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 ($L_\infty$), 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.
Mesopelagic fishes are not strongly exploited by fisheries, owing to their extreme dispersion (in the order of 1 g·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 Diaphininae (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 (Ø) 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 g·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 g·m⁻³), dark blue to high densities, white refers to unsampled sea areas, and yellow to land.](image-url)
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 Ø and mean asymptotic length (L∞) measured as standard length (SL).

| Species                        | L∞ (SL; cm) | K (year⁻¹) | Ø = logK + 2logL∞ |
|--------------------------------|-------------|------------|-------------------|
| Benthosema fibulatum           | 7.7         | 5.62       | 2.523             |
| Benthosema glaciale            | 8.3         | 0.20       | 1.139             |
| Benthosema glaciale            | 8.6         | 0.45       | 1.522             |
| Benthosema glaciale            | 8.5         | 0.36       | 1.415             |
| Benthosema glaciale            | 7.5         | 0.31       | 1.241             |
| Benthosema pterotum            | 6.8         | 1.81       | 1.923             |
| Benthosema suborbitale         | 3.3         | 3.65       | 1.599             |
| Ceratoscopelus maderensis      | 7.1         | 3.65       | 2.260             |
| Ceratoscopelus maderensis      | 7.9         | 1.30       | 1.909             |
| Diaphus dumerilii              | 7.5         | 1.83       | 2.011             |
| Diaphus dumerilii              | 6.9         | 3.81       | 2.259             |
| Diaphus watasei                | 15.1        | 0.80       | 2.261             |
| Diaphus watasei                | 15.1        | 0.80       | 2.261             |
| Electrona antarctica           | 9.7         | 0.25       | 1.374             |
| Electrona antarctica           | 12.9        | 0.17       | 1.452             |
| Electrona carlsbergi           | 9.7         | 0.55       | 1.711             |
| Electrona risso                | 6.1         | 3.03       | 2.052             |
| Gymnoscopelus braueri          | 13.3        | 0.29       | 1.712             |
| Krefftichthys anderssoni       | 6.9         | 0.71       | 1.524             |
| Lampanyctodes hectoris         | 10.0        | 0.31       | 1.491             |
| Lampanyctus regalis            | 26.5        | 0.20       | 2.150             |
| Lampanyctus ritteri            | 13.5        | 0.36       | 1.817             |
| Lepidophanes guentheri          | 7.3         | 1.83       | 1.988             |
| Lobianchia dofeini             | 4.6         | 1.39       | 1.467             |
| Lampanyctus centralis          | 11.1        | 1.29       | 2.201             |
| Myctophum nitidulum            | 10.0        | 0.42       | 1.623             |
| Myctophum punctatum            | 9.0         | 0.32       | 1.414             |
| Myctophum punctatum            | 10.5        | 0.17       | 1.262             |
| Notolichnus valdiviae           | 2.8         | 1.41       | 1.044             |
| Notoscoelopus elongatus         | 11.9        | 0.89       | 2.100             |
| Notoscoelopus kroyeri           | 14.9        | 0.20       | 1.647             |
| Scopelengys tristis            | 21.0        | 0.46       | 2.307             |
| Stenobrachius leucopsareri      | 10.5        | 0.33       | 1.561             |
| Stenobrachius leucopsareri      | 9.8         | 0.31       | 1.475             |
| Stenobrachius leucopsareri      | 14.3        | 0.24       | 1.698             |
| Stenobrachius leucopsareri      | 8.5         | 0.34       | 1.390             |
| Stenobrachius nannochir         | 13.0        | 0.42       | 1.851             |
| Symbolophorus californiens      | 13.5        | 0.43       | 1.894             |
| Triphoturus mexicanus           | 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 Ø = log(K) + (2/3)log(W∞).

| Species                        | W∞ (g)     | K (year⁻¹) | Ø                   |
|--------------------------------|------------|------------|---------------------|
| Thunnus albacares               | 198,940    | 0.250      | 2.93                |
| Morone saxatilis                | 17,543     | 0.186      | 2.10                |
| Mugil cephalus                  | 13,890     | 0.110      | 1.80                |
| Platichthys flesus              | 1058       | 0.229      | 1.38                |
| Cottus biflus                   | 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·L³, 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  | 27.6  |
| 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 Seamount | 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                                                     | Caught as bycatch of rock cod fishery [23]                                       |
| Antarctica                         | 1970: n.a.                                                                       | [21]                                                                             |
| South Africa                      | undated: 100–42,400 t·year⁻¹                                                     | Catch from log sheet records [24]                                                |
| Gulf of Oman                      | 1989: 1739 t                                                                       | [25]                                                                             |
| Iceland                            | 2009: >46,000 t; 2010: 18,000 t; 2013–2016: 0                                     |                              |
|                                  | 1980–1986: 500–2500 t·year⁻¹; 1987/88:                                            | [27]                                                                             |
|                                  | 14,000 t; 1988–1990: 23–29·10⁶ t·year⁻¹; 1990/91: 78,000 t; 1991/92: 51,000 t.     | [28]                                                                             |
| Northeast Atlantic                | April–June 1984: 0.024 t                                                        | Mainly used for fishmeal [26]                                                    |
| South Africa                      | 1969–1973: 82,000 t                                                               | [29]                                                                             |
| India                             | 2008 or earlier: 9600 t                                                          | [30]                                                                             |
| India/Kerala coast                | 2009: 2421 t; 2010: 2610 t; 2011: 2972 t                                         | [31]                                                                             |
| SW Indian Ocean and S. Atlantic   | 1992: 51,680 t                                                                    | [32]                                                                             |
| Philippines                       | Post WWII                                                                        | Number of boats, length of fishing trips, amount discarded and percentage of discards that are myctophids: see [29]; 2009–2010: 3676 t [36]; for India/Arabian Sea: 2010–2011: 2972 t [31] |
| Pakistan                          | 2016: n.a.                                                                       | [33]                                                                             |
| South Africa                      | 2015: 50,000 t                                                                    | [34]                                                                             |
| Iran                              | 1995–1998: 24–28·t·day⁻¹                                                         | [35]                                                                             |
| Oman                              | 1996, March: 446 t; 1996, April: 563 t; 1996, May: 1273 t                         | [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 *Electrona carsbergi* using midwater trawl was conducted by the USSR fleet between 1979 and 1986. The fishery was based on quasi-stationary aggregations of *E. carsbergi* 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 Statistical Bulletin.                                                                 |
| Indian sector of the Southern Ocean:      | A test fishery on *Electrona carsbergi* 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 *Diaphus suborbitalis* 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 fish-
ery 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 kg·h⁻¹ in the Sea of Okhotsk and 40 kg·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 t·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, 61,344·0.135/2 = 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 t·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](http://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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**References**

1. Gulland, J.A. (Ed.) Summary. In *The Fish Resources of the Ocean*; Fishing News Books: West Byfleet, UK, 1971; pp. 307–319.
2. Gjesaeter, J.; Kawaguchi, K. A review of the world resources of mesopelagic fish. In *FAO Fisheries Technical Paper 193*; FAO: Rome, Italy, 1980; 151p.
3. Radchenko, V.I. Mesopelagic fish community supplies “biological pump”. *Raffles Bull. Zool.* 2007, (Suppl. 14), 247–253.
4. Watanabe, H.; Moku, M.; Kawaguchi, K.; Ishimaru, K.; Ohno, A. Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. *Fish. Oceanogr.* 1999, 8, 115–127. [CrossRef]
5. Pauly, D. Ocean Ecology. In *Encyclopedia of Environmental Biology*; Nierenberg, W.A., Ed.; Academic Press: San Diego, CA, USA, 1995; Volume 3, pp. 1–17.
6. Moku, M.; Kawaguchi, K.; Watanabe, H.; Ohno, A. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. *Mar. Ecol. Prog. Ser.* 2000, 207, 129–140. [CrossRef]
7. Pakhomov, E.A.; Perissinotto, R.; McQuaid, C.D. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Prog. Ser.* 1996, 134, 1–14. [CrossRef]
8. Kaartvedt, S.; Staby, A.; Aksnes, D.L. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar. Ecol. Ser.* 2012, 456, 1–6. [CrossRef]
9. Irigoien, X.; A Klevjer, T.; Røstad, A.; Martinez, U.; Boyra, G.; Acuña, J.L.; Bode, A.; Echevarria, F.; González-Gordillo, J.I.; Hernandezleon, S.; et al. Large mesopelagic fish biomass and trophic efficiency in the open ocean. *Nat. Commun.* 2014, 5, 3271. [CrossRef]
10. Proud, R.; Handegard, N.O.; Kloster, R.J.; Cox, M.J.; Brierley, A.S. From siphonophores to deep scattering layers: Uncertainty ranges for the estimation of global mesopelagic fish biomass. *ICES J. Mar. Sci.* 2019, 76, 718–733. [CrossRef]
11. Anderson, T.R.; Martin, A.P.; Lampitt, R.S.; Trueman, C.N.; Henson, S.A.; Mayor, D.J. Quantifying carbon fluxes from primary production to mesopelagic fish using a simple food web model. *ICES J. Mar. Sci.* 2019, 76, 690–701. [CrossRef]
12. Froese, R.; Pauly, D. FishBase. World Wide Web Electronic Publication. 2021. Available online: [www.fishbase.org](http://www.fishbase.org) (accessed on 1 September 2021).
42. Ermakov, Y.K.; Karyakin, K.A. Bycatch composition in walleye pollock trawl fishery in the Okhotsk and Bering Seas. *Probl. Fish. [Voprosy Rybolovstva]* 2003, 4, 435–450. (In Russian)

43. Zolotov, A.O.; Buslov, A.V. Assessment of bycatch in the walleye pollock fishery by pelagic trawls in the western Bering Sea in 2002–2004. *Fisheries [Rybnoe Khozyaistvo]* 2006, 4, 37–41. (In Russian)