847.

Nolan, C.P. and Hogan, F. 2003. The reproductive biology of the longnose velvet dogfish, *Centroscymnus crepidater*, in the Northeast Atlantic. Poster Presentation. Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries, Queenstown, New Zealand, 1-5 December 2003.

Parsons, G.R. 1986. Observations on the reproductive biology of the marbled catshark, *Galeus arae antillensis*. Northeast Gulf Science 8(2):149-150.

Parsons, G.R., Ingram, G.W. Jr. and Havard, R. 2002. First record of the goblin shark *Mitsukurina owstoni*, Jordan (Family Mitsukurinidae) in the Gulf of Mexico. Southeastern Naturalist 1(2):189-192.

Quaranta, K.L., Didier, D.A., Long, D.J. and Ebert, D.A. 2006. A new species of chimaeroid, *Hydrolagus alphus* sp. nov. (Chimaeriformes: Chimaeridae) from the Galapagos Islands. Zootaxa 1377:33-45.

Orlov, A.M. and Biryukov, I.A. 2005. Catch of egg-capsules of female *Bathyraja violacea* (Rajidae) ready for deposition. Journal of Ichthyology 45(2):407-409.

Rey, J., de Sola, L.G. and Massutí, E. 2005. Distribution and biology of the blackmouth catshark *Galeus melastomus* in the Alboran Sea (Southwestern Mediterranean). Journal of Northwest Atlantic Fishery Science 35:215-223.

Richardson, A.J., Maharaj, G., Compagno, L.J.V., Leslie, R.W., Ebert, D.A. and Gibbons, M.J. 2000. Abundance, distribution, morphometrics, reproduction and diet of the Izak catshark. Journal of Fish Biology 56(3):552-576.

Rincon, G., Stehmann, M.F.W. and Vooren, C.M. 2001. Results of the research cruises of FRV 'Walther Herwig' to South America. LXXIV. *Benthobatis kreffti* n. sp. (Chondrichthyes, Torpediniformes, Narcinidae), a new deep-water electric ray from off south Brazil and the third species of the genus. Archive of Fishery and Marine Research 49(1):45-60.

Ruocco, N.L., Lucifora, L.O., Díaz de Astarloa, J.M. and Wöhler, O. 2006. Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the Southwest Atlantic. ICES Journal of Marine Science 63(1):105-116.

Ryland, J.S. and Ajayi, T.O. 1984. Growth and population dynamics of three *Raja* species (batoidei) in Carmarthen Bay, British Isles. Journal du Conseil International pour l'Exploration de la Mer 41:111-120.

Saemundsson, B. 1922. Zoologiske Meddelelser fra Island. XIV. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 74:159-201.

Sathyanesan, A.G. 1966. Egg laying of the chimaeroid fish *Hydrolagus colliei*. Copeia 1966(1):132-134.

Saunders, M.W. and McFarlane, G.A. 1993. Age and length at maturity of the spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. Environmental Biology of Fishes 38:49-57.

Serena, F., Cecchi, E., Mancusi, C. and Pajetta, R. 2006. Contribution to the knowledge of the biology of *Etmopterus spinax* (Linnaeus 1758) (Chondrichthyes, Etmopteridae). FAO Fisheries Proceedings 3(2):388-394.

Séret, B. 1987. *Halaelurus clevai*, sp. n., a new species of catshark (Scyliorhinidae) from off Madagascar, with remarks on the taxonomic status of the genera *Halaelurus* Gill and *Galeus* Rafinesque. J.L.B. Smith Institute of Ichthyology Special Publication 44:1-27.

Simpfendorfer, C.A. 1999. Mortality estimates, and demographic analysis, for the Australian sharpnose shark (*Rhizoprionodon taylori*) from northern Australia. Fishery Bulletin 97:978-986.

Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C. and Metcalfe, J.D. 2003. Seasonal movements and behaviour of basking sharks from archival tagging: No evidence of winter hibernation. Marine Ecology Progress Series 248:187-196.

Sion, L., D'Onghia, G. and Carlucci, R. 2002. A simple technique for ageing the velvet belly, *Etmopterus spinax* (Squalidae). Pp. 135-139. In: Vacchi, M., La Mesa, G., Serena, F. and Séret, B. (eds.). Proceedings of the 4th European Elasmobranch Association Meeting, Livorno, Italy.

Sion, L., D'Onghia, G., Tursi, A. and Mytilineou, Ch. 2003. First data on distribution and biology of *Squalus blainvillei* (Risso, 1826) from the eastern Mediterranean Sea. Journal of Northwest Atlantic Fishery Science 31:213-219.

Sminkey, T.R. and Tabit, C.R. 1992. Reproductive biology of the chain dogfish, *Scyliorhinus retifer*, from the Mid-Atlantic Bight. Copeia 1992(1):251-253.

Smith, S.E., Au, D.W. and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Marine and Freshwater Research 49:663-678.

Soundararajan, R. and Dam Roy, S. 2004. Distributional record and biological notes on two deep-sea sharks, *Centrophorus acus* Garman and *Squalus megalops* (Macleay), from Andaman waters. Journal of the Marine Biological Association of India 46(2):178-184.

Springer, S. 1979. A revision of the catsharks, family Scyliorhinidae. NOAA Technical Report NMFS Circular 422.

Springer, S. and Waller, R.A. 1969. *Hexanchus vitulus*, a new sixgill shark from the Bahamas. Bulletin of Marine Science 19:159-174.

Stehmann, M.F.W. 1990. Rajidae. Pp. 29-50. In: Quero, J.-C., Hureau, J.-C., Karrer, C., Post, A. and Sandanha, L. (eds.). Check-list of the fishes of the eastern tropical Atlantic, vol. 1. Junta Nacional de Investigaçao Cientifica e Tecnológica, Lisbon.

Stehmann, M.F.W. and Merrett, N.R. 2001. First records of advanced embryos and egg capsules of *Bathyraja* skates from the deep north-eastern Atlantic. Journal of Fish Biology 59(2):338-349.

Stevens, J.D. and McLoughlin, K.J. 1991. Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Australian Journal of Marine and Freshwater Research 42(2):151-199.

Stewart, A. 2000. False catshark – a real rarity. Seafood New Zealand 8(1):74-76.

Sulikowski, J.A., Kneebone, J., Elzey, S., Jurek, J., Danley, P.D., Huntting Howell, W. and Tsang P.C.W. 2005a. Age and growth estimates of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fishery Bulletin 103(1):161-168.

Sulikowski, J.A., Kneebone, J., Elzey, S., Jurek, J., Danley, P.D., Huntting Howell, W. and Tsang P.C.W. 2005b. The reproductive cycle of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fishery Bulletin 103(3):536-543.

Sulikowski, J.A., Kneebone, J., Elzey, S., Jurek, J., Howell, W.H. and Tsang, P.C.W. 2006. Using the composite variables of reproductive morphology, histology and steroid hormones to determine age and size at sexual maturity for the thorny skate *Amblyraja radiata* in the western Gulf of Maine. Journal of Fish Biology 69:1449-1465.

Sulikowski, J.A., Elzey, S., Kneebone, J., Jurek, J., Huntting Howell, W. and Tsang, P.C.W. 2007. The reproductive cycle of the smooth skate, *Malacoraja senta*, in the Gulf of Maine. Marine and Freshwater Research 58(1):98-103.

Sullivan, K.J. 1977. Age and growth of the elephantfish *Callorhinchus milii* (Elasmobranchii: Callorhynchidae). New Zealand Journal of Marine and Freshwater Research 11(4):745-753.

Sund, O. 1943. Et brugdebarsel. Naturen 67:285-286.

Tanaka, S. 1990. The structure of the dorsal spine of the deep sea squaloid shark *Centrophorus acus* and its utility for age determination. Bulletin of the Japanese Society of Scientific Fisheries 56(6):903-909.

Tanaka, S. and Mizue, K. 1977. Studies on sharks. - XI. Reproduction in female *Heptranchias perlo*. Bulletin of the Faculty of Fisheries, Nagasaki University 42:1-9.

Tanaka, S., Shiobara, Y., Hioki, S., Abe, H., Nishi, G., Yano. K. and Suzuki, K. 1990. The reproductive biology of the frilled shark, *Chlamydoselachus anguineus*, from Suruga Bay, Japan. Japanese Journal of Ichthyology 37(3):273-291.

Taniuchi, T. and Tachikawa, H. 1999. Geographical variation in age and growth of *Squalus mitsukurii* (Elasmobranchii: Squalidae) in the North Pacific. Pp. 321-328 In: Séret, B. and Sire, J.-Y. (eds.). Proceedings 5th Indo-Pacific Fish Conference, Noumea, New Caledonia, 3-8 November 1997. Soc. Fr. Ichtyol., Paris.

Taniuchi, T., Kobayashi, H. and Otake, T. 1984. Occurrence and reproductive mode of the false cat shark, *Pseudotriakis microdon*, in Japan. Japanese Journal of Ichthyology 31(1):88-92.

Taniuchi, T., Tachikawa, H., Shimizu, M. and Nose, Y. 1993. Geographical variations in reproductive parameters of shortspine spurdog in the North Pacific. Bulletin of the Japanese Society of Scientific Fisheries 59(1):45-51.

Templeman, W. 1984. Migrations of thorny skate, Raja radiata, tagged in the Newfoundland area. Journal of Northwest Atlantic Fishery Science 5(1):55-63.

Treloar, M.A. and Laurenson, L.J.B. 2005. Preliminary observations on the reproduction, growth and diet of *Urolophus cruciatus* (Lacépéde) and *Urolophus expansus*, McCulloch (Urolophidae) in southeastern Australia. Proceedings of the Royal Society of Victoria 117(2):341-347.

Trinnie, F.I. 2003. Demographic biology of *Urolophus paucimaculatus*, *Trygonoptera* sp. B, *U. cruciatus*, *U. expansus* and *U. bucculentus* (Batiodea: Urolophidae) in South-Eastern Australia. B.Sc. (Honours) Thesis. Deakin University, Warrnambool, Victoria, Australia.

Trunov, I.A. and Kukuev, E.I. 2005. New data on *Torpedo nobiliana* (Torpedinidae) from underwater rises of Azores Islands (Atlantic Ocean). Journal of Ichthyology 45(8):673-677.

Tursi, A., d'Onghia, G., Matarrese, A. and Piscitelli, G. 1993. Observations on the population biology of the blackmouth catshark *Galeus melastomus* (Chondrichthyes, Scyliorhinidae) in the Ionian Sea. Cybium 17(3):187-196.

Ungaro, N., Marano, G. and Musci, E. 1997. *Aspetti relativi alla riproduzione di selaci demersali nel bacino Adriatico sud-occidentale.* Biologia Marina Mediterranea 4(1):567-570.

Vaillant, L. 1901. Sur un griset (*Hexanchus griseus* L. Gm.) du golfe de Gascogne. Bulletin du Muséum d'histoire naturelle, Paris 7:202-204.

Veríssimo, A., Gordo, L., and Figueiredo, I. 2003. Reproductive biology and embryonic development of *Centroscymnus coelolepis* in Portuguese mainland waters. ICES Journal of Marine Science 60(6):1335-1341.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Human Biology 10:181-213.

Vooren, C. M. and Klippel, S. 2005. Biologia e status de conservação dos cações-anjo *Squatina guggenheim*, *Squatina occulta* and *Squatina argentina*. Pp. 57-82. In: Vooren. C.M. and Klippel, S. (eds.). Ações para a conservação de tubarões e raias no sul do Brasil. Igaré, Porto Alegre.

Walmsley-Hart, S.A., Sauer, W.H.H. and Buxton, C.D. 1999. The biology of the skates *Raja wallacei* and *R. pullopunctata* (Batoidea: Rajidae) on the Agulhas Bank, South Africa. South African Journal of Marine Science 21:165-179.

Watson, G. and Smale, M.J. 1998. Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Agulhas Bank, South Africa. Marine and Freshwater Research 49(7):695-703.

Watson, G. and Smale, M.J. 1999. Age and growth of the shortnose spiny dogfish *Squalus megalops* from the Agulhas Bank, South Africa. South African Journal of Marine Science 21:9-18.

Weng, K.C. and Block, B.A. 2004. Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. Fishery Bulletin 102(1):221-229.

Wetherbee, B.M. 1996. Distribution and reproduction of the southern lantern shark from New Zealand. Journal of Fish Biology 49(6):1186-1196.

White, W.T. and Potter, I.C. 2005. Reproductive biology, size and age compositions and growth of the batoid *Urolophus paucimaculatus*, including comparisons with other species of the Urolophidae. Marine and Freshwater Research 56(1):101-110.

Wilson, C.D. and Seki, M.P. 1994. Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean. Fishery Bulletin 92(4):851-864.

Yano, K. 1992. Comments on the reproductive mode of the false cat shark *Pseudotriakis microdon*. Copeia 1992(2):460-468.

Yano, K. 1993. Reproductive biology of the slender smoothhound, *Gollum attenuatus*, collected from New Zealand waters. Environmental Biology of Fishes 38(1-3):59-71.

Yano, K. 1995. Reproductive biology of the black dogfish, *Centroscyllium fabricii*, collected from waters off western Greenland. Journal of the Marine Biological Association of the United Kingdom 75(2):285-310.

Yano, K. and Tanaka, S. 1986. A telemetric study on the movements of the deep sea squaloid shark, *Centrophorus acus*. Pp. 372-380. In: Uyeno, T., Arai, R., Taniuchi, T. and Matsuura,

K. (eds.). Indo-Pacific Fish Biology. Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, Tokyo.

Yano, K. and Tanaka, S. 1988. Size at maturity, reproductive cycle, fecundity and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coelolepis* in Suruga Bay, Japan. Bulletin of the Japanese Society of Scientific Fisheries 54(2):167-174.

Yano, K., Mochizuki, K., Tsukada, O. and Suzuki, K. 2003. Further description and notes of natural history of the viper dogfish, *Trigonognathus kabeyai* from the Kumano-nada Sea and the Ogasawara Islands, Japan (Chondrichthyes: Etmopteridae). Ichthyological Research 50(3):251-258.

Yano, K., Stevens, J.D. and Compagno, L.J.V. 2004. A review of the systematics of the sleeper shark genus *Somniosus* with redescritpions of *Somniosus* (*Somniosus*) *antarcticus* and *Somniosus* (*Rhinoscymnus*) *longus* (Squaliformes: Somniosidae). Ichthyological Research 51:360-373.

Yano, K., Stevens, J.D. and Compagno, L.J.V. 2007. Distribution, reproduction and feeding of the Greenland shark *Somniosus* (*Somniosus*) *microcephalus*, with notes on two other sleeper sharks, *Somniosus* (*Somniosus*) *pacificus* and *Somniosus* (*Somniosus*) *antarcticus*. Journal of Fish Biology 70:374-390.

Zeiner, S.J. and Wolf, P.G. 1993. Growth characteristics and estimates of age at maturity of two species of skates (*Raja binoculata* and *Raja rhina*) from Monterey Bay, California. NOAA Technical Report NMFS 115:87-90.

SECTION III.
DEEPWATER CHONDRICHTHYANS AND FISHERIES

There is a general lack of available trade and landings data for deepwater chondrichthyans (Cavanagh and Kyne 2005). Indeed, statistics are often lacking for catches of sharks, rays and chimaeras in general. Globally, the chondrichthyan fishes represent approximately 1% of total fisheries production (Bonfil 1994), although the reported catch has been increasing over the past three decades (Stevens et al. 2000, FAO FIGIS database). Many deepwater species are taken as bycatch, often discarded, or landed under generic species-codes such as 'shark' or 'other'. It has been suggested that 50% of the world's catch of chondrichthyans is taken as bycatch (Stevens et al. 2000) and while Bonfil (1994) suggested that the actual annual catch of chondrichthyans may be twice as high as the reported catch, Clarke et al. (2006) postulated that the biomass of shark involved in the shark fin trade is 3–4 times higher than reported catch statistics indicate.

As traditional marine resource stocks are depleted, global demand for fish products increases and fishing technology advances, fisheries are moving into deeper water and new commercial deepwater fisheries are continuing to develop (Gordon 1999, Lack et al. 2003, Morato et al. 2006). The lack of accurate catch data, including the under-reporting of catches, the lack of recording bycatch, poor taxonomic resolution and species-identification, and illegal fishing, makes an assessment of the global catch of deepwater chondrichthyans extremely difficult.

This Section reviews available fisheries data on deepwater chondrichthyans utilizing FAO (the United Nation's Food and Agriculture Organization) fisheries statistics to overview trends in global and regional production of deepwater chondrichthyans. There are considerable limitations to this data and these are discussed in this Section. Additionally, a number of case studies are presented covering southern Australia, the Northeast Atlantic, the Azores, the Maldives and Namibia. For some of these case studies, actual catch data is not available, but they are discussed to demonstrate a collapse in a deepwater shark fishery (Maldives) and approaches to the precautionary management of a developing deepwater shark fishery (Namibia).

GLOBAL PRODUCTION OF DEEPWATER CHONDRICHTHYANS, 1950-2004

Status: Increasing but fluctuating trend in global production. Poor data resolution and under-reporting make this analysis of questionable accuracy, and together with bycatch issues and illegal fishing, make an assessment of global trends extremely difficult.

The FAO FIGIS database provides global production statistics for fish and other living marine resources for the years 1950 to 2004. Data were extracted for production statistics of all 'deepwater' chondrichthyans, that is for species or species groups that are listed in Section I of this report (annotated checklist of deepwater chondrichthyans). Table 3.1 outlines the FAO database categories and their corresponding scientific names that were used in this analysis.

Global and regional (by major ocean region) production figures are presented for 1950–2004 for all deepwater species categories combined. The major ocean regions used are based upon the FAO's Major Fishing Areas for Statistical Purposes as outlined in the introduction of Section I of this report. Data for major ocean regions were compiled by extracting data for all deepwater species categories for each FAO Fisheries Area within that region. Within the FAO database there were no data for the following FAO Areas: Arctic Sea (FAO Fisheries Area 18), Southeast Atlantic (47), Western Indian (51), Eastern Indian (57), Western Central Pacific (71), Southeast Pacific (87), Antarctic areas nei (FAO Area 98) and Marine areas outside the Antarctic (99). The major ocean regions are thus as follows: Indo-West Pacific - Northwest Pacific (61) and Southwest Pacific (81); Eastern Pacific - Northeast Pacific (67) and Eastern Central Pacific (77); Western Atlantic - Northwest Atlantic (21), Western Central Atlantic (31) and Southwest Atlantic (41); Eastern Atlantic - Northeast Atlantic (27), Eastern Central Atlantic (34) and Mediterranean and Black Sea (37); and, Antarctic Seas - Antarctic Atlantic (48), Antarctic Indian (58) and Antarctic Pacific (88).

Limitations of using global FAO fisheries data

Some FAO database species categories used in this analysis are likely to include captures made in shelf or epipelagic waters (those waters <200m). Examples include the Argentine angelshark *Squatina argentina*, which has been taken in various fisheries off southern Brazil, both on the shelf and the upper slope, and the bigeye thresher *Alopias superciliosus*, taken in pelagic longline fisheries, mostly in the epipelagic zone at night. However, they are included here as these species have been considered 'deepwater' species under the definition provided in Section I of this report. Some broad species categories included in the analyses also likely include shelf captures, for example the FAO category dogfish sharks etc. nei (=Squaliformes) likely includes shelf captures of species such as *Squalus megalops* (but not of *Squalus acanthias* which is primarily a shelf species and which by far represent the greatest volume of landed squaloid globally – this species has a separate FAO species category not here included).

The FAO databases rely on the reporting of catch, landing and production statistics by national reporting offices. However, reporting is not consistent across all countries and hence there is a vast under-reporting of catches to FAO. Many nations for which there is poor fisheries management and statistical reporting (usually under-developed nations) do not report catches to FAO. However, this problem is not only restricted to poorer nations, with some developed countries also failing to report their catches to FAO. This under-reporting severely limits the accuracy of the FAO data. Illegal fishing is also not factored into these analyses and contributes to the underestimation of global figures.

Overall, the global volumes and trends provided here represent considerable underestimates; not only because of unreported catches, but since several broad FAO species categories are not included in these analyses which would include deepwater species. These broad categories (FAO category name followed by corresponding scientific name in parentheses) are: various sharks nei (Selachians); torpedo rays (*Torpedo* spp); sharks, rays, skates, etc. nei (Elasmobranchii); rays and skates nei (Rajidae); rays, stingrays, mantas nei (Rajiformes); *Raja* rays nei (*Raja* spp); dogfishes and hounds nei (Squaliformes, Scyliorhinidae); catsharks, etc. nei (Scyliorhinidae); and, catsharks, nursehounds nei (*Scyliorhinus* spp). It is impossible to separate the catch statistics attributed to deepwater versus shelf species in these broad groupings and thus they are excluded from the analyses.

Global production

Reported global catch of deepwater chondrichthyans (all 'deepwater' categories specified in Table 3.1) for 1950 was 18245t, showing a steady increase to 30304t in 2004. There were two considerable peaks in reported production, one in the early 1970s to the mid 1980s (peaking at 44413t in 1975) and the other during the 1990s (peaking at 59393t in 1996). The latter peak was followed by a rapid decline to 27026t in the year 2000, before beginning to rise slightly until the end of the time-series (Figure 3.1).

The global trend is largely influenced by the trends in production figures from the Eastern and Western Atlantic. The decline after the 1996 peak is a result of a reduction in reported catch from the Western Atlantic and the slight increase at the end of the global time-series, a result of increases in reported catch from the Eastern Atlantic. This ocean region has shown an upward trend in reported catches across the time-series. It is the Atlantic were at present the bulk of deepsea fishing activities occur, with little contribution from the other major ocean regions. The exception is during the 1950s where the bulk of reported catches came from the Indo-West Pacific. From initial reported catches of ~10000t in the 1950s, reported catches from the Indo-West Pacific declined consistently to <1000t in 1967 with low reported catches until 1975. From 1976 to 1990 there were no reported catches for the deepwater species categories and reported catches in the 1990s were generally low, reaching ~5000t at the end of the time-series. Reported catches from the Eastern Pacific have maintained low levels across the time-series (generally <3000t) with slight peaks in 1979 (4086t) and 1987 (3666t). At present, deeper water chondrichthyan fishing is generally limited in the Eastern Pacific region (skates are targeted in some areas) and reported catches are very low (2-6t) towards the end of the time-series. The contribution to reported global production from the Antarctic Seas region is minor and is not illustrated in Figure 3.1. Catches in any deepwater category were not reported until 1999 and were between 7 and 62t annually for the period 1999 to 2004.

It is difficult to relate causative effects to the trends in global and regional reported catches. It is uncertain if peaks and troughs are related to market forces, stock collapse, fishery shifts or changes in reporting. The data used are simple reported landings and are not standardized for effort. It also needs to be re-emphasized that this analysis is under the considerable limitations outlined previously.

Figure 3.2 shows a comparison between global reported catches from *deepwater* chondrichthyans and global reported catches of *all* chondrichthyans for the time period 1950–2004. Specified deepwater catches represent only 1.8–7.5% of all chondrichthyans across the time period (6.7% in 1950, 3.7% in 2004). To highlight the non-specific reporting of chondrichthyan catches, global reported catch of all chondrichthyans was compared with catches reported in 'other' non-specified categories (the FAO species categories: sharks, rays, skates, etc. nei; catsharks, etc. nei; catsharks, nursehounds nei; dogfish sharks, etc. nei; dogfish sharks nei; dogfishes and hounds nei; rays, stingrays, mantas nei; rays and skates nei; and, various sharks nei). Reporting under these categories represented 57.5–73.0% of all reported catches, demonstrating the poor species-specific reporting of chondrichthyan fisheries statistics. The extent to which deepwater chondrichthyans are included within these broad non-specific categories is unknown and as such the global and regional trends presented here, while providing a general overview, should be interpreted with caution.

Table 3.1. FAO FIGIS database categories included in analyses and their corresponding scientific names. nei, not elsewhere included.

FAO database category	**Scientific name**
Angular roughshark	*Oxynotus centrina*
Antarctic starry skate	*Amblyraja georgiana*
Arctic skate	*Amblyraja hyperbora*
Argentine angelshark	*Squatina argentina*
Basking shark	*Cetorhinus maximus*
Bathyraja rays nei	*Bathyraja* spp
Bigeye thresher	*Alopias superciliosus*
Birdbeak dogfish	*Deania calcea*
Black dogfish	*Centroscyllium fabricii*
Blackmouth catshark	*Galeus melastomus*
Blue skate	*Dipturus batis*
Bluntnose sixgill shark	*Hexanchus griseus*
Bramble shark	*Echinorhinus brucus*
Chimaeras, etc. nei	Chimaeriformes
Cuckoo ray	*Leucoraja naevus*
Dark ghost shark	*Hydrolagus novaezealandiae*
Dark-belly skate	*Bathyraja meridionalis*
Dogfish sharks, etc. nei	Squaliformes
Dusky catshark	*Bythaelurus canescens*
Eaton's skate	*Bathyraja eatonii*
Greenland shark	*Somniosus microcephalus*
Gulper shark	*Centrophorus granulosus*
Kerguelen sandpaper skate	*Bathyraja irrasa*
Kitefin shark	*Dalatias licha*
Lanternsharks nei.	*Etmopterus* spp
Leafscale gulper shark	*Centrophorus squamosus*
Little sleeper shark	*Somniosus rostratus*
Longnose velvet dogfish	*Centroselachus crepidater*
Longnosed skate	*Dipturus oxyrhynchus*
McCain's skate	*Bathyraja maccaini*
Murray's skate	*Bathyraja murrayi*
Pacific sleeper shark	*Somniosus pacificus*
Portuguese dogfish	*Centroscymnus coelolepis*
Rabbit fish	*Chimaera monstrosa*
Ratfishes nei	*Hydrolagus* spp
Sailfin roughshark	*Oxynotus paradoxus*
Sailray	*Dipturus lintea*
Shagreen ray	*Leucoraja fullonica*
Spotted ratfish	*Hydrolagus colliei*
Starry ray	*Amblyraja radiata*
Straightnose rabbitfish	*Rhinochimaera atlantica*
Velvet belly	*Etmopterus spinax*

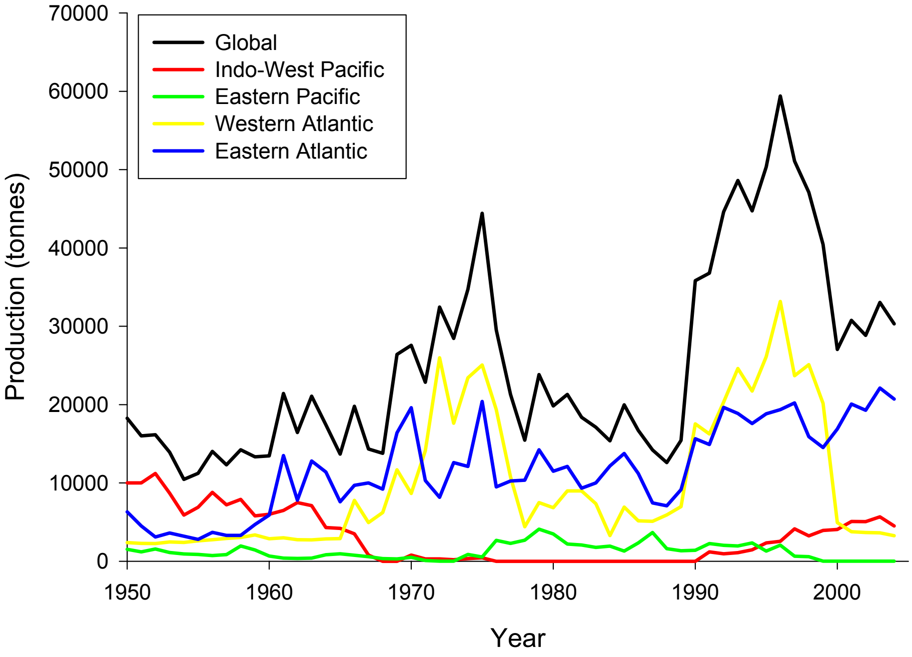


Figure 3.1. Global deepwater chondrichthyan production 1950–2004 from the FAO FIGIS database (global production statistics). Global, all FAO Fisheries Areas combined; Indo-West Pacific, FAO Areas 61, 81; Eastern Pacific, FAO Areas 67, 77; Western Atlantic, FAO Areas 21, 31, 41; Eastern Atlantic, FAO Areas 27, 34, 37.

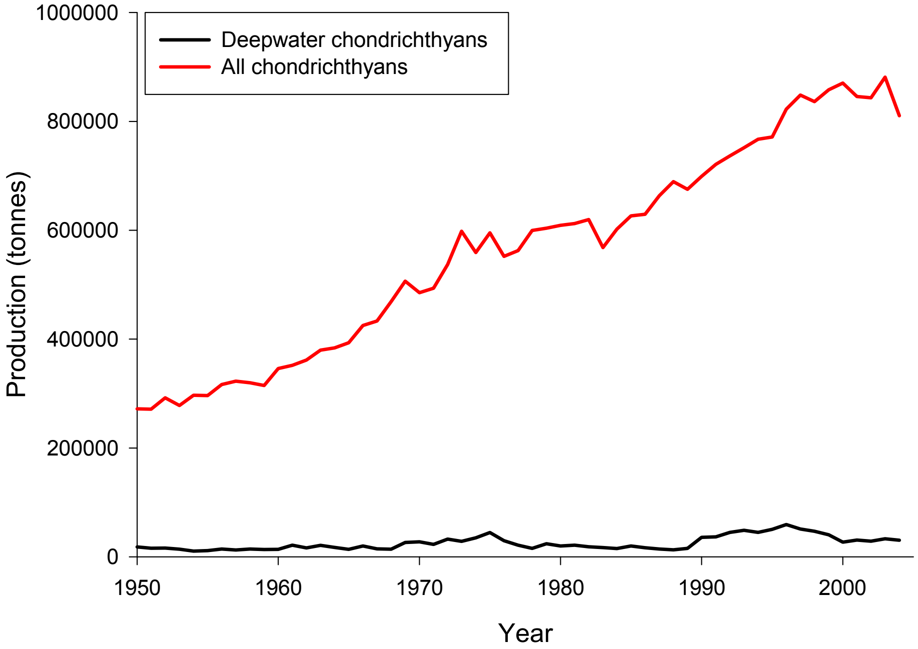


Figure 3.2. Comparison of global chondrichthyan (all species – shallow, deep and pelagic) and global deepwater chondrichthyan production 1950–2004 from the FAO FIGIS database (global production statistics).

CASE STUDY 1. AUSTRALIAN SOUTHERN AND EASTERN SCALEFISH AND SHARK FISHERY

Status: Intensive fishing has depleted upper slope species, 98-99% decline for Centrophorus *spp over twenty-year period. Declines documented for several other upper slope chondrichthyans. Mid-slope species now managed, but continuing pressure on the upper slope.*

The Australian Southern and Eastern Scalefish and Shark Fishery (SESSF) extends across southern and southeastern Australia over an extensive area of the Australian Fishing Zone. The SESSF is a Commonwealth-managed fishery, that is, it is managed by the Australian Federal Government (in cooperation with State fisheries agencies) through the Australian Fisheries Management Authority (AFMA). The SESSF is a complex multi-species, multi-gear fishery that comprises several sectors including the Commonwealth Trawl Sector (CTS) (formerly known as the South East Trawl Fishery (SETF)), the Great Australian Bight Trawl Sector, the East Coast Deepwater Trawl Sector, and the Gillnet, Hook and Trap Sectors. Deepwater sharks are caught across the SESSF, although it is the CTS that is responsible for the majority of the deepwater shark catch (Daley et al. 2002).

Daley et al. (2002) undertook a catch analysis of deepwater squaloid sharks from southern Australia and most of this introductory information is drawn from that source. Little information is available on the catch of deepwater sharks from the earlier years of slope fishing, which developed off the east coast (the state of New South Wales) in the 1970s and off the southern states of Victoria and Tasmania in the 1980s. Initial catch levels off NSW were reportedly high and as there was no market for deepwater shark carcasses, discarding levels were also very high (Daley et al. 2002). Logbook data showed that substantial amounts of deepwater shark were taken off NSW in the 1980s and fisheries-independent surveys on the NSW upper slope have shown the depletion of the upper-slope resource (Graham et al. 2001).

In Australia, there are two main domestic fish markets where the vast majority of shark landings are sold: Sydney (NSW) and Melbourne (Victoria). Victorian regulations on the mercury content of shark flesh restricted any targeting of large deepwater sharks off Victoria and Tasmania before the regulation was eased in 1995. Daley et al. (2002) believes that there would have been significant discarding prior to that time. A number of market and management changes led to an increased interest in the deepwater dogfish resource, and the targeting of slope species. These included the development of a liver oil market (considerably higher value than flesh), relaxation of the Victorian mercury content regulations and the introduction to the fishery of a quota management system for target teleost (bony) fishes (Daley et al. 2002). Once quotas were introduced, fishers sought alternative species that were not under quota, including deepwater sharks. A discussion follows on logbook data presented by Daley et al. (2002) from 1986 to 1999, 'mid-slope' species catch data provided by AFMA from 1997–2006, and the results of fishery-independent surveys of the NSW upper-slope as presented by Graham et al. (2001).

Daley et al. (2002) reported a 75% decline in the SETF catch rates of upper-slope dogfish from 1986 to 1999, and a 59% decline in the logbook reported catch of *Centrophorus* spp off NSW. *Centrophorus* spp and other squaloids were essentially depleted on the upper slope before the late 1990s (Graham et al. 2001) with the largest declines apparent from the 200–399m and 400–649m depth ranges off NSW (Daley et al. 2002). The majority of the dogfish catch in the SETF for 1999 and 2000 was taken from the 'mid-slope' (650–1200m) (Daley et al. 2002).

Over the past few years, AFMA has introduced management for deepwater sharks within the SESSF. In 2003, trip limits were first imposed for landings of *Centrophorus* in Commonwealth waters, although the landing of mid-slope deepwater dogfishes was largely unregulated until 2005. However, from 2003 the landing of dogfishes (including mid-slope species) required the landing of both the liver and carcass so that accurate landing information may be obtained. Due to the difficulty in accurately identifying many deepwater dogfish species, AFMA introduced a 'basket' quota management system for the SESSF in 2005. This 'basket' included various species of mid-slope dogfishes, many considered 'discard' species and the quota system set a Transferable Allowable Catch for 2005 and 2006 at around half the reported 2004 catch (200t). Shark species covered under this quota are shown in Table 3.2. Note that the quota does not include *Squalus* dogfishes (outer shelf and upper slope species), known locally as 'greeneye' sharks (*Squalus megalops*, *S. mitsukurii* and *S.* sp. F) and catches of these remain unregulated. *Centrophorus* spp (upper slope species) remain managed under individual trip limits.

Landings data for 'deepwater sharks' (i.e. 'mid-slope' species) from all Sectors of the SESSF, provided by AFMA are shown in Figure 3.3. Landings peaked in 2002–2004 before the quota was introduced. A bycatch-only TAC of 22t has been introduced for 2007 as a precautionary management measure. The data provided by AFMA are based on Catch Disposal Records and the reliability of this data is questionable, particularly prior to 2000 when the Catch Disposal Records were introduced (M. Piasente, pers. comm.).

With a lack of species-specific reporting of catches it can not be determined from the industry data presented by Daley et al. (2002) which species have been most affected. This information, however, can be drawn from fisheries-independent surveys undertaken on the NSW upper slope. Graham et al. (2001) compared catches of chondrichthyans in three areas of the upper slope off NSW at depths of 200–605m from standardized surveys undertaken in 1976–1977 and 1996–1997. A summary of changes in chondrichthyan populations is given in Table 3.3. The largest declines occurred amongst the *Centrophorus* species; *C. harrissoni* and *C.* cf. *uyato* taken in 1996–97 at 0.3% of the 1976–77 catch level, and *C. moluccensis* at 1.6% of 1976–77 levels. Changes in relative abundance of greater than -90% were also demonstrated for *Heptranchias perlo*, *Squalus mitsukurii*, *S.* sp. F, *Squatina* sp. A and *Hydrolagus ogilbyi*. *Deania quadrispinosum* and skates (*Dipturus* spp) declined by >80%. The only chondrichthyan to show an increase in relative abundance was *Squalus megalops*, increasing by 18% across the three study areas. This is an abundant small dogfish, also common on the outer shelf and likely to be recruiting from there to the upper slope (Graham et al. 2001). It may also have benefited from the decline of other species. It is clear that two decades of intensive trawl fishing by the SETF caused the collapse of chondrichthyan populations on the upper slope off NSW. Continued exploitation after 1996 and targeting of deepwater sharks on the 'mid slope' (650–1200m) added to the pressures already faced by these species. It is also important to note when considering catch data that localised extirpations for many mid-slope species may have gone unnoticed due to vessels moving from seamount to seamount during fishing operations.

Considering the productivity analyses undertaken in Section II of this report, populations of these species, particularly the overexploited *Centrophorus* spp, will take considerable time to recover. A recent ban on commercial trawling at depths >700m in the SESSF (>750m in the Great Australian Bight) should have significant conservation benefits for deepwater chondrichthyans (Department of Agriculture, Fisheries and Forestry media release DAFF07/005A, 29 January 2007). However, while a bycatch only TAC is in place for 'deepwater sharks' (mid-slope species), ongoing fishing pressure on the upper slope will continue to impact some of the most unproductive shark species (e.g. *Centrophorus*) through bycatch.

Table 3.2. Mid-slope deepwater shark species covered under the 'deepwater shark' quota in Australia's Southern and Eastern Scalefish and Shark Fishery. Courtesy of AFMA.

Family	AFMA common Name	Scientific name	Other local common names
Centrophoridae	Brier shark	*Deania calcea*	birdbeak dogfish, deepwater dogfish, platypus shark, roughskin dogfish
	Longsnout dogfish	*Deania quadrispinosum*	
Etmopteridae	Bareskin dogfish	*Centroscyllium kamoharai*	
	Smooth lanternshark	*Etmopterus bigelowi*	black shark, seal shark
	Short-tail lanternshark	*Etmopterus brachyurus*	
	Pink lanternshark	*Etmopterus dianthus*	
	Lined lanternshark	*Etmopterus dislineatus*	
	Blackmouth lanternshark	*Etmopterus evansi*	
	Pygmy lanternshark	*Etmopterus fusus*	
	Southern lanternshark	*Etmopterus granulosus**	
	Blackbelly lanternshark	*Etmopterus lucifer*	
	Mollers lanternshark	*Etmopterus molleri*	
	Slender lanternshark	*Etmopterus pusillus*	
Somniosidae	Portuguese dogfish	*Centroscymnus coelolepis*	
	Golden dogfish	*Centroselachus crepidater*	black shark, longnose dogfish, roughskin dogfish, small spine dogfish, smallspine shark
	Owstons dogfish	*Centroscymnus owstoni*	black shark, roughskin dogfish, smallspine dogfish, smallspine shark
	Plunkets dogfish	*Proscymnodon plunketi*	
Dalatiidae	Black shark	*Dalatias licha*	kitefin shark, seal shark

*Although listed by AFMA, this species does not occur in Australian waters and is referable to *E. baxteri*.

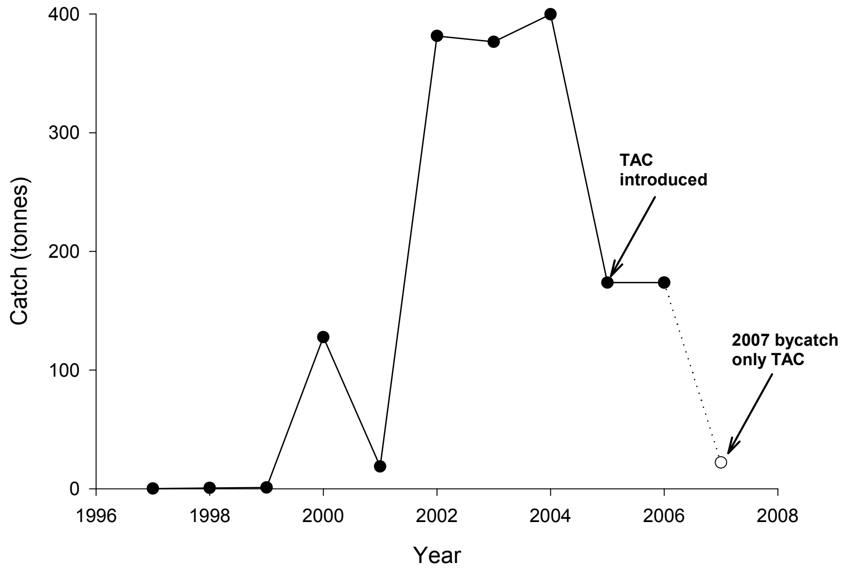


Figure 3.3. Landings of 'deepwater shark' ('mid-slope' species listed in Table 3.2) from the Australia Southern and Eastern Scalefish and Shark Fishery for the period 1997 to 2006. A 'deepwater shark' quota was introduced in 2005, and a bycatch-only quota of 22t for 2007. Data provided by AFMA.

Table 3.3. Changes in the relative abundance of chondrichthyan species on the NSW upper slope between 1976–77 and 1996–97. Data from Graham et al. (2001).

Family	Species	Trend	Extent of change
Hexanchidae	*Heptranchias perlo*	Decline	-91.4%
Squalidae	*Squalus megalops*	Increase	+18.0%
	Squalus mitsukurii & *Squalus* sp. F	Decline	-97.3%
Centrophoridae	*Centrophorus harrissoni*	Decline	-99.7%
	Centrophorus moluccensis	Decline	-98.4%
	Centrophorus cf. *uyato*	Decline	-99.7%
	Deania quadrispinosum	Decline	-87.3%
Squatinidae	*Squatina* sp. A	Decline	-96.0%
Pristiophoridae	*Pristiophorus* sp. A	Decline	-47.9%
Scyliorhinidae	*Cephaloscyllium* sp. A	Decline	-31.9%
Rajidae	*Dipturus* spp[1]	Decline	-83.2%
Chimaeridae	*Hydrolagus ogilbyi*[2]	Decline	-96.4%

[1] Comprises *Dipturus australis**, *D. gudgeri*, *D. whitleyi**, *D.* sp. A*, *D.* sp. B, *D.* sp. C, *D.* sp. J, *D.* sp. J. (*primarily shelf species); [2] Possibly includes catches of *H. lemures*.

CASE STUDY 2. NORTHEAST ATLANTIC DEEPWATER FISHERIES

Status: Stocks of the most commonly caught species, the leafscale gulper shark Centrophorus squamosus *and the Portuguese dogfish* Centroscymnus coelolepis*, are depleted. Little data on other species, but some declines are also evident.*

The most common commercially-encountered deepwater sharks in the Northeast Atlantic are the leafscale gulper shark *Centrophorus squamosus*, birdbeak dogfish *Deania calcea*, black dogfish *Centroscyllium fabricii*, velvet belly *Etmopterus spinax*, great lanternshark *E. princeps*, Portuguese dogfish *Centroscymnus coelolepis*, longnose velvet dogfish *Centroselachus crepidater*, knifetooth dogfish *Scymnodon ringens* and the kitefin shark *Dalatias licha* (Basson et al. 2002, ICES 2005). Some scyliorhinid catsharks (*Apristurus* and *Galeus* spp) are also locally common, particularly the blackmouth catshark *G. melastomus* (Basson et al. 2002).

Fisheries research in the Northeast Atlantic is coordinated through ICES (the International Council for the Exploration of the Sea) using data reported from a system of regional Sub areas. The majority of deepwater shark fishing activities occur in northern ICES Sub areas (Sub areas V, VI, VII, XII), particularly around the Rockall Trough and on the Porcupine Bank slopes, which lay to the west of the British Isles (Clarke et al. 2002). Species are taken in multi-species trawl and multi-species and directed longline fisheries. France, Iceland, Ireland, Norway, Portugal, Spain and the UK are the main countries in the region landing deepwater sharks (Walker et al. 2005). The most commonly landed species are *C. squamosus* and *C. coelolepis*, and it is these two species which are the primary focus of this case study. ICES (2006) presented limited landings data for other deepwater shark species in the Northeast Atlantic, however no CPUE data are available. It has only been since 1988 that *C. squamosus* and *C. coelolepis* have begun to be landed, initially by the French, then the Spanish and later by other nations (Heessen 2003, ICES 2006). The short time-period of the fisheries has generally limited assessments of trend data, until recently when ICES presented a series of CPUE trends for these species to advise that the stock had been depleted (ICES 2005).

Prior to the ICES advice, Basson et al. (2002) reported a declining trend for French trawl *C. squamosus* and *C. coelolepis* CPUE over a short time-series of 1990–1998 in ICES Sub areas VI and VII and Division Vb (the area to the West of the British Isles). They used production models to undertake biomass estimates, with results indicating that the exploitable biomass of these two species in those regions was below 50% virgin biomass. However, the short time-series and the effects of fishing at different depths constrain their results. They also made the observation that the French trawl fleet was moving into deeper water to exploit sharks as well as other fish (Basson et al. 2002).

As part of the European-wide DELASS project (Development of Elasmobranch Assessments) (Heessen 2003) stock assessments were attempted for these two species for the Northeast Atlantic as a whole. Although Heessen (2003) reports evidence of a decline in abundance (from CPUE data) for the two species combined in ICES Sub areas V, VI and VII, the stock assessment was unsuccessful due to a short time-series, a lack of species-specific data and a poor understanding of the stock structure of the species in the region.

In 2005, ICES advised a zero catch limit for *C. squamosus* and *C. coelolepis* in ICES areas (i.e. the Northeast Atlantic) (ICES 2005). ICES (2005) noted that exploitation increased significantly from the commencement of fishing at the end of the 1980s while CPUE declined considerably for French, Irish, Norwegian, Portuguese and Scottish trawlers and longliners from 1994 to 2005 in the northern region (ICES Sub areas VI, VII and XII). Longline CPUE for ICES Sub area IX appears to be stable, although the time-series is short (2001 to 2006) (ICES 2006).

Jones et al. (2005) provided further evidence of considerable declines for these two species utilising fisheries-independent data. Trawl surveys undertaken to the west of Scotland between 1998 and 2004 were compared with historical trawl survey data from 1970 to 1978. The historical data is pre-exploitation of deepwater marine resources in the region. There were considerable declines in CPUE between the 1970s surveys and the recent surveys for *C. squamosus* and *C. coelolepis* as well as for *D. licha* and *D. calcea* (1998–2004 survey catches 62–99% lower than 1970s surveys) (Jones et al. 2005). CPUE increased considerably for *C. crepidater* as the result of two unusually large catches in 1998. CPUE also increased for *G. melastomus*, and were comparable between the surveys for *E. spinax* and *Apristurus* spp (Jones et al. 2005). Separate preliminary analysis of the survey data from 1998 to 2004, although a short time-series, showed that CPUE continued to decline for *C. squamosus* and *C. coelolepis* (Jones et al. 2005).

CASE STUDY 3. AZORES KITEFIN SHARK FISHERY

Status: Fisheries for kitefin shark Dalatias licha *ceased in 2001 due to poor market value of livers. A considerable biomass decline is apparent for the stock.*

The kitefin shark *Dalatias licha* was targeted in an artisanal longline (handline) fishery in the Azores from 1972 to 2001. It was also taken in an industrial benthic gillnet fishery from 1980 onwards. Catch and CPUE data are provided in Heessen (2003) and are graphed in Figure 3.4. The catch is dominated by the benthic gillnet fishery which shows three peaks, in its second year (1981) at 667t, in 1984–85 at 842–814t and in 1991at 794t. Catch then declined rapidly to 148t in 1996 and <1t in 2000 and 2001. CPUE in the gillnet fishery peaked in the late eighties-early nineties before declining to initial levels by 1998. Catch in the handline fishery peaked in 1979–1980 at 232–227t before declining to <100t where is remained relatively stable (with some fluctuations) until the early 1990s. Catch then gradually declined to ~11t in 2001. CPUE fluctuated throughout the period of the fishery with a rapid increase in 1996, the last year for which CPUE data are presented in Heessen (2003).

The poor market value of kitefin livers apparently underlies the decline in landings, rather than the collapse of the stock. The species is no longer targeted around the Azores but taken as bycatch in other demersal fisheries (Heessen 2003).

Heessen (2003) undertook a stock assessment for *D. licha* around the Azores and modelled biomass time-series trends based on the catch and CPUE data from the longline and gillnet fisheries. A continuous decline in the predicted biomass was demonstrated from the commencement of fishing in 1972, through the 1970s and 1980s. The severity of the decline (i.e. the slope of the predicted biomass time-series) was greater after the gillnet fishery commenced in 1980. The model suggested that the stock begins to rebuild as the fishery comes to its end. The model also gave estimated probabilities of 51–85% that the stock was overexploited (based on comparing estimated biomass in 2001 with predictions of Maximum Sustainable Yield) (Heessen 2003).

A considerable biomass decline is apparent from nearly 30 years of fishing pressure for the Azores kitefin shark stock, which was likely exploited beyond sustainable levels. A cessation of fishing suggests that the stock will likely begin to recover, but the overall result appears to suggest local depletion of the population (Heessen 2003).

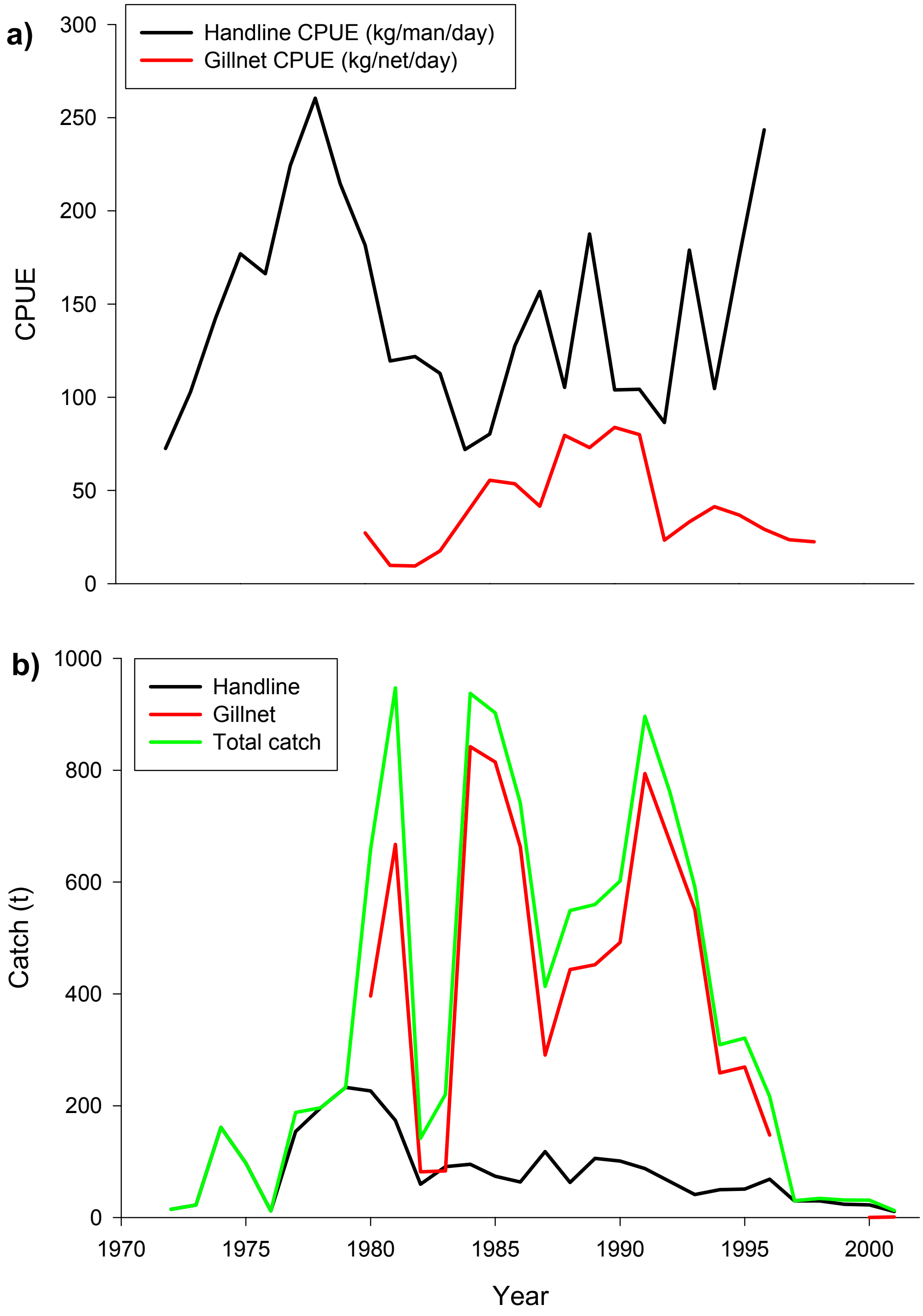


Figure 3.4. a) CPUE, and **b)** catch data for the Azores kitefin shark *Dalatias licha* artisanal longline (handline) and industrial benthic gillnet fisheries from 1972 to 2001. Data from Heessen (2003).

CASE STUDY 4. MALDIVES GULPER SHARK FISHERY

Status: Complete collapse of the gulper shark fishery (targeted for liver oil) after only ~20 years of exploitation.

The exploitation of gulper shark (*Centrophorus* spp) in the Maldives commenced in 1980 using multi-hook handlines (vertical longlines). Sharks were targeted for their livers, which yield a high-value oil (squalene) product that was exported to the Japanese market. Adam et al. (1998) identified three species of gulper shark from the Maldives, the Taiwan gulper shark *Centrophorus niaukang*, the leafscale gulper shark *C. squamosus* and the Mosaic gulper shark *C. tessellatus*. *Centrophorus niaukang* was reported to be the most common species taken in the liver oil fishery (Adam et al. 1998). However, the authors recognise the taxonomic problems associated with the genus and note that their identifications are somewhat tentative. Hence, the actual composition of the Maldivian *Centrophorus* fauna remains unresolved.

Anderson and Ahmed (1993) surveyed shark fishing activities around the Maldives, reporting 31 full-time and 274 part-time vessels, operating from 37 islands involved in the gulper shark fishery. There are no time-series data of catches available for the fishery (M.S. Adam, pers. comm.), only export figures for shark liver oil. Anderson and Ahmed (1993) reported export figures from 1980 to 1991, and a review of government-produced Basic Fisheries Statistics for the Maldives from 1995 to 2002 found that additional figures were available only for the years 1996, 1997, 2001 and 2002 (MOFA 1996, 1997, MOFAMR 2001, 2002). Gulper shark liver oil exports are shown in Figure 3.5. Exports peaked rapidly in 1982 (87400 litres) before showing a general downward trend until 1989. Exports then increased again in 1990 and 1991 while the remaining data shows exports at very low levels up to 2002. This marked the effective end of the fishery due to stock collapse from overfishing of the resource (R.C. Anderson, pers. comm.).

The Maldives *Centrophorus* fishery was short-lived, commencing in 1980 and closing just over 20 years later due to population depletion. The present status of the stock is unknown, but fishing for gulper sharks has ceased. The resource was probably fished beyond sustainable levels in its early years.

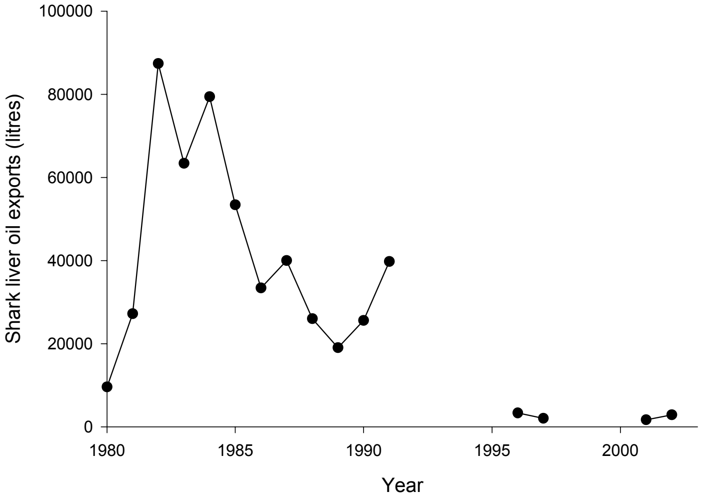


Figure 3.5. Gulper shark (*Centrophorus* spp) liver oil exports from the Maldives from 1980 to 2002. Data for 1980–1991 from Anderson and Ahmed (1993), data for 1996 from MOFA (1996), data for 1997 from MOFA (1997), data from 2001 from MOFAMR (2001) and data from 2002 from MOFAMR (2002). Data could not be sourced for intervening years.

CASE STUDY 5. NAMIBIAN DIRECTED EXPLORATORY DEEPWATER SHARK FISHERY

Status: Short-term fishing rights granted to explore the deepwater shark resource. No commercial licences granted at this stage due to inadequate biomass data. Namibia is taking a precautionary approach to the development of any deepwater shark fishing.

Two fishing companies were granted exploratory rights in 2000 to target deepwater dogfishes off Namibia utilising set nets. The primary target species were the leafscale gulper shark *Centrophorus squamosus*, the longsnout dogfish *Deania quadrispinosum* and the Portuguese dogfish *Centroscymnus coelolepis*. The Namibian government has taken a precautionary approach to the management of deepwater shark fishing, attempting to balance the exploitation of a potentially valuable resource with an understanding of the biological vulnerability of the group (NATMIRC 2003). As such, the exploratory licences were governed by rigid management measures including monitoring and logbook recording of all individuals caught by species and sex (NATMIRC 2003).

Monitoring conducted on three trips between January and June 2002 on one licensed exploratory vessel documented the landing of 131.3t of trunks and 4.5t of fins from *C. squamosus*, and 15.8t of trunks, 9t of fillets and 11.8t of livers from *D. quadrispinosum*, totalling ~172t of deepwater shark product (NATMIRC 2003). The identification of some deepwater dogfishes has been problematic (H. Holtzhausen, pers. comm.) and this may affect species composition data. This exploratory fishing vessel also landed deepwater skate products, with an additional 10.1t of skate wings being recorded during these three trips (NATMIRC 2003). The most commonly harvested skates are the African softnose skate *Bathyraja smithii* and the ghost skate *Rajella dissimilis* (Holtzhausen and Kaanandunge 2003).

The exploratory directed deepwater shark licences expired in January 2006 and as yet there has been no decision made as whether to grant commercial rights to the fishery (H. Holtzhausen, pers. comm.). Insignificant abundance and biomass data to set effective Total Allowable Catches has meant that commercial licences have not yet been granted. Surveys are ongoing to obtain such data in order to make an assessment of the long-term sustainability of the resource, and the level at which the stocks can be exploited if commercial licences are granted (H. Holtzhausen, pers. comm.).

Deepwater dogfishes (including *C. squamosus*, *D. quadrispinosum*, *C. coelolepis* and the shortspine spurdog *Squalus mitsukurii*) are also taken as bycatch by the Namibian Non-directed trawl fishery at depths of 400–1000m (NATMIRC 2003). Species-specific catch data for this fishery is not available as these bycatch species are generally recorded in the 'shark' or 'other' logbook categories (NATMIRC 2003, H. Holtzhausen, pers. comm.).

SECTION III LITERATURE

Adam, M.S., Merrett, N.R. and Anderson, R.C. 1998. Additions to the fish fauna of the Maldives. Part 1: An annotated checklist of the deep demersal fishes of the Maldive Islands. Ichthyological Bulletin of the JLB Smith Institute of Ichthyology 67(Part 1):1-19.

Anderson, R.C. and Ahmed, H. 1993. The shark fisheries of the Maldives. Ministry of Fisheries and Agriculture, Republic of Maldives, Malé and FAO, Rome.

Basson, M., Gordon, J.D.M., Large, P., Lorance, P., Pope, J. and Rackham, B. 2002. The effects of fishing on deep-water fish species to the west of Britain. Joint Nature Conservation Committee Report No. 324. JNCC, Petersborough.

Bonfil, R. 1994. Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper 341:1-119.

Cavanagh, R.D. and Kyne, P.M. 2005. The conservation status of deep-sea chondrichthyan fishes. Pp. 366-380. In: Shotton, R. (ed.). Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries. Part 2: Conference poster papers and workshop papers. Queenstown, New Zealand, 1-5 December 2003 and 27-29 November 2003 Dunedin, New Zealand. FAO Fisheries Proceedings No. 3/2. FAO, Rome.

Clarke, M., Girard, M., Hareide, N.-R., Lorance, P. and Officer, R. 2003. Approaches to assessment of deepwater sharks in the Northeast Atlantic. NAFO Scientific Council Research Document 02/136.

Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H. and Shivji, M.S. 2006. Global estimates of shark catches using trade records from commercial markets. Ecology Letters 9:1115-1126.

Daley, R., Stevens, J. and Graham, K. 2002. Catch analysis and productivity of the deepwater dogfish resource in southern Australia. FRDC Final Report, 1998/108. Fisheries Research and Development Corporation, Canberra.

Gordon, J.D.M. 1999. Management considerations of deep-water shark fisheries. FAO Fisheries Technical Paper 378/2:774-818.

Graham, K.J., Andrew, N.L. and Hodgson, K.E. 2001. Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. Marine and Freshwater Research 52:549-561.

Heessen, H.J.L. (ed.). 2003. Development of elasmobranch assessments DELASS. Final Report of DG Fish Study Contract 99/055.

Holtzhausen, J.A. and Kaanandunge, D. 2003. The emerging fishery for deep sea chondrichthyan fishes off Namibia, south-western Africa. Abstract. Conservation and management of deepsea chondrichthyan fishes. Joint FAO and IUCN Shark Specialist Group Pre-conference Meeting in conjunction with Deepsea 2003. University of Otago, Portobello Marine Laboratory, Portobello, New Zealand, 27-29 November 2003.

ICES. 2005. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2005. Volume 1-11. 1403pp.

ICES. 2006. Report of the Working Group on Elasmobranch Fishes (WGEF), 14-21 June 2006, ICES Headquarters. ICES CM 2006/ACFM:31. 291 pp

Jones, E., Beare, D., Dobby, H., Trinkler, N., Burns, F., Peach, K. and Blasdale, T. 2005. The potential impact of commercial fishing activity on the ecology of deepwater chondrichthyans from the west of Scotland. ICES CM 2005/N:16.

Lack, M., Short, K. and Willock, A. 2003. Managing risk and uncertainty in deepsea fisheries: lessons learned from orange roughy. TRAFFIC Oceania and WWF Endangered Seas Programme.

MOFA. 1996. Basic fisheries statistics Jan – Dec 1996. Economic Planning and Coordination Section, Ministry of Fisheries and Agriculture, Malé.

MOFA. 1997. Basic fisheries statistics Jan – Dec 1997. Economic Planning and Coordination Section, Ministry of Fisheries and Agriculture, Malé.

MOFAMR. 2001. Basic fisheries statistics Jan – Dec 2001. Economic Planning and Coordination Section, Ministry of Fisheries, Agriculture and Marine Resources, Malé.

MOFAMR. 2002. Basic fisheries statistics Jan – Dec 2002. Economic Planning and Coordination Section, Ministry of Fisheries, Agriculture and Marine Resources, Malé.

Morato, T., Watson, R., Pitcher, T.J. and Pauly, D. 2006. Fishing down the deep. Fish and Fisheries 7:24-34.

NATMIRC (National Marine Information and Research Centre). 2003. The Namibian Plan of Action for the Conservation and Management of Sharks (NPOA). NATMIRC, Swakopmund, Namibia.

Stevens, J.D., Bonfil, R., Dulvy, N.K. and Walker, P.A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science 57(3):476-494.

Walker, P., Cavanagh, R.D., Ducrocq, M. and Fowler, S.L. 2005. Northeast Atlantic (including Mediterranean and Black Sea). Pp. 71-95. In: Fowler, S.L., Cavanagh, R.D., Camhi, M., Burgess, G.H., Cailliet, G.M., Fordham, S.V, Simpfendorfer, C.A. and Musick, J.A. Sharks, rays and chimaeras: the status of the chondrichthyan fishes. IUCN SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, U.K.