

Article

The Biology of Mesopelagic Fishes and Their Catches (1950–2018) by Commercial and Experimental Fisheries

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Abstract: Following a brief review of their biology, this contribution is an attempt to provide a global overview of the catches of mesopelagic fishes (of which 2.68 million tonnes were officially reported to the FAO) throughout the world ocean from 1950 to 2018, to serve as a baseline to a future development of these fisheries. The overview is based on a thorough scanning of the literature dealing with commercial or experimental fisheries for mesopelagics and their catches, and/or the mesopelagic bycatch of other fisheries. All commercial (industrial and artisanal) fisheries for mesopelagic fishes were included, as well as experimental fisheries of which we were aware, while catches performed only to obtain scientific samples were omitted. The processes of generating bycatch and causing discards are discussed, with emphasis on Russian fisheries. From peer-reviewed and gray literature, we lifted information on mesopelagic fisheries and assembled it into one document, which we then summarized into two text tables with catch data, one by country/region, the other by species or species groups.

Keywords: Myctophiformes; reconstructed fisheries catch; *Sea Around Us*; bycatch; discards; growth

1. Introduction

The ocean's deep scattering layer (DSL), discovered in WWII, was quickly identified as caused by a multitude of mesopelagic organisms, notably lanternfishes of the Myctophidae family (Figure 1). It took several decades for mesopelagic fishes to be perceived as a potential resource [1], before a global review of estimates of their abundance was assembled [2].

Mesopelagic fish, most of which belong to the lanternfish family Myctophidae (Table S1, Supplementary Materials), live during daytime, at depths between 200 and 1000 m, and perform a diel migration between these often hypoxic depths and the near water surface at night [3–5]. They are largely quiescent during the day, but feed actively at night, mostly on crustaceans (copepods, amphipods, and euphausiids [6,7]).

There is at present a lively debate on the abundance and biomass of mesopelagic fishes, mainly Myctophidae and their relatives [8]. The net estimated midwater fish biomass, about

1 billion tonnes, may have been systematically underestimated, and could be in excess of 11–15 billion tonnes [9]. The most recent estimates, mainly using a combination of acoustics and ecosystem modeling, downscaled these estimates to 3.8–8.3 billion tonnes [10], and as low as 2.4 billion tonnes [11]. This highlights enormous knowledge gaps, and filling them is urgently needed for modeling the physiological ecology of mesopelagic fish, their trophic pathways within the mesopelagic food webs, and links to primary production in the surface waters. This contribution is the first to emphasize the catches of mesopelagic fishes made throughout the world oceans since 1950, to serve as a baseline to a future development of these fisheries. Only in the Discussion do we turn to the issue of net avoidance, which mars debates on the global abundance of mesopelagics.

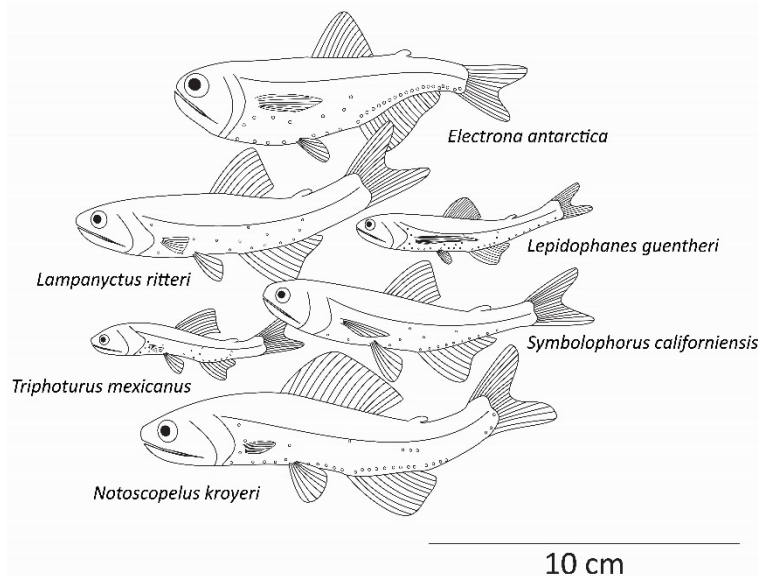


Figure 1. Lanternfishes of the family Myctophidae (order Myctophiformes).

2. Materials and Methods

FishBase [12] was used to assemble a list of mesopelagic fish consisting of all species of the order Myctophiformes, consisting of the family Neoscopelidae and Myctophidae, and the latter's 5 subfamilies. This list was then complemented, where available, with the maximum (standard) length of each species, their depth range, and their trophic level, as determined by studies of their zooplanktonic diet. Trophic levels are also assigned by FishBase using the maximum size reached by a species and the diet composition of taxonomically close relatives [13].

The asymptotic length (L_{∞}), the growth coefficient (K), and the usually negative age at a length of zero (t_0), that is, the parameters of the von Bertalanffy growth function (VBGF) available in FishBase, were assembled for each species. This enables estimates of the potential productivity of an assemblage of mesopelagic species. Furthermore, the inclusion of mesopelagics in ecosystem models was quantified using EcoBase, the database of Ecopath or EwE models [14].

A thorough scanning of the literature was conducted, using both search engines and the classic snowball technique applied to references, to obtain the bulk of the literature dealing with historic fisheries catches of mesopelagic fishes. Included were all commercial (industrial and artisanal) fisheries for mesopelagic fishes, as well as test (or experimental) fisheries. However, catches performed only to obtain scientific samples were omitted.

As the majority of mesopelagic fisheries accounts were brief mentions in papers covering other topics, we lifted the paragraphs with information on mesopelagic fisheries and assembled them into our Online Supplementary Material. We summarized into text tables catch data by country/region and by species, and created a global cumulative catch map, covering the years 1950 to 2018. The catch map can be compared with a new version of the biomass map of Gjøsaeter and Kawaguchi [2], which was redrawn using ArcGIS

9.0, a tool not available in 1980. This implied checking that the density estimates for each stratum defined by Gjøsaeter and Kawaguchi [2] were consistent with their text and with each other.

3. Results

Mesopelagic fishes are not strongly exploited by fisheries, owing to their extreme dispersion (in the order of $1 \text{ g} \cdot \text{m}^{-3}$), but are important prey items to a number of species targeted by fisheries. As such, they must be included in models of ocean ecosystems, and indeed they are. In EcoBase, the database of Ecopath or EwE models [14], of the 200 models of ecosystems likely to have mesopelagic fishes as a component, 155 models include myctophids or mesopelagics as an explicit state variable. These 155 models represent a valuable source of information on the dynamics and trophic ecology of mesopelagic fishes, a theme that is not further elaborated upon here.

A total of 254 species of the order Myctophiformes are included in Table S1, including six species in the family Neoscopelidae and 248 in the family Myctophidae. The latter family is subdivided in the Diaphinae (80 spp.), Gymnoscopelinae (18 spp.), Lampanyctinae (71 spp.), Myctophinae (78 spp.), and Notolychninae (1 sp.). Their reported depth ranges are replaced by a single depth of occurrence in some cases for species that need more study. This also applies to the maximum lengths, for which the length of the holotypes had to be substituted in cases where field samples of length-frequency data are missing.

The growth performance (\emptyset) of 39 populations of 28 mesopelagic species (Table 1) compared with other pelagic species (Table 2) is very low, which is reasonable given that they spend about half of their time in cold, often hypoxic habitat (where, however, they are protected from predation by other fish), and given that most perform vertical migration twice daily, both of which require resources that cannot be devoted to somatic growth [15].

Figure 2 summarizes the immense work of Gjøsaeter and Kawaguchi [2], who assembled a global database of mesopelagic density estimates, which they raised to the level of the global ocean. Their work provides the geographic framework within which fisheries catches can be interpreted, regardless of the catchability of the equipment used to sample mesopelagic fishes.

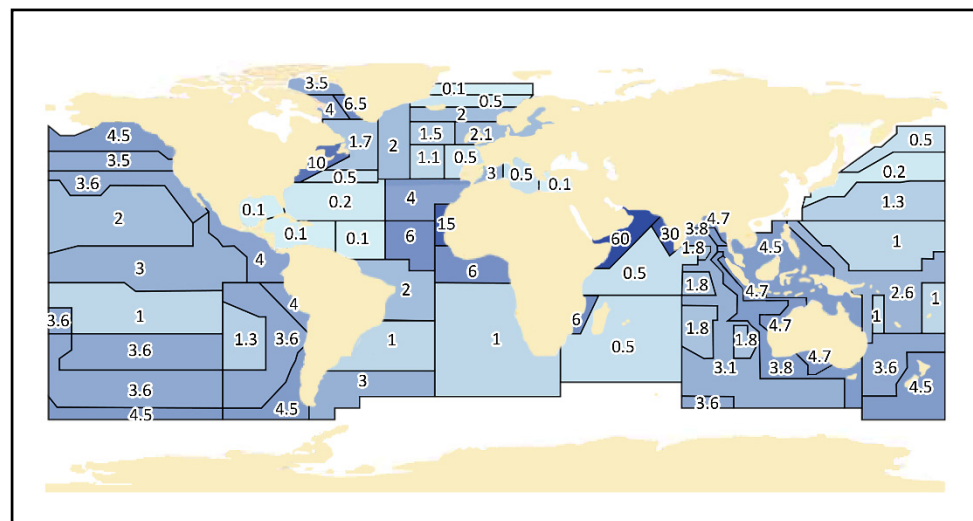


Figure 2. Biomass of mesopelagics (in $\text{g} \cdot \text{m}^{-3}$) based on data in Gjøsaeter and Kawaguchi [2], with mean estimates per stratum corrected using ESRI's ArcGIS 9.0. Light blue refers to low densities of mesopelagics (with means in $\text{g} \cdot \text{m}^{-3}$), dark blue to high densities, white refers to unsampled sea areas, and yellow to land.

Table 1. Growth parameters of 39 populations of 28 mesopelagic species obtained from FishBase (www.fishbase.org; accessed on 8 June 2021), which provides details on ageing methods, sampling location, and sources not presented in this table. The mean growth coefficient (K) values were computed from the mean $\bar{\phi}$ and mean asymptotic length (L_{∞}) measured as standard length (SL).

Species	L_{∞} (SL; cm)	K (year ⁻¹)	$\bar{\phi} =$ $\log K + 2\log L_{\infty}$
<i>Benthoosema fibulatum</i>	7.7	5.62	2.523
<i>Benthoosema glaciale</i>	8.3	0.20	1.139
<i>Benthoosema glaciale</i>	8.6	0.45	1.522
<i>Benthoosema glaciale</i>	8.5	0.36	1.415
<i>Benthoosema glaciale</i>	7.5	0.31	1.241
<i>Benthoosema pterotum</i>	6.8	1.81	1.923
<i>Benthoosema suborbitale</i>	3.3	3.65	1.599
<i>Ceratoscopelus maderensis</i>	7.1	3.65	2.260
<i>Ceratoscopelus maderensis</i>	7.9	1.30	1.909
<i>Diaphus dumerilii</i>	7.5	1.83	2.011
<i>Diaphus dumerilii</i>	6.9	3.81	2.259
<i>Diaphus watasei</i>	15.1	0.80	2.261
<i>Diaphus watasei</i>	15.1	0.80	2.261
<i>Electrona antarctica</i>	9.7	0.25	1.374
<i>Electrona antarctica</i>	12.9	0.17	1.452
<i>Electrona carlsbergi</i>	9.7	0.55	1.711
<i>Electrona risso</i>	6.1	3.03	2.052
<i>Gymnoscopelus braueri</i>	13.3	0.29	1.712
<i>Kreftlichthys anderssoni</i>	6.9	0.71	1.524
<i>Lampanyctodes hectoris</i>	10.0	0.31	1.491
<i>Lampanyctus regalis</i>	26.5	0.20	2.150
<i>Lampanyctus ritteri</i>	13.5	0.36	1.817
<i>Lepidophanes guentheri</i>	7.3	1.83	1.988
<i>Lobianchia dofleini</i>	4.6	1.39	1.467
<i>Metelectrona ventralis</i>	11.1	1.29	2.201
<i>Myctophum nitidulum</i>	10.0	0.42	1.623
<i>Myctophum punctatum</i>	9.0	0.32	1.414
<i>Myctophum punctatum</i>	10.5	0.17	1.262
<i>Notolychnus valdiviae</i>	2.8	1.41	1.044
<i>Notoscopelus elongatus</i>	11.9	0.89	2.100
<i>Notoscopelus kroyeri</i>	14.9	0.20	1.647
<i>Scopelogadus tristis</i>	21.0	0.46	2.307
<i>Stenobrachius leucopsarus</i>	10.5	0.33	1.561
<i>Stenobrachius leucopsarus</i>	9.8	0.31	1.475
<i>Stenobrachius leucopsarus</i>	14.3	0.24	1.698
<i>Stenobrachius leucopsarus</i>	8.5	0.34	1.390
<i>Stenobrachius nannochir</i>	13.0	0.42	1.851
<i>Symbolophorus californiensis</i>	13.5	0.43	1.894
<i>Triphoturus mexicanus</i>	7.9	0.63	1.593
Means	10.24	0.532	1.7467

Table 2. Comparison between the growth performance of mesopelagic fishes with that of other teleosts using the growth performance index $\bar{\phi} = \log(K) + (2/3)\log(W_{\infty})$.

Species ¹	W_{∞} (g)	K (year ⁻¹)	$\bar{\phi}$
<i>Thunnus albacares</i>	198,940	0.250	2.93
<i>Morone saxatilis</i>	17,543	0.186	2.10
<i>Mugil cephalus</i>	13,890	0.110	1.80
<i>Platichthys flesus</i>	1058	0.229	1.38
<i>Cottus bubalis</i>	102	0.230	0.70
Mesopelagics ²	10.7	0.532	0.413

¹ These 5 non-mesopelagic species are documented in [16], with *M. saxatilis* listed as *R. lineatus*. ² From the last row of Table 1, and assuming the length–weight relationship $W = 0.01 \cdot L^3$, where L is in cm and W is in g.

Table 3 summarizes Gjøsaeter and Kawaguchi's [2] results by the statistical areas used by the Food and Agriculture Organization of the United Nations (FAO) to present the fisheries landings reported by their member countries [17]. As may be seen, the sum of the biomass presented by Gjøsaeter and Kawaguchi [2] for each of the 15 FAO areas is 797 million t (Column A in Table 3), while the sum of the biomass in each FAO area based on subareas mentioned in their text is 945 million t (Column B). Remarkably similar biomass estimates were obtained by [18], albeit with a different approach, i.e., modeling of the pelagic biomass spectrum and the mesozooplankton standing stock in the top 100 m layer as a predictor of midwater fish total biomass (Column C). The mesopelagic fish biomass within the depth range 100–1000 m calculated is similar to that of Gjøsaeter and Kawaguchi [2]. Estimated biomass by FAO areas ranged between 495 and 987 million t (average 741). In the Atlantic, Indian, and Pacific oceans, mesopelagic fish biomass was 156 (range 103–210), 198 (130–266), and 387 (262–511) million t, respectively (Table 11 in [18]). Finally, the synthesis redone with the mesopelagic density estimates was checked for internal consistency, and the marine surface areas recomputed by ArcGIS 9.0 yielded a global biomass of 999 million, i.e., 1 billion t (column D).

Table 3. Biomass of mesopelagic fishes (millions t) by FAO Statistical Area, as estimated by Gjøsaeter and Kawaguchi [2] (G&K) in columns A (G&K's estimates in tables) and B (G&K's estimates in text), C (Tseilin's [18] averaged from lower and higher limits of biomass estimates), and by Lam and Pauly [19] in column D (new estimates).

FAO Area	A	B	C	D
Northwest Atlantic (21)	14.9	14.8	24.0	22.0
Northeast Atlantic (27)	14.7	14.7	18.5	15.9
Western Central Atlantic (31)	1.9	19.4	17.0	2.3
Eastern Central Atlantic (34)	77.5	77.0	16.0	80.7
Mediterranean Sea (37)	2.5	2.5	8.5	3.0
Southwest Atlantic (41)	33.0	39.0	40.0	33.4
Southeast Atlantic (47)	17.8	18.0	32.5	20.4
Western Indian Ocean (51)	133.0	257.0	123.9	263.2
Eastern Indian Ocean (57)	92.9	94.0	74.0	202.6
Northwest Pacific (61)	48.6	49.0	22.0	52.5
Northeast Pacific (67)	26.8	27.0	14.0	27.8
Western Central Pacific (71)	51.3	52.0	24.0	85.4
Eastern Central Pacific (77)	129.0	129.0	146.0	35.0
Southwest Pacific (81)	101.0	101.0	52.5	99.9
Southeast Pacific (87)	52.1	51.0	123.5	54.9
Total	797.0	945.0	611.4	999.0

Figure 3 summarizes the landings (i.e., the catch that is not discarded) officially reported to the FAO by its member countries, i.e., mainly the U.K. (South Georgia and Sandwich Islands, reporting 47%), South Africa (Atlantic and Cape, 37%), and Iceland (13%). As may be seen in Figure 3, two species, *Lampanyctodes hectoris* and *Electrona carlsbergi*, contributed about 80% of the reported landings.

Table 4 summarizes the historic mesopelagic fish caught from the waters of different countries and regions that we were able to identify, while Table 5 summarizes the results of some test fisheries by the former USSR (see Supplementary Materials for more details). Figure 4 is a graphical summary of these data, accounting both for quantitative information (via different colors for the EEZ of countries with reported catches) and qualitative information, via blue dots where the sizes and exact locations of (occasional) mesopelagic catches remains unknown.

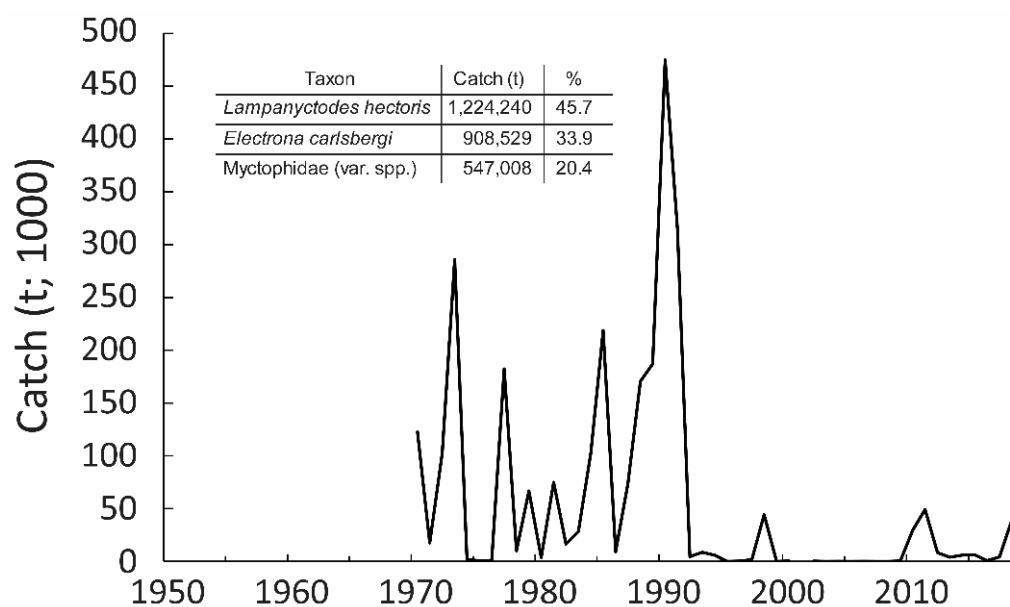


Figure 3. Landings officially reported to the FAO by its member countries totaling 2.68 million tonnes from 1950–2018, mainly the U.K. (South Georgia and Sandwich Islands, reporting 47%), South Africa (Atlantic and Cape, 37%), and Iceland (13%).

Table 4. Catch information for 20 mesopelagic fishes depicted in Figure 3 by country/region and year.

Country or Region	Year(s): Catch (t)	Remarks (Source)
South Georgia/Ob and Lena Seamounts	1988–1990: 20,000 t·year ⁻¹ ; 1991: 78,488 t; 1992: TAC of 200,000 t	Fishery appears to have lasted from 1985 to 1992 [20,21]
South Africa	1960: 1134 t; 1973: 42,560 t	[22]
Antarctica	1970: n.a.	Caught as bycatch of rock cod fishery [23]
South Africa	undated: 100–42,400 t·year ⁻¹	[21]
Gulf of Oman	1989: 1739 t.	Catch from log sheet records [24]
Iceland	2009: >46,000 t; 2010: 18,000 t; 2013–2016: 0	[25]
Antarctica	1980–1986: 500–2500 t·year ⁻¹ ; 1987/88: 14,000 t; 1988–1990: 23–29·10 ³ t·year ⁻¹ ; 1990/91: 78,000 t; 1991/92: 51,000 t.	Mainly used for fishmeal [26]
Northeast Atlantic	April–June 1984: 0.024 t	[27]
South Africa	1969–1973: 82,000 t	Purse seine fishery [28]
India	2008 or earlier: 9600 t	Number of boats, length of fishing trips, amount discarded and percentage of discards that are myctophids: see [29]; 2009–2010: 3676 t [30]; for India/Arabian Sea: 2010–2011: 2972 t [31]
India/Kerala coast	2009: 2421 t; 2010: 2610 t; 2011: 2972 t	[32]
SW Indian Ocean and S. Atlantic	1992: 51,680 t	Fishery began in 1977 and ceased due to a decrease in catches [32]
Philippines	Post WWII	No catch given [33]
Pakistan	2016: n.a.	[34]
South Africa	2015: 50,000 t	Combined TAC for lanternfish and lightfish [35]
Iran	1995–1998: 24–28 t·day ⁻¹	[36]
Oman	1996, March: 446 t; 1996, April: 563 t; 1996, May: 1273 t	Fishery was over after 123 fishing days, with an average catch of 20 t·day ⁻¹ [36]
Southeast Atlantic	1973: 42,000 t; 1980: <1000 t·year ⁻¹ ; 1982–1983: <1000 t year ⁻¹ ; 1979 and 1981: 10,000 t each	[37]
Southern Ocean	1988/89: 30,000 t	[38]
South Africa	2011: 7000 t; 2012: 50,000 t; 2013: 1000 t	[39]
South Africa	1971–2010: 162,444 t; 2011–2012: 9486 t	Figure A.1 in [40]
South Africa	1969–1973: 1134–42,560 t	[41]
Uruguay	1966: 15 t	[41]

Table 5. Results of some test and exploratory mesopelagic fisheries by the ex-USSR (L. K. Pshenichnov, pers. obs.).

Area	Fisheries
Atlantic sector of the Southern Ocean	A test fishery on <i>Electrona carsbergi</i> using midwater trawl was conducted by the USSR fleet between 1979 and 1986. The fishery was based on quasi-stationary aggregations of <i>E. carsbergi</i> within 49–55° S and 49° W–20° E. Catches ranged between 3 and 30 t per hour trawling. Official statistics for these catches are archived in the CCAMLR <i>Statistical Bulletin</i> .
Indian sector of the Southern Ocean:	A test fishery on <i>Electrona carsbergi</i> concentrations was conducted by JugRybPoisk trawlers between 1986 and 1988 using midwater trawls in an area with the coordinates 42–45° S and 47–60° E. The catch/effort was 4 to 7 tonnes per hour trawling. In the area defined by the coordinates 50–51° S and 28–29° E, the catch/effort was 8 to 25 t per hour trawling.
Indian Ocean Equatorial Seamount, 00°25' S–56° E	A stock assessment of <i>Diaphus suborbitalis</i> was performed in the 1980s using midwater trawl. Individual catches ranged from 1 to 4 t per hour trawling. The biomass estimates were 35,000 t in 1984 and 13,000 t in 1987.

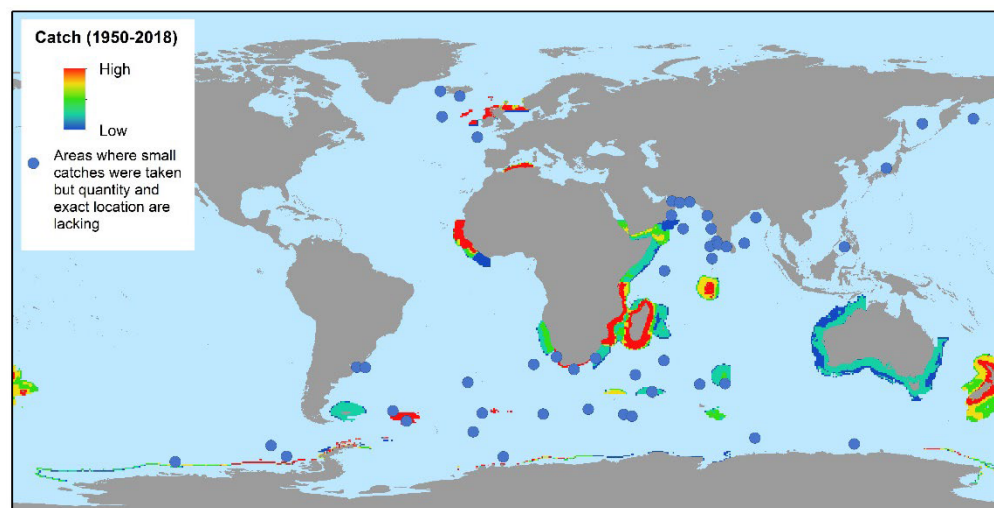


Figure 4. Sea Around Us reconstructed catches of mesopelagic fishes for the period 1950–2018 in the global oceans. Areas where small catches are taken (blue dots) but where quantity and exact location are unknown are listed in the Supplementary Materials and/or mentioned in the text.

4. Discussion

As might be seen from Figure 4, most of the mesopelagic catches reported or documented in various reports were made in the Southern Hemisphere, from the southern Atlantic and Indian Oceans, all the way to southern Australia and New Zealand. Within that broad area, the southern tip of Africa and the western Indian Ocean appear to be the only areas where commercial fisheries for mesopelagic fishes have been seriously attempted or operating (see also Figure 2 for its high biomasses in the northwestern Indian Ocean and the FAO data in Figure 3).

Another spot is the northwest Atlantic, from Iceland to British Isles; however, there, the fisheries for mesopelagic fish appear to have ceased.

Overall, the high number of blue dots in Figure 4, mainly representing ill-documented trial fisheries, suggests that the majority of fisheries for mesopelagic fishes, from 1950 to the present have been ad hoc and lacking continuity.

As a result of this lack of continuity, the evaluation of industrial trawl fishing impact on mesopelagic fish populations is also fraught with uncertainties. Commercial trawl nets are designed to minimize catching of undersized fish, and their mesh size does not effectively retain small and fragile organisms such as mesopelagic fish. For example, trawl nets used in the North Pacific by the fishery for walleye pollock (*Gadus chalcogrammus*)

should have a mesh size not less than 10 cm, set to avoid bycatch of juvenile pollock below 35 cm.

When mesopelagic fish enter the mouth of a pelagic trawl along with the targeted fish, four different processes may occur: (i) they manage to leave the trawl net through the meshes of the cod end or other part of the net, while the target fish are retained; (ii) some of the mesopelagics may become stuck near the knots of the net while the target fish end up in the cod end; (iii) some of the mesopelagics are retained in the cod end, especially near the end of a trawl haul, particularly when its meshes are blocked by other fishes; and (iv) the mesopelagics are ingested within the trawl net by larger fishes. Unfortunately, detailed quantitative information on these four processes are not available.

Based on one of the author's field observations (V.I. Radchenko, unpublished data), last-minute ingestion by larger fish (item iv) affects about 4% of the mesopelagic bycatch, while the other three processes (i to iii) are about equal, and thus would each impact 32% of the bycatch. Fish stuck near the knots of trawl nets (item iii) usually suffer heavy damage to their bodies and lose their scale; these fish are shaken out and discarded.

Fish that leave a trawl net (i) without contact with the net and/or other individual fish are rare. These contacts lead to body integument damage and scale loss. Thus, despite efforts to spare undersized fish, a sizable fraction will leave the net in a damaged state. These damaged fish are likely to die from their injuries, or may become more vulnerable to piscine, mammalian, or avian predators.

It is only the process in (iii) that a bycatch is produced that may be retained and landed, e.g., for use in producing fish feed for aquaculture. At well-organized production facilities, the bycatch and the offal from target species are used to make fishmeal and fish oil, which minimizes discarding. For example, in 2016, Russia produced 92,134 t of fishmeal from 1,500,000 t of raw fish and offal (head, guts, etc.). However, mesopelagic fish are not appreciated in fishmeal plants due to their high wax ester content, which affects fishmeal and fish oil quality. Thus, mesopelagic fish are not even mentioned among bycatch of the walleye pollock fishery in the Sea of Okhotsk [42], nor in the Bering Sea [43]; in the following, we briefly explore why it may be so.

In 1990, Russian fishery scientists conducted detailed trawl surveys to study the mesopelagic fauna in the Sea of Okhotsk (February to March, and November to January) and the Bering Sea (April to November) that coincided with the main walleye pollock fishery seasons in both seas (details in [3]). In these surveys, commercial trawl nets equipped with a fine-mesh insert (10 mm), along the entire length from the trawl wings to the cod end (total length 137 m), were used, which allowed for the avoidance of small fish getting stuck in the net, or escaping through its meshes. Within the 200–500 m depth layers, the average nighttime mesopelagic fish catch was $135 \text{ kg}\cdot\text{h}^{-1}$ in the Sea of Okhotsk and $40 \text{ kg}\cdot\text{h}^{-1}$ in the Bering Sea. Northern smooth-tongue (*Leuroglossus schmidti*) contributed 76% of the catch in the Sea of Okhotsk, while light-rayed lanternfish (*Stenobrachius leucopsarus*) contributed 93% in the Bering Sea [3].

In 2016, the Russian fishing fleet caught about 767,000 t of walleye pollock in the Sea of Okhotsk by pelagic trawls, with the average of about $12.5 \text{ t}\cdot\text{h}^{-1}$; during about 8000 vessel-days, the fleet performed a total of 20,000 trawl hauls that required 61,344 h, or 3.13 h per haul. If 50% of these trawl operations were conducted at night, when mesopelagic fish occur in the upper pelagic layers, $61,344 \cdot 0.135 / 2 = 4140$ t of mesopelagic fish every year enter the net of pelagic trawls targeting walleye pollock in the Sea of Okhotsk. Given the relative importance assumed for the above processes (i) to (iv), various amounts of wounded or dead fish, or of landed bycatch, would be generated, but each would be of a small fraction of $4140 \text{ t}\cdot\text{year}^{-1}$, which is a tiny fraction (0.054%) of the annual catch of the target fish.

Thus, by extension, it may be assumed that the massive pelagic trawl fisheries that occur in different parts of the world, and which do not target mesopelagics, do not generate a large, unaccounted-for bycatch of mesopelagics.

This is reassuring, but it does not change the fact that catches, whether targeted or as bycatch, have been underreported to the FAO. This will forever result in biased baselines. The *Sea Around Us* will still endeavor to account, in its catch database (see www.seaaroundus.org), for the bycatch of mesopelagics as meticulously as for reported catches. This is because it is only if we account for all catches extracted from the oceans that we can ensure their fisheries operate on a sustainable basis.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/jmse9101057/s1>, Table S1: Species of fish in FishBase belonging to the Myctophiformes, Text: Quotes with diverse information of mesopelagic fisheries and their catches.

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Article

The Biology of Mesopelagic Fishes and Their Catches (1950–2018) by Commercial and Experimental Fisheries

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Abstract: Following a brief review of their biology, this contribution is an attempt to provide a global overview of the catches of mesopelagic fishes (of which 2.68 million tonnes were officially reported to the FAO) throughout the world ocean from 1950 to 2018, to serve as a baseline to a future development of these fisheries. The overview is based on a thorough scanning of the literature dealing with commercial or experimental fisheries for mesopelagics and their catches, and/or the mesopelagic bycatch of other fisheries. All commercial (industrial and artisanal) fisheries for mesopelagic fishes were included, as well as experimental fisheries of which we were aware, while catches performed only to obtain scientific samples were omitted. The processes of generating bycatch and causing discards are discussed, with emphasis on Russian fisheries. From peer-reviewed and gray literature, we lifted information on mesopelagic fisheries and assembled it into one document (see Online Supplementary Material), which we then summarized into two text tables with catch data, one by country/region, the other by species or species groups.

Keywords: Myctophiformes; reconstructed fisheries catch; *Sea Around Us*; bycatch; discards; growth

Table S1. Species of fish in FishBase belonging to the Myctophiformes (n=254), Neoscolopelidae (n=6) and Myctophidae (n=248), and considered to contribute the bulk of mesopelagic fishes. Where available, the depth range (or a single depth of occurrence), maximum recorded length and trophic level are provided (see www.fishbase.org). Note: Lmax is the maximum length in standard length (SL).

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
	Family Neoscopelidae	entry 1	data	data
1	<i>Neoscopelus macrolepidotus</i>	300–1180	25.0	4.2
2	<i>Neoscopelus microchir</i>	250–700	30.5	3.2
3	<i>Neoscopelus porosus</i>	454–642	18.3	3.6
4	<i>Scopelengys clarkei</i>	0–1000	--	3.2
5	<i>Scopelengys tristis</i>	400–1830	20.0	3.1
6	<i>Solvomer arenidens</i>	1241–2022	--	3.2
	Family Myctophidae			
	Subfamily Diaphinae			
7	<i>Diaphus adenomus</i>	180–600	18.0	3.2
8	<i>Diaphus aliciae</i>	489	6.0	3.1
9	<i>Diaphus anderseni</i>	100–560	3.2	3.1
10	<i>Diaphus antonbruuni</i>	500	5.5	3.1
11	<i>Diaphus arabicus</i>	0–468	--	3.1
12	<i>Diaphus basileusi</i>	120	16.4	3.2
13	<i>Diaphus bertelseni</i>	0–300	9.1	3.1
14	<i>Diaphus brachycephalus</i>	200–600	6.0	3.1
15	<i>Diaphus burtoni</i>	312	--	3.1
16	<i>Diaphus chrysohynchus</i>	213–587	1.1	3.0
17	<i>Diaphus coeruleus</i>	457–549	13.7	3.9
18	<i>Diaphus confusus</i>	562	--	3.1
19	<i>Diaphus dahlgreni</i>	320	--	3.1
20	<i>Diaphus danae</i>	350	12.6	3.3
21	<i>Diaphus dehaveni</i>	247	--	3.1
22	<i>Diaphus diadematus</i>	350	4.2	3.1
23	<i>Diaphus diademophilus</i>	0–1808	4.9	3.1
24	<i>Diaphus drachmanni</i>	300	--	3.1
25	<i>Diaphus dumerilii</i>	0–805	8.7	3.0
26	<i>Diaphus effulgens</i>	0–6000	15.0	3.0
27	<i>Diaphus ehrhorni</i>	382	--	3.1
28	<i>Diaphus faustinoi</i>	540	--	3.1
29	<i>Diaphus fragilis</i>	15–1313	12.3	3.1
30	<i>Diaphus fulgens</i>	85–1000	4.5	3.1
31	<i>Diaphus garmani</i>	0–2091	6.0	3.1
32	<i>Diaphus gigas</i>	100–839	--	3.1
33	<i>Diaphus handi</i>	774	--	3.1
34	<i>Diaphus holti</i>	40–777	7.0	3.1
35	<i>Diaphus hudsoni</i>	0–840	8.4	3.3
36	<i>Diaphus impostor</i>	0–140	--	3.1
37	<i>Diaphus jenseni</i>	350–1389	5.0	3.1
38	<i>Diaphus kapalae</i>	0–290	--	3.1
39	<i>Diaphus knappi</i>	122–664	17.3	3.2
40	<i>Diaphus kora</i>	0–387	--	3.1
41	<i>Diaphus kuroshio</i>	100–1537	6.3	3.1
42	<i>Diaphus lobatus</i>	--	--	3.1
43	<i>Diaphus lucidus</i>	0–2999	11.8	3.0
44	<i>Diaphus lucifrons</i>	564	--	3.1
45	<i>Diaphus luetkeni</i>	40–750	6.0	3.8
46	<i>Diaphus malayanus</i>	1000–2000	4.5	3.1

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
47	<i>Diaphus mascarensis</i>	237–800	14.4	3.2
48	<i>Diaphus meadi</i>	250	5.4	3.0
49	<i>Diaphus megalops</i>	1–528	8.5	3.1
50	<i>Diaphus metopoclampus</i>	90–1085	7.5	3.3
51	<i>Diaphus minax</i>	476	--	3.1
52	<i>Diaphus mollis</i>	50–600	6.6	3.0
53	<i>Diaphus nielseni</i>	--	4.0	3.1
54	<i>Diaphus ostenfeldi</i>	350	12.0	3.2
55	<i>Diaphus pacificus</i>	--	--	3.1
56	<i>Diaphus pallidus</i>	310	--	3.1
57	<i>Diaphus parini</i>	320	--	3.1
58	<i>Diaphus parri</i>	350–1071	6.5	3.1
59	<i>Diaphus perspicillatus</i>	0–1500	7.1	3.1
60	<i>Diaphus phillipsi</i>	588–1330	7.7	3.1
61	<i>Diaphus problematicus</i>	40–820	10.5	3.0
62	<i>Diaphus rafinesquii</i>	40–2173	9.0	3.4
63	<i>Diaphus regani</i>	750	1.4	3.0
64	<i>Diaphus richardsoni</i>	350–1000	6.0	3.1
65	<i>Diaphus rivatoni</i>	0–152	9.0	3.1
66	<i>Diaphus roei</i>	558	--	3.1
67	<i>Diaphus sagamiensis</i>	549	--	3.1
68	<i>Diaphus schmidti</i>	100–1400	5.3	3.2
69	<i>Diaphus signatus</i>	1270	4.0	3.1
70	<i>Diaphus similis</i>	0–631	7.2	3.1
71	<i>Diaphus splendidus</i>	0–8000	9.0	3.0
72	<i>Diaphus suborbitalis</i>	387–1537	7.3	3.1
73	<i>Diaphus subtilis</i>	40–750	8.5	3.1
74	<i>Diaphus taaningi</i>	40–475	7.0	3.3
75	<i>Diaphus termophilus</i>	40–850	8.0	3.1
76	<i>Diaphus theta</i>	10–3400	9.3	3.2
77	<i>Diaphus thiollierei</i>	--	10.0	3.3
78	<i>Diaphus trachops</i>	100–686	6.3	3.1
79	<i>Diaphus umbroculus</i>	311	--	3.1
80	<i>Diaphus vanhoeffeni</i>	40–750	4.2	3.1
81	<i>Diaphus watasei</i>	100–2005	17.0	3.2
82	<i>Diaphus whitleyi</i>	311	--	3.1
83	<i>Diaphus wisneri</i>	50–375	--	3.1
84	<i>Idiolychnus urolampus</i>	124–582	11.0	3.2
85	<i>Lobianchia dofleini</i>	0–4000	5.0	3.0
86	<i>Lobianchia gemellarii</i>	25–800	6.0	3.0
	Subfamily Gymnoscopelinae			
87	<i>Gymnoscopelus bolini</i>	4200	28.0	3.3
88	<i>Gymnoscopelus braueri</i>	2700	13.2	3.2
89	<i>Gymnoscopelus fraseri</i>	50–250	8.8	3.2
90	<i>Gymnoscopelus hintonoides</i>	2200–2350	14.0	3.2
91	<i>Gymnoscopelus microlampas</i>	200–500	11.7	3.0
92	<i>Gymnoscopelus nicholsi</i>	300	15.7	3.4
93	<i>Gymnoscopelus opisthopterus</i>	550–900	16.2	3.3
94	<i>Gymnoscopelus piabilis</i>	--	14.6	3.2

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
95	<i>Hintonia candens</i>	--	13.0	3.2
96	<i>Lampanyctodes hectoris</i>	--	7.0	3.2
97	<i>Lampichthys procerus</i>	1–2000	8.2	3.1
98	<i>Notoscopelus bolini</i>	1–1300	10.2	3.1
99	<i>Notoscopelus caudispinosus</i>	1–360	14.0	3.2
100	<i>Notoscopelus elongatus</i>	45–1000	14.2	3.4
101	<i>Notoscopelus japonicus</i>	391–794	13.3	3.2
102	<i>Notoscopelus kroyeri</i>	0–1000	14.3	3.2
103	<i>Notoscopelus resplendens</i>	777–2121	9.5	3.0
104	<i>Scopelopsis multipunctatus</i>	3–2000	8.1	3.0
Subfamily Lampanyctinae				
105	<i>Bolinichthys distofax</i>	100–690	9.0	3.1
106	<i>Bolinichthys indicus</i>	25–900	4.5	3.1
107	<i>Bolinichthys longipes</i>	50–1021	5.0	3.1
108	<i>Bolinichthys nikolayi</i>	25–1760	4.1	3.0
109	<i>Bolinichthys photothorax</i>	40–750	7.3	3.0
110	<i>Bolinichthys pyrsobolus</i>	60–778	9.2	3.1
111	<i>Bolinichthys supralateralis</i>	40–850	11.7	3.1
112	<i>Ceratoscopelus maderensis</i>	51–1480	8.1	3.3
113	<i>Ceratoscopelus townsendi</i>	100–500	15.1	3.5
114	<i>Ceratoscopelus warmingii</i>	391–2056	8.1	3.4
115	<i>Lampadena anomala</i>	330–2000	18.0	3.2
116	<i>Lampadena atlantica</i>	60–1000	20.0	3.2
117	<i>Lampadena chavesi</i>	40–800	8.0	3.1
118	<i>Lampadena dea</i>	1500–2390	8.9	3.1
119	<i>Lampadena luminosa</i>	50–1021	20.0	3.2
120	<i>Lampadena notialis</i>	1–800	13.9	3.2
121	<i>Lampadena pontifex</i>	1–750	11.0	3.1
122	<i>Lampadena speculigera</i>	1–1000	15.3	3.2
123	<i>Lampadena urophaos</i>	50–1000	20.0	3.2
124	<i>Lampadena yaquinae</i>	100–2056	13.0	3.2
125	<i>Lampanyctus acanthurus</i>	930–1537	13.0	3.3
126	<i>Lampanyctus achirus</i>	--	16.2	3.2
127	<i>Lampanyctus alatus</i>	40–1500	6.1	3.2
128	<i>Lampanyctus ater</i>	60–1100	14.0	3.2
129	<i>Lampanyctus australis</i>	--	13.1	3.3
130	<i>Lampanyctus bristori</i>	--	14.2	3.2
131	<i>Lampanyctus crocodilus</i>	1–1200	30.0	3.2
132	<i>Lampanyctus crypticus</i>	--	9.8	3.2
133	<i>Lampanyctus cuprarius</i>	40–1000	7.9	3.3
134	<i>Lampanyctus fernae</i>	1–750	9.1	3.2
135	<i>Lampanyctus festivus</i>	40–1052	13.8	3.3
136	<i>Lampanyctus gibbsi</i>	--	12.2	3.2
137	<i>Lampanyctus hawaiiensis</i>	300–850	8.1	3.1
138	<i>Lampanyctus hubbsi</i>	1–2500	3.0	3.1
139	<i>Lampanyctus idostigma</i>	100–500	9.6	3.2
140	<i>Lampanyctus indicus</i>	--	8.0	3.1
141	<i>Lampanyctus intricarius</i>	40–750	20.0	3.4
142	<i>Lampanyctus isaacsi</i>	0–2300	13.3	3.2

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
143	<i>Lampanyctus iselinoides</i>	64	--	3.2
144	<i>Lampanyctus jordani</i>	588–3400	14.0	3.3
145	<i>Lampanyctus lepidolychnus</i>	312–332	11.9	3.2
146	<i>Lampanyctus lineatus</i>	60–1150	23.7	3.0
147	<i>Lampanyctus macdonaldi</i>	60–1464	16.0	3.1
148	<i>Lampanyctus macropterus</i>	0–2091	6.8	3.2
149	<i>Lampanyctus niger</i>	100–1015	11.1	3.1
150	<i>Lampanyctus nobilis</i>	100–1000	12.4	3.1
151	<i>Lampanyctus omostigma</i>	3000	2.6	3.1
152	<i>Lampanyctus parvicauda</i>	100–500	--	3.2
153	<i>Lampanyctus photonotus</i>	40–1100	8.5	3.2
154	<i>Lampanyctus phyllisae</i>	--	15.1	3.2
155	<i>Lampanyctus pusillus</i>	40–850	4.3	3.4
156	<i>Lampanyctus regalis</i>	772–3400	17.2	3.2
157	<i>Lampanyctus ritteri</i>	20–1095	12.0	3.4
158	<i>Lampanyctus simulator</i>	0–500	9.3	3.2
159	<i>Lampanyctus steinbecki</i>	80–100	3.8	3.1
160	<i>Lampanyctus tenuiformis</i>	1537	15.3	3.3
161	<i>Lampanyctus turneri</i>	1757	7.0	3.2
162	<i>Lampanyctus vadulus</i>	0–370	9.9	3.2
163	<i>Lampanyctus wisneri</i>	600–650	8.8	3.1
164	<i>Lepidophanes gaussi</i>	0–850	5.0	3.1
165	<i>Lepidophanes guentheri</i>	40–750	7.8	3.0
166	<i>Parvilux boschmai</i>	--	--	3.2
167	<i>Parvilux ingens</i>	100–500	16.4	3.1
168	<i>Stenobranchius leucopsarus</i>	31–3400	10.7	3.2
169	<i>Stenobranchius nannochir</i>	441–3400	11.0	3.0
170	<i>Taaningichthys bathyphilus</i>	400–1550	8.0	3.1
171	<i>Taaningichthys minimus</i>	90–800	6.5	3.1
172	<i>Taaningichthys paurolychnus</i>	900–2000	9.5	3.2
173	<i>Triphoturus mexicanus</i>	25	5.7	3.3
174	<i>Triphoturus nigrescens</i>	100–1000	8.1	3.1
175	<i>Triphoturus oculeum</i>	770–3243	--	3.2
Subfamily Myctophinae				
176	<i>Benthoosema fibulatum</i>	1–2000	8.0	3.2
177	<i>Benthoosema glaciale</i>	1–1407	10.3	3.1
178	<i>Benthoosema panamense</i>	--	4.5	3.1
179	<i>Benthoosema pterotum</i>	10–300	5.7	3.1
180	<i>Benthoosema suborbitale</i>	50–2500	3.9	3.4
181	<i>Centrobranchus andreae</i>	650	6.5	3.4
182	<i>Centrobranchus breviostris</i>	--	4.0	3.3
183	<i>C. choerocephalus</i>	1050	4.0	3.3
184	<i>Centrobranchus nigroocellatus</i>	1–700	5.0	3.4
185	<i>Ctenoscopelus phengodes</i>	--	9.3	3.4
186	<i>Dasyscopelus asper</i>	244–1948	6.5	3.7
187	<i>Dasyscopelus obtusirostris</i>	1–700	7.8	3.4
188	<i>Dasyscopelus selenops</i>	40–500	6.4	3.3
189	<i>Dasyscopelus spinosus</i>	1–700	9.0	3.5
190	<i>Diogenichthys atlanticus</i>	1–1050	2.9	3.1

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
191	<i>Diogenichthys laternatus</i>	1–2091	4.0	3.2
192	<i>Diogenichthys panurgus</i>	366	2.3	3.1
193	<i>Electrona antarctica</i>	1–1010	11.5	3.2
194	<i>Electrona carlsbergi</i>	1–1008	11.2	3.3
195	<i>Electrona paucirastra</i>	--	7.0	3.3
196	<i>Electrona risso</i>	90–1485	8.2	3.4
197	<i>Electrona subaspera</i>	--	12.7	3.3
198	<i>Gonichthys barnesi</i>	1–1000	5.0	3.2
199	<i>Gonichthys cocco</i>	1–1450	6.0	3.2
200	<i>Gonichthys tenuiculus</i>	--	4.1	3.2
201	<i>Gonichthys venetus</i>	--	--	3.2
202	<i>Hygophum atratum</i>	600–3132	4.9	3.2
203	<i>Hygophum benoiti</i>	51–700	5.5	3.0
204	<i>Hygophum bruuni</i>	--	--	3.2
205	<i>Hygophum hanseni</i>	57–728	6.7	3.2
206	<i>Hygophum hygomii</i>	1–1485	6.8	3.0
207	<i>Hygophum macrochir</i>	1–750	6.0	3.2
208	<i>Hygophum proximum</i>	1–1000	5.0	3.2
209	<i>Hygophum reinhardtii</i>	1–1050	6.0	3.2
210	<i>Hygophum taaningi</i>	250–1000	6.1	3.2
211	<i>Krefflichthys anderssoni</i>	2700	7.1	3.1
212	<i>Loweina interrupta</i>	60–800	3.9	3.2
213	<i>Loweina rara</i>	1–1050	4.5	3.2
214	<i>Loweina terminata</i>	1–825	3.0	3.1
215	<i>Metelectrona ahlstromi</i>	1–2000	--	3.3
216	<i>Metelectrona herwigi</i>	98	5.5	3.2
217	<i>Metelectrona ventralis</i>	0–426	10.7	3.3
218	<i>Myctophum affine</i>	0–600	7.9	3.0
219	<i>Myctophum aurolaternatum</i>	--	11.0	3.5
220	<i>Myctophum brachygnathum</i>	--	--	3.4
221	<i>Myctophum fissunovi</i>	--	7.0	3.4
222	<i>Myctophum indicum</i>	--	--	3.4
223	<i>Myctophum lunatum</i>	--	5.7	3.3
224	<i>Myctophum lychnobium</i>	1–1000	3.8	3.2
225	<i>Myctophum nitidulum</i>	412–1537	8.3	3.4
226	<i>Myctophum orientale</i>	--	--	3.4
227	<i>Myctophum ovcharovi</i>	40–90	7.2	3.4
228	<i>Myctophum punctatum</i>	1–1000	11.0	3.4
229	<i>Protomyctophum andriashewi</i>	50–332	6.0	3.4
230	<i>Protomyctophum arcticum</i>	90–1600	6.0	3.1
231	<i>Protomyctophum beckeri</i>	1–2100	3.5	3.2
232	<i>Protomyctophum bolini</i>	364–728	6.7	3.0
233	<i>Protomyctophum chilense</i>	1–400	--	3.3
234	<i>Protomyctophum choriodon</i>	--	9.5	4.2
235	<i>Protomyctophum crockeri</i>	100–500	3.7	3.2
236	<i>Protomyctophum gemmatum</i>	2000	8.6	3.4
237	<i>Protomyctophum luciferum</i>	2000	6.1	3.5
238	<i>Protomyctophum mcginnisi</i>	--	--	3.3
239	<i>Protomyctophum normani</i>	--	5.6	3.3

No.	Species (Families, Subfamilies)	Depth range (m)	Lmax (SL, cm)	Trophic level
240	<i>Protomyctophum parallelum</i>	2500	5.0	3.3
241	<i>P. subparallelum</i>	350	3.6	3.2
242	<i>Protomyctophum tenisoni</i>	96	5.4	3.3
243	<i>Protomyctophum thompsoni</i>	785–1500	5.2	3.3
244	<i>Symbolophorus barnardi</i>	100–800	11.6	3.1
245	<i>Symbolophorus boops</i>	0–500	13.1	3.5
246	<i>Symbolophorus californiensis</i>	557–1497	11.0	3.1
247	<i>Symbolophorus evermanni</i>	100–500	8.0	3.4
248	<i>Symbolophorus krefftii</i>	1–150	11.2	3.2
249	<i>Symbolophorus reversus</i>	--	8.9	3.2
250	<i>Symbolophorus rufinus</i>	0–850	9.4	3.2
251	<i>Symbolophorus veranyi</i>	0–800	12.0	3.3
252	<i>Tarletonbeania crenularis</i>	0–710	10.4	3.1
253	<i>Tarletonbeania taylori</i>	0–1500	7.0	3.3
Subfamily Notolychninae				
254	<i>Notolychnus valdiviae</i>	25–700	5.2	3.1

Quotes. The following consists of quotes with diverse information of mesopelagic fisheries and their catches.

“During the late 1970s and early 1980s, the severe depletion of demersal fish stocks (most notably *Nothotenia rossii*) was followed in the second half of the latter decade by harvesting of benthopelagic species such as toothfish species with variable year class strengths (*C. gunnari*) and mesopelagic species such as *E. carlsbergi*. [...] Economic considerations effectively ended the *E. carlsbergi* fishery at the end of the 1991/92 season [1], while other fishing grounds, such as the Ob and Lena Seamounts, were effectively closed from the mid-1990s onwards” [2].

“Recently a fortuitous fishery for the lanternfish *Lampanyctodes hectoris* has developed incidental to the anchovy/pilchard fishery off the western coast of South Africa [3]. Annual landings of lanternfishes (mostly *L. hectoris*) were 1,134 metric tons or 0.3 percent of the pelagic fishery catch in this region in 1969 and increased to 42,560 metric tons or 10.45 percent of the catch in 1973” [4].

“There are reports of fishery for mesopelagics especially myctophids, the most well-known is the purse seine fishery for *Lampanyctodes hectoris* off South Africa [5] and also in erstwhile USSR where they fish off West Africa and off Southern Australia. Due to its high lipid (wax esters) content most of the myctophids are unpalatable for consumption and is used for the production of fish meal, fish oil and fish silage. But some species (*Diaphus coeruleus* and *Gymnoscopelus nicholski*) have been fished for human consumption [6,7]. During the 70’s *Gymnoscopelus bolini* and *G. nicholski*, caught as bycatch in the Antarctic marbled rock cod fishery has been smoked for human consumption. In India, however there have been no reports of a myctophid fishery and its use for human consumption” [8].

“Commercial lanternfish fisheries include limited operations off South Africa, in the sub-Antarctic and in the Gulf of Oman [9–12]. But majority of the myctophids are not used for direct human consumption owing to their high lipid or wax ester content, therefore they are used as predator fish feed, poultry feed, animal feed and crop fertilizers [8,13,14]. Exceptions to this are *Diaphus coeruleus*, *Gymnoscopelus nicholski* and *G. bolini* which were considered edible in the Southwest Indian Ocean and Southern Atlantic in the late 1970s [8,15–17]. There are no reports of human consumption of myctophids in India [8,17]. Lekshmy et al. [13] have carried out various methods for processing and utilization of *Benthosema pterotum*. They have also carried out nutritional evaluation of fish meal, dry fish and fish hydrolysate using casein protein as reference on rats for palability. However, one cannot ignore the processing difficulties on a large scale. An industrial fishery for

Lampanyctodes hectoris in South African waters closed in the mid-1980s due to processing difficulties caused by the high oil content of the fish [17]. Interestingly, in eastern South Atlantic, this particular species accounted for around 42,560 tonnes (10.45%) of pelagic catch in 1973 [16] [18].

“A single haul off Argentina yielded 30 tonnes (33 tons) of *Diaphus dumerilii* in one hour. [...]. Limited commercial exploitation occurs off South Africa, where annual purse seine landings (mainly of *Lampanyctodes hectoris*) have fluctuated between 100 and 42,400 tonnes (110 to 46,725 tons). The lanternfishes are reduced to fish meal and fish oil. Because of lanternfishes' high oil content, processing plants are forced to mix them with other species to prevent clogging the machinery. Around South Georgia and Shag rocks, experimental fishing on *Electrona carlsbergi* (mainly juveniles) averaged about 20,000 tonnes (22,000 tons) per year between 1988 and 1990, but increased dramatically to 78,488 tonnes (86,494 tons) in 1991. The Commission for the Conservation of Antarctic Marine Living Resources therefore introduced a 20,000 tonne (220,400 ton) TAC (total allowable catch) for the species for the 1992 season” [19].

“During 1989–1990, 8 cruises were carried out using this vessel in the region, not only for trial fishing but also for estimating the biomass of lantern fish (myctophids) resources” [20].

“According to [21], fishermen in Suruga Bay who eat large quantities of *Diaphus* spp. sort out and discard *B. pterotum* as inedible. That does not mean that this huge production is useless; fish oil and protein have other uses than direct human consumption. Studies in India [9,14] show that meal and hydrolysate from *B. pterotum* are excellent protein supplements in fish and poultry feeds. These myctophids are readily fished; Norwegian results reached 100 tons hr⁻¹ with a sonar-guided, 750 m² (15 × 50 m) double warp trawl (which is a seriously large piece of gear)” [22].

“Pearlside fishery of 2009 landed more than 46,000t; landing in 2010 was 18,000t and decreased until 2013–2016 had 0 landings despite some trials” [23].

“The target species of the fishery are or have been marbled notothenia (*Notothenia rossii*), mackerel icefish (*Champsocephalus gunnari*), grey notothenia (*Lepidonotothen* (= *Notothenia squamifrons*), Günther's notothenia (*Patagonotothen guntheri*), sub-Antarctic lanternfish (indiscriminately recorded as *Electrona carlsbergi*) and Patagonian toothfish (*Dissostichus eleginoides*). [...] Owing to their small size Günther's notothenia and lanternfish have been used for fish meal, while the other species have been fished primarily for direct human consumption [24]. [...] After the successive depletion of the demersal fish stocks, harvesting of (benthopelagic) Patagonian toothfish and (pelagic) sub-Antarctic lanternfish started in the second half of the 1980s [...] Economical considerations prompted the cessation of the fishery on lanternfish after the 1991/92 season. [...] The stock of sub-Antarctic lanternfish has yet to be properly assessed following a tentative assessment in 1991 [...], although a substantial fishery with annual catches of several tens of thousand tonnes has been conducted on the stock for a number of years” [25].

“After most of the demersal (bottom-dwelling) fish stocks were depleted, which happened before CCAMLR came into force, benthopelagic (living off the bottom) Patagonian toothfish and mesopelagic (living in oceanic midwater) sub-Antarctic lanternfish began to be harvested in the second half of the 1980s [...]. By the end of the 1980s, fishing for most species was either prohibited, as in the case of the marbled rockcod, or was limited by total allowable catches (TACs). [...] Economic considerations prompted the cessation of the fishery for lanternfish after the 1991/92 season. [...] The Soviet Union began a trawl fishery for lanternfish (reported indiscriminately as *E. carlsbergi*) in the Antarctic Polar Front in the 1980s, with annual catches initially varying between 500 and 2,500 tonnes. Catches increased from 1987/88 by 14,000 to 23,000–29,000 tonnes in the two subsequent seasons, and peaked in 1990/91 (78,000 tonnes) and 1991/92 (51,000 tonnes) [...]. The fishery lapsed in the 1992/93 season, as it was no longer considered to be economically viable” [26].

“Iceland has in the last few years collected information on mesopelagic fish in the Irminger Sea during their investigations on redfish and have also done some exploratory fishing trials. In Faroese waters Russian trawlers fishing for blue whiting have occasionally reported significant by-catches of mesopelagic fish, and the Faroese Fisheries Laboratory and the Marine Research Institute in Iceland have done some exploratory fishing, but so far without any success” [27].

“Since 2002, the Federation of Vessel owners, in cooperation with the Marine Research Institute in Reykjavík have conducted several experimental cruises. So far, none of the trials have resulted in commercially exploitable catches. The experiments were performed along the Reykjanes Ridge with commercial vessels, using a Gloria #1280 type trawl. Modifications was made on the belly part and the cod end had 9 mm mesh size. In summary there were low catch rate in all hauls, but also low acoustic recordings during the surveys, according to the fishermen. Highest catch rate during these experiments was 3 t/h of *Maurolicus muelleri*” [27].

“In the Gulf of Oman, the only myctophid present is *Benthoosema pterotum* and Iranian fishers have started a commercial fishery for myctophids in their part of the Gulf of Oman [28].

“In spite of its abundance in world oceans, currently only a few commercial myctophid fisheries exist, which include limited operations off South Africa, in the sub- Antarctic, and in the Gulf of Oman [5,19,29]. Global catch of myctophids during 1970–2010, varied between a few tonnes to a maximum of 42,400 t reported during 1973 [30]. Though not commercially exploited in India, these resources have been reported as bycatch of deep-sea shrimp trawlers operating from southwest coast of India [31–33]. [It was reported that] the annual catch of myctophids during 2010–11 was 2972 t and the catch was supported mainly by five species viz., *Diaphus watasei*, *D. garmani*, *Benthoosema fibulatum*, *Myctophum obtusirostre* and *Neoscopilus microchir*. Boopendranath et al. [34] reported the annual catch of myctophids, caught as bycatch in the deep-sea shrimp trawlers operating off southwest coast of India, as 3676 t, with a catch rate of 19.87 kg h⁻¹” [35].

“Myctophids are fairly abundant in Philippine waters, but are rarely caught by fishermen except when they are attracted by light at night in the open seas” [36].

“Myctophids form bycatch in deep sea shrimp trawls with an annual average catch of 2668 t during 2009–2011 in Kerala coast. Fishery occurred almost round the year with peak during November - February. [...] Along the south-west coast of India, lantern fish (Order Myctophiformes) forms a major portion (20–35%) of the bycatch in the deep-sea shrimp trawls [37]. These fishes, when landed are mostly used for fishmeal or manure production” [33].

“Fishermen in Suruga Bay, Central Japan used *Diaphus* spp. as food [21]. Commercial fishery for *Diaphus coeruleus* and *Gymnoscopelus nicholski* (edible species) in the south-west Indian Ocean and southern Atlantic began in 1977 and catch by former USSR countries reached 51,680 t in 1992, after which the fishery ceased due to decrease in catch. Despite this, the Commission for Conservation of Antarctic Marine Living Resources (CCAMLR) still permits Total Allowable Catch (TAC) of 200,000 t for this resource from the area under its jurisdiction. Industrial purse seine fishery for *Lampanyctodes hectoris* was developed in South African waters and closed in the mid-1980s due to processing difficulties caused by the high oil content in the fish [17]. Lanternfishes are harvested commercially only off South Africa and in the sub-Antarctic [19,38] [...] Catch comprised of five species viz., *Diaphus watasei* (74.23%), *Neoscopilus microchir* (20.57%), *Benthoosema fibulatum* (1.94%), *Diaphus garmani* (1.69%) and *Myctophum obtusirostre* (1.58%) [...] *D. watasei* and *N. microchir* were available round the year whereas, other species occurred only seasonally. *D. watasei* was found to be dominant among the myctophids” [33].

“After a long period of high expectations, a commercial fishery for these mesopelagic fishes was initiated in the Persian side of the Oman Sea” [39].

“The federal government has prepared a draft Deep-Sea Fishing Policy for issuance of 50 Licenses for Tuna long Liners, Squid Jigger, Mesopelagic fishing to foreign flagged vessels and 6000 licenses to local fishing vessels” [40].

“Management measures: (1) TAC combined for lantern and lightfish: 50,000 t; (2) Minimum mesh size of 28 mm; (3) Sardine bycatch limitation (anchovy-directed operations); (4) Closed season from 1 November to 14 January; (5) ‘Landings monitored and estimated at factory landing sites” [41].

“During commercial fishing trials in 1995–1998, using a pelagic trawl with cod-end mesh size of 10 mm, the average catch was between 24 and 28 t day⁻¹ in Iranian waters [...]. During trial commercial fishing in Oman waters in 1996, total monthly catches of myctophids for the months of March, April and May were 446, 1563 and 1273 t, respectively. Over 123 fishing days this gave an average catch of 20 t day⁻¹. However, catches declined during early summer and the trial was therefore discontinued” [42].

“[A] fishery for two species of myctophids which are considered edible viz., *Diaphus coeruleus* and *Gymnoscopelus nicholski* existed in the Southwest Indian Ocean and Southern Atlantic during 1977–1992 and catches up to 51,680 t has been reported in 1992. Shotton [43] has reported regarding an industrial purse seine fishery for *Lampanyctodes hectoris* in South African waters which was closed in the mid-1980s due to processing difficulties caused by the high oil content of the fish. Qeshm Fish Process Company in Iran produces fish meal and oil, mainly based on lantern fish and the plant has a nominal capacity of 3,600 tons of lanternfish per day, out of which approximately 700 tons of fish meal and 70 tons of fish oil are obtained (QFPCO 2011)” [44].

“Special attention should be paid here to numerous species from the group of Myctophidae, pelagic Gobidae and other snail-sized fish (below 10 cm in length) forming dense shoals identified as sound scattering layers. The exploitation of their stocks was begun by the Republic of South Africa (Divisions 1.4 and 1.6) when 11- and 12.7-mm mesh purse seines were introduced, although these fish inhabit the whole ICSEAF Area. At first their catches were quite substantial, equaling, for instance, 42,000 tons (mostly *L. hectoris*) for Division 1.6 in 1973. Between 1978 and 1983, the catches considerably, not exceeding 1,000 tons, with the exception of 1979 and 1981, when 10,000 tons were taken [5] (Newman, 1977)” [45].

“*Lampanyctodes hectoris* have accounted for 0.3–10.45% (1134–42,560 metric tons) of the total fish landed by South African pelagic fishing boats operating in the cold water off the west coast of south Africa during the years 1969–1973 [3]. Approximately 15 tons of another species, *Diaphus dumerilii*, were taken in a single haul at a depth of 260–265 m off Uruguay [46]” [38].

“Myctophids have been targeted by commercial fisheries in the Southern Ocean, notably in the northern Scotia Sea area where ex-Soviet Union vessels targeted *Electrona carlsbergi* at or just south of the Polar Front to the north of South Georgia [47]. Catches peaked at around 30,000 tonnes in the 1988/89 season, with the fish converted to meal, but since 1990 there has not been a targeted fishery” [48].

“An annual PUCL for mesopelagic fish of 50,000 t was introduced in 2012, following increased catches of lantern- and light fish by the experimental pelagic trawl fishery in 2011, when just over 7000 t of these species were landed. Since then, however, catches have not exceeded 1000 t. It is anticipated that catches of mesopelagic fish may again increase in 2014 with resumption of this experiment” [49].

“While under limited commercial exploitation in the southern Benguela, the mesopelagic catch has historically fluctuated between 100 and 42,400 tonnes and has accounted for some 10% of the total annual catch made by South Africa’s small pelagic fishery in some years [...] However, the fishery intermittently closed during mid-80s due to processing difficulties caused by the high wax ester content of the fish [...]. In addition to the commercial purse-seine fishery, DAFF granted two-year permits in 2010 for an experimental mid-water trawl fishery targeting mesopelagic and pelagic stocks. Of the total

catch reported for both years combined (9486.5 tonnes), 83% consisted of *L. hectoris* and 4% of *M. walvisensis*" [50].

"Some Icelandic companies are developing the maurolic fishery (*Maurolicus muelleri*) in areas south of Iceland. While he is not always successful, at the end of January, there were several successful days before main concentrations of maurolic migrated to the west.

According to the information of the First Officer and skipper of the "Faxi RE" trawler, the fishery began in the area of the Grindavík Deep, then moved south of the Eldey area. All three HB Grandi trawlers were fishing. The catches were 70 to 80 tons for long trawls. In the same area there were 12 other vessels of other companies. The "Faxi RE" used a midwater trawl with a small-mesh insert. But it seems that for a more successful harvest, a smaller mesh trawl and additional knowledge will be required. The fish is small enough. The optimal time for catching it is daytime only." [51].

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