ISSN 1198-6727

Fisheries Centre Research Reports

2022 Volume #30 Number #4

Marine and Freshwater Miscellanea IV

Institute for the Oceans and Fisheries,
The University of British Columbia, Canada

Cite as:
D. Pauly and E. Chu (eds). 2022. *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver. 118 pp.

ISSN 1198-6727

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Preface

Like its predecessors[1,2,3], this Fisheries Centre Research Report is a grab-bag of contributions of which a few could have been submitted to peer-reviewed journals but weren't and others contributions that couldn't, because of their subject matter or irreverent style.

The three contributions on sturgeon and which were drafted in support of an international project that was not funded and thus could not get started.

Two others deal with aspects of fish respiration, in the giant Mekong catfish and in the writing of George Cuvier, while two others deal with the reconstruction of fisheries catches; one is about the freshwater fisheries of Quebec, the other about the global catch of sponge fisheries, both from 1950 to the near present.

The remaining contributions comprise 3 articles on sardinella in West Africa, basic traits in sharks and rays, and the "fishing down" phenomenon in the Bohai Sea in the Chinese Northeast, and 3 short accounts with observations by one of us (D.P.) on a trip to India and on receiving science awards, which does make one think.

We hope that readers will find one or two items that they find interesting in this grab-bag.

Daniel Pauly and Elaine Chu
Vancouver, November 2022

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[1] Pauly, D. and V. Ruiz-Leotaud (Editors). 2018. *Marine and Freshwater Miscellanea*. Fisheries Centre Research Reports 26(2), 83 p.

[2] Pauly, D. and V. Ruiz-Leotaud (Editors). 2020. *Marine and Freshwater Miscellanea II*. Fisheries Centre Research Reports 28(2), 141 p.

[3] D. Pauly and E. Chu (Editors). 2021. *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Reports 29(1), 115 p.

Foreword

And then there were four.

This is the fourth collection of articles, authored or co-authored by Daniel Pauly, which, as he says "could have been submitted to peer-reviewed journals but weren't and others contributions that couldn't, because of their subject matter or irreverent style." Daniel Pauly has earned the right to be humorous about his research through decades of hard work, deep understanding of the subject matter and exceptional research. In fact, he'd be hard pressed not to have a lighter side; science is not without its quirks and foibles, and it often takes a sense of humour to make it through.

More importantly, Daniel Pauly has an absolute commitment to publishing scientific knowledge so that it can be known and used by others, rather than having the works staying as unpublished papers or files in the cabinet or hard drive where no one know or has access to. Such a commitment is amongst the many qualities that make him one of the most influential living marine scientists.

In this collection of articles, jointly edited with Elaine Chu, Daniel juxtaposes the Meking catfish and tuna, looks at freshwater catches in Quebec before rushing to Senegal and northwest Africa to check on sardinella stocks, then talks about sharks and rays, sturgeons and sponges (separately, not all together). He switches gears and talks about a brief meeting with the Dalai Lama, and provides two award acceptance speeches.

Definitely a wide-range of subjects, but all presented with Daniel's unique grace and style.

Enjoy!

Regards,

Prof. William Cheung
Director, Institute for the Oceans and Fisheries
The University of British Columbia

Does the Mekong giant catfish *Pangasianodon gigas* grow as fast as a tuna?[1]

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Abstract

Tentative parameters of the von Bertalanffy growth function (VBGF) of the Mekong giant catfish (*Pangasianodon gigas* Chevey, 1931) in the wild were estimated as $L_\infty = 300$ cm (total length), K = 0.085 year^{-1} and $t_0 = -1.115$ year based on scattered information in the existing literature. These parameters suggest that *P. gigas* grows almost as fast as Atlantic bluefin tuna (*Thunnus thynnus*), which is attributed to the fact that adult *P. gigas* are air-breathers.

Introduction

The very high growth rates of air-breathing fishes are often noted in aquaculture manuals and invasive species reports (Knight 2010; Mäkinen *et al.* 2013). Yet, despite the growing literature on bi-modal respiratory behavior in aquatic animals, such information remains largely anecdotal. It is the purpose of this contribution to evaluate one such anecdote, the growth of the Mekong giant catfish (*Pangasianodon gigas* Chevey, 1931).

An FAO report on the fishes of the Mekong River delta states that this species shows “one of the fastest growth rates of any fish in the world, reaching 150 to 200 kg in 6 years” (Rainboth 1996, p. 153) and a 1991 revision of the Pangasiidae Family even reports a growth of “at least 200 kg in its first three years” (Roberts and Vidthayanon 1991, p. 97). The author of a major book on air-breathing fishes, Graham (1997, p. 256) suggested that “the growth rate of *Pangasius* is said to rival that of pelagic species such as tuna, a rare phenomenon for a freshwater species”.

This statement can be tested if “*Pangasius*” is understood as the now invalid synonym of *Pangasianodon gigas*, which was treated as a subgenus of *Pangasius* by Roberts and Vidthayanon (1991, p. 102)[2]. The Mekong giant catfish and the Chao Phraya giant catfish (*Pangasius sanitwongsei* Smith, 1931) are the only members of the Pangasiidae that reach sizes similar to those of tuna, thus enabling comparisons of their growth rate across their entire size range. This small contribution presents a test of this claim. Given the tentative nature of the data at hand, no formal statistical test, whether ‘frequentist’ or Bayesian, will be

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[1] Cite as: Pauly, D. and J. Müller. 2022. Does the Mekong giant catfish *Pangasianodon gigas* grow as fast as a tuna? p. 5-12. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

[2] Graham’s nomenclatural references are often imprecise and despite the otherwise very important contributions of his book, it is sometimes hard to identify the exact species he had in mind. In some cases, he refers to names that were invalid for as long as 50 years at the time of publication, for example in the cases of *Pseudosphromenus cupanus*, which is referred to as “*Macropodus*” *cupanus* (Cuvier 1831), or *Macropodus ocellatus* Cantor, 1842 (referred to as *M. “chinensis”*). His statement that some *Macropodus* species are mouth brooders (Graham 1997, p. 250) suggest an even wider nomenclatural confusion and raise the question whether he did not confuse them with *Betta* spp., perhaps from the similar-looking *B. pugnax* species group. Graham also refers to *Pangasianodon hypophthalmus* as “*Pangasius*” which suggest that he used the same genus name for *P. gigas*.

performed but the following calculations will hopefully inspire future research on the growth of large air-breathing fishes.

The Mekong giant catfish (*Pangasianodon gigas*) reaches a length of 300 cm (Baird *et al.* 1999) and weight of 350 kg (Kottelat 2001), data that are indeed similar to the maximum sizes reported for the 3 bluefin tuna species and for yellowfin tuna (i.e., *Thunnus* spp., see FishBase; www.fishbase.org). The notion that *P. gigas* reaches these large sizes as rapidly as these tuna species is, however, a strong claim because large tuna possess gills with very narrow interlamellar spaces and huge large surface area (Muir and Hughes 1969), which provides them with the large amount of oxygen required to sustain their elevated metabolism; Mekong giant catfish do not have such extraordinarily large gills.

In contrast to tuna, whose growth has been studied by numerous authors (see FishBase), the growth of Mekong giant catfish has not yet been well studied. Its growth in captivity has been reported upon (Lorenzen *et al.* 2006), but there are apparently no studies of its growth in the wild. Roberts and Vidthayanon (1991, pp. 119-120) mention specular growth rates in the early juvenile stages but their information is only based on personal communication. In their account, the fishes' growth accelerates again during their second year, which is atypical for both marine and freshwater fishes and has so far only been demonstrated in *Arapaima gigas* (Schinz, 1822), also an air-breathing species (Wosnitza-Mendo 1984; Pauly 2019).

In addition to these more anecdotal accounts, Lorenzen *et al.* (2006) have presented two estimates of the parameters of the von Bertalanffy Growth Function (VBGF) for *P. gigas* from which a single growth curve for the for the remaining few specimens in the wild may be inferred. These two methods are presented here, following a presentation of the VBGF and related concepts.

The VBGF for length has the form:

$$L_t = L_\infty \cdot (1-e^{-K\cdot(t-t_0)}) \qquad \text{...1)}$$

where L_t is the mean length at age t of the fish in question, L_∞ their asymptotic length, i.e., the mean length that would be attained after an infinitely long time, K a growth coefficient expressing how fast the asymptotic size is approached (here in year^{-1}) and t_0 is a parameter adjusting for the fact that VBGF usually fails to describe the growth of the earliest (larval and post-larval) stages of fishes.

The growth in length of fish with similar shapes can be compared using the parameter *Ø',* (Pauly 1998), defined by the equation

$$Ø' = \log(K) + 2\cdot\log(W_\infty) \qquad \text{...2)}$$

which has a normal distribution when applied to numerous populations of the same species, e.g., in skipjack tuna *Katsuwonus pelamis* (see figure 9.4, p. 263 of Longhurst and Pauly 1987).

The VBGF for growth in weight is

$$W_t = W_\infty \cdot (1-e^{-K\cdot(t-t_0)})^b \qquad \text{...3)}$$

where W_∞ is the asymptotic weight, as derived from a length-weight relationship (LWR) of the form $W = a\cdot L^b$ (Froese 2006), with b often taking values of, or near 3. One of the advantages of a growth curve in weight is that it allows for comparing the growth performance of fishes of widely different shapes through the index

$$Ø = \log(K) + 2/3\log(W_\infty) \qquad \text{...4)}$$

(Pauly 1998), which also is normally distributed when within taxa with similar life histories.

The first estimate

Lorenzen *et al.* (2006) wrote that *P. gigas* "*are widely stocked into 'semi-natural' reservoirs in Thailand, where they appear to survive and grow well but are not known to mature or spawn. Stocking and recapture data were analysed for Sirikit reservoir in Thailand [and grow parameters] were estimated as* L_∞ *= 210 cm and K= 0.2 year*$^{-1}$*. [...] . The stocked fish thus appear to grow at a higher rate but to a lower asymptotic size than the wild fish in the Mekong. This is consistent with the general observation that cultured fish, even after release, show an accelerated life history (Lorenzen 2000, Thorpe 2004).*"

Lorenzen *et al.* (2006) provide no textual details beyond the statement that "*no data were collected for the first 7.5 years after release*" and they did not specify the method they used to estimate growth parameters from the growth increment data that they casually mention. However, the graph they presented suggests that the stocked and released fish whose length increments were used to compute growth parameters were rather large, and thus did not grow much. This should result in a rather uncertain estimate of the parameter K, because it is the more rapid growth of younger/small fish which stabilizes the estimation of this parameters.

The second estimate

Lorenzen *et al.* (2006) used the maximum size (they) recorded for *P. gigas,* i.e., 290 cm as an estimate of L_∞. However, the length type was not specified. There are 92 mentions of the word 'length' (or 'lengths') in Lorenzen *et al.* (2006), but only one of 'total length' (TL). Given this single mention, and especially because assuming that fork length (FL) or standard length (SL) was used in the 91 remaining instances would generate unrealistically high maximum weights in conjunction with the length-weight relationship (LWR) mentioned below, we suggest that Lorenzen *et al.* (2006) used TL throughout.

To estimate K, they plotted the values of L_∞ and K in the compilation of Pauly (1980) as ln(K) vs. ln(L_∞), from which they derived $K = 3.3492 \cdot L_\infty^{0.6673}$. They then solved the equation for L_∞ = 290 cm (TL), which yielded K = 0.08 year^{-1}. They thought these values were reasonable and used them for assessing the (dire) state of their population in the Mekong basin.

The estimates of K in Pauly (1980) which will have most influenced this empirical equation (via a lever effect) will have been his largest species, i.e., the basking shark *Cetorhinus maximus* with L_∞ = 1226 cm (and not '226' cm as stated in Table 1 of Pauly 1980) and K = 0.045 year^{-1}, and the white sturgeon *Acipenser transmontanus,* with L_∞ = 350 and 300 cm, and K = 0.5 and 0.04 year^{-1}, respectively. These fishes are not known to be particularly fast growing, and thus Lorenzen *et al.*'s empirical equation may not predict values of K that are too high, even though some fast-growing fish (incl. tuna species) were also included in the dataset they used.

Combining the first and the second estimate

Applying Equation (2) to the first and the second estimate of growth parameters of *P. gigas* yields estimates of *Ø'* = 3.94 and 3.83, respectively, with an average *Ø'* = 3.88. The lower value of *Ø'* suggests that the second estimate of *K* = 0.08 year^{-1} for 'wild' *P. gigas* was not excessively high.

Generally, L_∞ is slightly larger than the largest fish in a population, or L_{max} (Taylor 1958; Froese, and Binohlan 2000), and thus, for *P. gigas,* 300 cm may be more appropriate as estimate of L_∞ than L_{max} = 290 cm. Combined with an estimate of L_∞ = 300 cm, the mean *Ø'* yields an estimate of K = 0.085 year^{-1}.

An estimate of t_0 is provided, in the absence of any other estimate, by the empirical equation of Pauly (2019), which suggests that

$$\log(-t_0) = -0.3922 - 0.2752 \cdot \log(L_\infty) - 1.038 \cdot \log(K) \qquad \ldots 5)$$

which here yields $t_0 = -1.115$ years.

The set of values for the growth parameters of *P. gigas* in the wild is very tentative, but it is based on broader considerations than the previous estimates and, therefore, may be more accurate.

Comparing the growth of *P. gigas* with that of tuna

Lorenzen *et al.* (2006) presented an LWR for *P. gigas*, i.e., $W = 0.04 \cdot L^{2.8}$, where weight is in g and length in cm. Thus, based on the previous considerations, its VBGF for weight growth is

$$W_t = 345{,}000 \cdot (1 - e^{-0.085 \cdot (t + 1.115)})^{2.8} \qquad \ldots 6)$$

which leads, via Equation (4) to an estimate of $\text{Ø} = 2.62$, which is close to estimates of Ø for bluefin tuna (*Thunnus thynnus*; red dots in Figure 1), and within the ellipsoids that could be drawn around the Scombridae family (green dots in Figure 1).

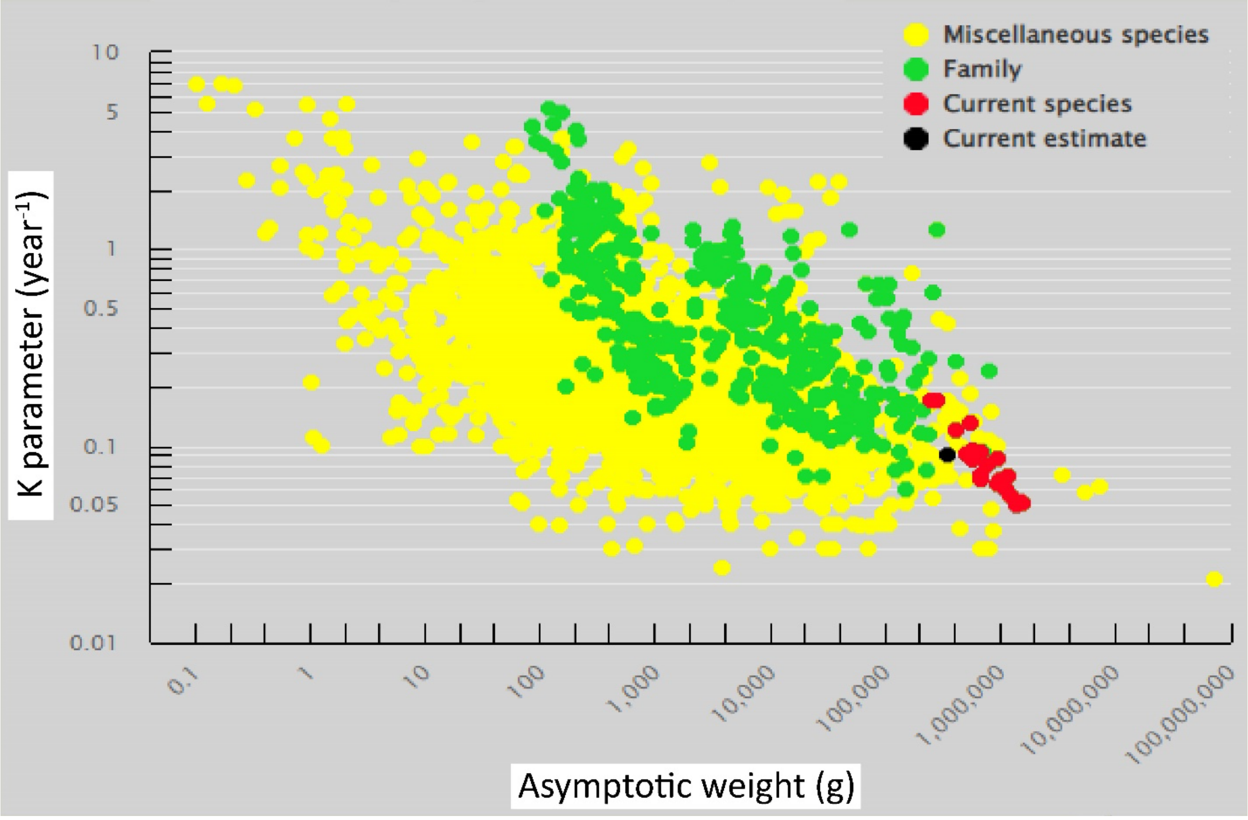

Figure 1. Auximetric plot of the fish with weight growth parameters in FishBase (www.fishbase.org), with each dot representing a K & W_∞ pair, i.e., the mean growth curve of the individual of a fish population. The non-Scombridae are represented by yellow dots ('Miscellaneous species'), the fast-growing Scombridae (mackerels, tuna, etc.) by green dots ('Family'), and Atlantic bluefin tuna by red dots ('Current species'). The black dot ('Current estimate') represents the tentative growth curve for *P. gigas* (W_∞ = 345 kg and K = 0.085 year^{-1}), which is suggested here to grow almost as fast as bluefin tuna.

Figure 1 suggests that the Mekong giant catfish *Pangasianodon gigas* (black dot) grows almost as fast as Atlantic bluefin tuna (red dots), commonly and justifiably seen as the fastest-growing tuna. Thus, *P. gigas* is indeed a very fast-growing fish.

A total length of 300 cm in *P. gigas* roughly corresponds to fork length of 266 cm, which is smaller than the asymptotic fork lengths estimated by various researchers for Atlantic bluefin tuna. However, using the mean value of $\O' = 4.00$ in Atlantic tuna, which refers to LF, a estimate of K can be derived for hypothetical bluefin that would reach only 266 cm LF. This estimate of K would be 0.14 year^{-1}; inserted into Equation (5), these estimates yield $t_0 \approx -0.2$ years. Figure 2A compares the growth curves *in length* for these two species, and also gives the impression that their growth is not very different.

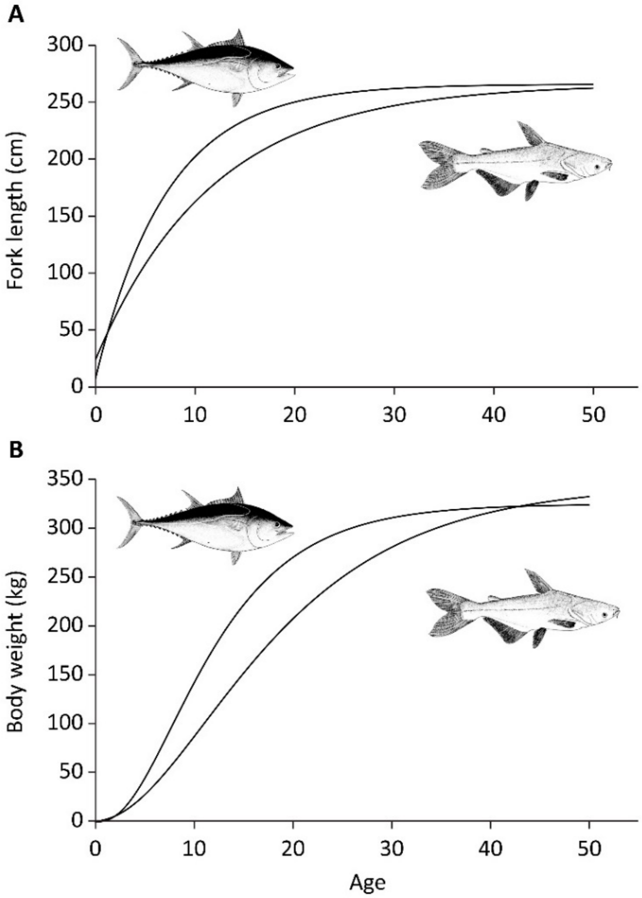

Figure 2. Growth curves in length (A) and weight (B) of (hypothetical) bluefin tuna and Mekong giant catfish, all assuming an asymptotic length of 266 cm (FL; see text).

However, when comparing growth *in weight* between these two species (Figure 2B), what appears as a small difference in Figures 1 and 2A turns out to be substantial, with young tuna growing faster. This fast growth is made possible by huge gills, which supply the oxygen required to sustain a metabolic rate almost equivalent to that of a similar-sized mammal. Even by breathing air, *P. gigas* does not match the growth of Atlantic bluefin tuna, although it does grow very fast.

Lefevre *et al.* (2013), presumably because their first author believes that growing fish can always meet their oxygen requirements via their gills, failed to understand why they devoted energy to breathing air (see also Pauly 2021). Thus, they write that "*[t]hough air-breathing is usually considered a beneficial* *behaviour, we show that surfacing does indeed incur an energetic cost. Though air-breathing is important to swimming in hypoxia (McKenzie et al. 2012), it remains unclear what mechanisms drive the air-breathing behaviour in* [Pangasianodon] hypophthalmus *in normoxia*."

This self-created conundrum is easily resolved: air breathing is not only "*a beneficial behavio*r" in *Pangasianodon* species, but absolutely necessary, because large individuals of this genus cannot meet their oxygen requirements by relying only on their gills at higher temperatures, even in normoxic water (see Mitamura *et al*. 2009, fig. 4). Being a migratory species, *P. gigas* experiences a relatively wide range of temperatures compared to other tropical freshwater fishes: it spawns in the cool regions of Chiang Rhai and Chiang Kong in Northern Thailand (Eva *et al*. 2016; Ngamsiri *et al*. 2007; Pholprasith and Tavarutmaneegul 1997) and moves downstream into the lower delta region. The temperatures at its most northern habitats range from 18 to 26°C between January and August (Zhang *et al*. 2007), whereas the water in the delta is typically 10°C warmer. Some authors (Ngamsiri *et al*. 2007; Hogan *et al*. 2001; Pholprasit 1989) assume a historical distribution of *P. gigas* in the Chinese province of Yunnan where water temperatures can be as low as 14-16°C in the cold season and rarely exceed 22°C in the summer (Wang *et al*. 2014; Zhang *et al*. 2007). Hogan *et al*. (2001) and Hogan (2004) hypothesize that *P. gigas* might still be present in southern China and that its decline in Yunnan could be attributed to deforestation and the construction of dams in this region.

Even in the warmer regions of the delta, *P. gigas* may not constantly be exposed to the upper extremes of its thermal tolerance range. Like other large species of the Mekong delta, it is often reported in the vicinity of, or even inside, deep river pools (Eva *et al*. 2016). Some of these deep holes reach depths of up to 90 m (Gupta and Liew 2007) but it is unclear to which depths the Mekong giant catfish actually dives. Even in stagnant and warm water bodies such as the Mae Peum reservoir in Thailand, depths of only 6 to 12 m provide temperature differences of up to 6 °C between the water surface and the bottom (Mitamura *et al*. 2009). In this reservoir, *P. gigas* surfaces frequently in the hot season but less so in January and February, when the deeper water columns are well-oxygenated (Mitamura *et al*. 2009, fig. 6).

As for Graham's claim of 1997, which appears credible when growth in length is considered (Figure 2A) is less convincing when growth in weight is considered (Figure 2B), at least when bluefin tuna is used as representative of 'tuna'. However, the fact that a fish that inhabits warm and often deoxygenated freshwater bodies can reach growth rates that equal those of large marine fishes is remarkable in itself. There are only a few examples of very big tropical freshwater teleosts and those for which rapid growth rates are reported are typically air-breathers, for example, *Clarias gariepanus* Burchell, 1822, supposedly the fastest-growing large freshwater fish of Africa, and *Arapaima gigas* from South America, the largest scaled freshwater species in the world (Wosnitza-Mendo 1984).

Acknowledgements

We thank Ms. Elaine Chu for Figure 2.

References

Baird, I.G., V. Inthaphaisy, P. Kisouvannalath, B. Phylavanh and B. Mounsouphom. 1999. *The fishes of southern Lao*. Lao Community Fisheries and Dolphin Protection Project. Ministry of Agriculture and Forestry, Lao PDR.161 p.

Cantor, T. 1842. General features of Chusan, with remarks on the flora and fauna of that island. *Annals and Magazine of Natural History*, 9: 265–278, 360–370, 481–493.

Chevey, P. 1931. Sur un nouveau silure géant du Bassin du Mékong *Pangasianodon gigas* nov. g., nov. sp. *Bulletin de la Société Zoologique de France,* 55(7) : 536–542

Cuvier, G. and A. Valenciennes. 1831. *Histoire naturelle des poissons. Tome septième. Livre septième. Des Squamipennes. Livre huitième. Des poissons à pharyngiens labyrinthiformes. Volume 7.* F. G. Levrault, Paris. i-xxix + 531 p., 170–208 pls.

Eva, B., P. Harmony, G. Thomas, G. Francois, V. Alice, M. Claude, and D. Tony. 2016. Trails of river monsters: detecting critically endangered Mekong giant catfish *Pangasianodon gigas* using environmental DNA. *Global Ecology and Conservation*, 7: 148–156

Froese R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology,* 22: 241–253.

Froese, R. and C. Binohlan. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, 56(4): 758–773.

Graham, J.B. 1997. *Air-breathing fishes: Evolution, Diversity and Adaptation*. Academic Press, San Diego. 299 p.

Gupta, A. and S.C. Liew. 2007. The Mekong from satellite imagery: A quick look at a large river. *Geomorphology*, 85(3-4): 259–274.

Hogan, Z.S. 2004. Threatened fishes of the world: *Pangasianodon gigas* Chevey, 1931 (Pangasiidae). *Environtmental Biology of Fishes*, 70: 210.

Hogan, Z.S., N. Pengbun and N. van Zalinge. 2001. Status and conservation of two endangered fish species, the Mekong giant catfish *Pangasianodon gigas* and the giant carp *Catlocarpio siamensis*. Cambodia's Tonle Sap River. *Natural History Bulletin of the Siam Society*, 49: 269–282.

Knight, J.D.M. 2010. Invasive ornamental fish: a potential threat to aquatic biodiversity in peninsular India. *Journal of Threatened Taxa,* 2(2)**:** 700–704.

Kottelat, M. 2001. *Fishes of Laos*. WHT Publications Ltd., Colombo 5, Sri Lanka. 198 p.

Lefevre S, T. Wang, N.T. Phuong and M. Bayley. 2013. Partitioning of oxygen uptake and cost of surfacing during swimming in the air-breathing catfish *Pangasianodon hypophthalmus*. *Journal of Comparative Physiology B*, 183(2): 215–21.

Lefevre, S., D.J. McKenzie and G.E. Nilsson. 2017a. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology,* 23: 3449–3459.

Lefevre, S., D.J. McKenzie and G.E. Nilsson. 2017b. In modelling effects of global warming, invalid assumptions lead to unrealistic projections. *Global Change Biology,* 24: 553–556.

Longhurst, A. and D. Pauly. 1987. *Ecology of Tropical Oceans*. Academic Press, San Diego. 407 p.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish stocking programmes. *Canadian Journal of Fisheries and Aquatic Sciences,* 57: 2374–2381.

Lorenzen, K., N. Sukumasavin and Z. Hogan. 2006. Development of a conservation strategy for the critically endangered Mekong giant catfish: quantitative assessment report. *Mekong Giant Catfish Working Group Report* 3.

Mäkinen, T., O.L.F Weyl, K.-A. van der Walt and E.R. Swartz. 2013. First record of an introduction of the giant pangasius, *Pangasius sanitwongsei* Smith 1931, into an African river. *African Zoology,* 48(2) : 388–391.

McKenzie, D.J., J.F. Steffensen, E.W. Taylor and A.S. Abe. 2012. The contribution of air-breathing to aerobic scope and exercise performance in the banded knifefish *Gymnotus carapo* L. *Journal of Experiental Biology,* 215: 1323–1330.

Mitamura, H., N. Arai, Y. Yamagishi, Y. Kawabata, Y. Mitsunaga, M. Khachaphichat and T. Viputhanumas. 2009. Habitat use and movement of hatchery-reared F2 Mekong giant catfish in the Mae Peum reservoir, Thailand, studied by acoustic telemetry. *Fisheries Science*, 75(1): 175–182.

Muir B.S. and G.M. Hughes. 1969. Gill Dimensions for Three Species of Tunny. *Journal of Experemental Biology,* 51: 271–285.

Ngamsiri, T., M. Nakajima, S. Sukmanomon, N. Sukumasavin, W. Kamonrat, U. Na-Nakorn and N. Taniguchi. 2007. Genetic diversity of wild Mekong giant catfish Pangasianodon gigas collected from Thailand and Cambodia. *Fisheries Science,* 73(4): 792–799.

Thorpe, J.E. 2004. Life history responses of fishes to culture. *Journal of Fish Biology,* 65: 263–285.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer,* 39(3): 175–192.

Pauly. D. 1998. Beyond our original horizons: the tropicalization of Beverton and Holt. *Reviews in Fish Biology and Fisheries,* 8(3): 307–334.

Pauly D. 2019. *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals – 2nd Edition.* International Ecology Institute, Oldendorf/Luhe, Germany. 279 p.

Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7(2). doi.org/10.1126/sciadv.abc6050

Pholprasith, S. and P. Tavarutmaneegul. 1997. *Biology and culture of Mekong giant catfish Pangasianodon gigas (*Chevey 1930*). Extension Paper No. 31.* National Inland Fisheries Institute, Bangkok. 79 p.

Pholprasit, S. 1989. On the induced breeding of the Mekhong giant catfish (*Pangasianodon gigas* Chevey). In *12. Conference on Science and Technology of Thailand, Bangkok (Thailand)*, 20-22 Oct 1986.

Rainboth, W.J. 1996. *Fishes of the Cambodian Mekong. FAO species identification field guide for fishery purposes*. FAO, Rome. 265 p.

Roberts, T.R. and C. Vidthayanon. 1991. Systematic revision of the Asian catfish family Pangasiidae, with biological observations and descriptions of three new species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 143: 97–143.

Schinz, H.R. 1822. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie. Mit vielen Zusätzen versehen von H. R. Schinz. Cotta, Stuttgart & Tübingen. v. 2: i-xvi + 1–835.

Smith, H.M. 1931. Descriptions of new genera and species of Siamese fishes. *Proceedings of the United States National Museum,* 79(2873): 1–48, Pl. 1.

Taylor, C.C. 1958. Cod growth and temperature. *ICES Journal of Marine Science*, 23: 366-370.

Thorpe, J.E., 2004. Life history responses of fishes to culture. *Journal of Fish Biology*, 65: 263–285.

Wang, X., P. Liang, C. Li and F. Wu. 2014. Analysis of regional temperature variation characteristics in the Lancang River Basin in southwestern China. *Quaternary international*, 333: 198–206.

Wosnitza-Mendo, C. 1984. The growth of *Arapaima gigas* (Cuvier) after stocking in a Peruvian lake. *Archiv für Fischereiwissenschaft,* 35: 1–5.

Zhang, Y., F.U. Gao, D. He and S. Li. 2007. Comparison of spatial-temporal distribution characteristics of water temperatures between Lancang River and Mekong River. *Chinese Science Bulletin*, *52*(2): 141–147

GEORGES CUVIER "ON THE RESPIRATION OF FISHES"[1]

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Abstract

This brief account is the authors' translation of the section on fish respiration originally titled '*De la respiration*' on p. 517-519 in Volume 1 of Cuvier and Valenciennes' '*Histoire naturelle des poissons*' (1828), of which the famous French ichthyologist Georges Cuvier was the sole author. This book was published at a time when there was no scientific consensus of what breathing in water actually entailed. Particular attention was given to identifying Cuvier's sources, here detailed in form of extensive endnotes.

On the respiration of fishes[i]

It is through the almost infinite subdivision of the surface of gill lamellae that the blood of fish is affected by the surrounding liquid. This liquid is water, which fish cause to flow across its gills, through movements of their jaws and of their operculum and hyoid organs. This respiration is as required for fish as is the breathing of air to other animals.

[Fish] give the same impression of distress [as any animal] when they cannot breathe, and they die rapidly. However, the effect of water on blood is much weaker than that of air. Water [itself] does not contribute to respiration, nor does the oxygen that is a component of water [molecules]. Rather, it is only the small quantity of dissolved oxygen that it contains that is used for fishes' respiration.

If the [oxygen] is removed by boiling the water, it will quickly kill them. It is even necessary for many fishes to breathe air [directly], especially when the water they inhabit is devoid [of oxygen][ii]. There are, with regard to this, very convincing experiments in which it was sufficient for the water surface to be covered with gauze for the fish to become asphyxiated.

In the respiration of fishes, like in that of higher animals, atmospheric air, like the air that is dissolved in water, loses its oxygen.[iii]

Overall, oxygen uptake is very low[iv], and it has been calculated that a man consumes fifty thousand times more [oxygen] than a tench[v] [*Tinca tinca*]. All the oxygen [consumed] doesn't come back in the form of carbon dioxide; some remains in the fish's body, which also keeps a sizeable proportion of nitrogen, perhaps used in filling their gas bladders.

There are also fishes that swallow atmospheric air and convert oxygen into carbon dioxide by passing it through their intestine. This is the case with the weatherfish [*Misgurnus fossilis*], according to the strange

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[1] Cite as: Pauly, D. and J. Müller. 2022. Georges Cuvier "On the respiration of fishes", p. 13-15. *In:* Pauly, D. and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

experiments of M. Ehrmann[vi]. Indeed, in all [fishes], a similar transformation occurs on the skin and under the scales.

When fishes are outside the water, they die, not because of a lack of oxygen, but because their gills dry up[vii], so that the blood cannot flow easily through them. This is the reason why the species in which the gill openings are small, as in eel [*Anguilla anguilla*] or those that have an organ that keeps some water, as in anabas [*Anabas testudineus*] or snakehead [*Channa striata*], can survive exposure to air, while those that have wide open gills, as in herring [*Clupea harengus*], die as soon as they are taken out of the water.

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[i] [This is an extract, originally titled '*De la respiration*' from p. 517–519 in Volume 1 of Cuvier and Valenciennes' '*Histoire naturelle des poissons'* (1828), of which G. Cuvier was the sole author. The translation from the French is by Daniel Pauly and his insertions (and those of Johannes Müller) are [in square brackets]. The original text, in the fashion of its time, did not consist of clearly separated sentences and paragraphs; here, they were introduced to facilitate reading. The original spelling of quotes and references in French and German was retained: they are not typos, and the original footnotes are here endnotes]

[ii] [What Cuvier describes here is not necessarily air-breathing in itself (since his knowledge of air-breathing fishes was still rather limited), but more likely aquatic surface breathing, i.e., gulping at the water surface that allows air to diffuse in water more easily].

[iii] Spallanzani [L. . 1803. Mémoire sur les la respiration, traduit en français par J. Senebier d'après un manuscrit inédit. Genève, 8^o ; modified from *Dean's Bibliography of Fishes*, vol. 2, p. 47] has shown that fish absorb oxygen and convert it in [carbon dioxide]. M[onsieur] Silvestre has shown that they breathe atmospheric air, or air dissolved in water, but not the oxygen of water [molecules]. MM de Humboldt and Provençal, who applied the methods of advanced chemistry to this question, have obtained the [same] results as reported here. Their memoir is part of the memoirs of the Société d'Arcueil, vo. II, p. 359 and following, and in the Observations zoologiques of M. de Humboldt, vol. II, p. 194. [Alexander von Humboldt, Recueil d'observations de zoologie et d'anatomie comparée : faites dans l'océan atlantique, dans l'intérieur du nouveau continent et dans la mer du sud pendant les ans 1799, 1800, 1801, 1802 et 1803, Paris 1811].

[iv] [Jean Senebier and Lazzaro Spallanzani, Rapports de l'air avec les êtres organisés ou traites de l'action du poumon, Genève, 1807 : "Je les retirai de l'eau de chaux dans le même moment ; les branchies de la tanche non respirante étoient saines et d'un rouge un peu obscur: celles de la tanche qui avoit respiré étoient livides et noirâtres, un sang corrompu s'attachoit au doigt qui les touchoit. Je recueillis avec soin les deux précipités, et quand chacun d'eux eut été également séché, je les trouvai rigoureusement égaux ; chacun d'eux pesa 66,35 milligrammes, ou un grain 1/4 ; je voulus peser de nouveau les cartes dont je m'étois servi et dont les poids étoient, mais je trouvai que celle sur laquelle j'avois mis le précipité de la tanche respirante pesoit un grain de plus que l'autre. D'où il paroîtroit que l'acide carbonique produit par la tanche non respirante auroit été plus fort d'un grain, que celui de la tanche respirante, ce qui ne s'accorderoit pas avec le résultat précédent, mais je m'aperçus que la tanche non respirante étoit plus grande que l'autre: aussi je conclus encore que l'acide carbonique dégagé par les tanches dans l'eau de chaux est un produit du corps de l'animal , et qu'il ne sauroit être celui des branchies]"

[v] [Cuvier's claim that a man consumes 50,000 times more oxygen than a tench was clearly taken from Provençal and Humboldt (1809, p. 387), who states that an experiment by Antoine Lavoisier suggested that a 'man' consumes in six hours the oxygen one cubic meter of air, which they then suggest is 50,000 time as much as a tench would require in the same period. This claim can be verified using data in von Bertalanffy (1951, p. 241), pertaining to carp (*Cyprinus carpio*), a relative of the tench. There, a carp of 206 g is reported to consume 89.7 cm^3 of oxygen (presumably at 1 atm) per hour, while a person of 60 kg is reported to consume 200 cm^3 per hour. According to this, a carp consumes 206 x 89.7 = 18,478 cm^3 of oxygen per hour, while a person consumes 60,000 x 200 = 12,000,000 cm^3 per hour. Since 12,000,000/18,478 = 649, the figure of 50,000 is 77 times too high. Accounting for the fact that tench are less active than carp, and thus consume less oxygen, and that a 'man' could weight more than 60 kg and thus consume more oxygen would reduce the 77 times figure; however, the 50,000 times figure would still be far too high.

There is, however, another, more instructive comparison between the respiration of tench and human. It is that the tench spend about 30 % of their overall metabolic rate (i.e., oxygen supply) on breathing, while for humans, the corresponding figure is about 2 % (Schuman and Piiper 1966).

Bertalanffy, L. von. 1951. *Theoretische Biologie —zweiter Band: Stoffwechsel, Wachstum*. A Francke Verlag, Bern.

Provençal, J.-M. and F.H. von Humboldt. 1809. Recherches sur la respiration des poissons. *Mémoires de Physique et de Chimie de la Société d'Arcueil*, 2: 359–404.

Schumann, D. and J. Piiper. 1966. Der Sauerstoffbedarf der Atmung bei Fischen nach Messungen an der narkotisierten Schleie (*Tinca tinca*). *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere*, 288(1): 15–26.

[vi] Erman, P. 1808. Untersuchungen über das Gas in der Schwimmblase der Fische, und über die Mitwirkung des Darmkanals zum Respirationsgeschäfte bei der Fischart *Cobitis fossilis* (Schlammspeitzger). *Annalen der Physik*, 10: 113–160].

[vii] Edward [W. F. 1824]. *De l'influence des agens physiques sur la vie*, p. 124 [Chez Crochard, Libraire].

A reconstruction of the freshwater catch of fisheries in Quebec (1950 to 2020)[1]

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Abstract

A reconstruction of the total freshwater catch in Quebec is presented which is based the analysis of secondary data. A thorough search of online literature and datas*et al*lowed adding estimates of unreported catches to the officially reported catch (in tonnes) in the 71 years from 1950 to 2020. This catch is reported by species and sector (industrial, artisanal, recreational, and indigenous/subsistence). This reconstruction showed that the freshwater catch in Quebec is largely dominated by the recreational sector, and that there has been a slight decrease in total catch from the end of the 20th century. Therefore, because it omits recreational and indigenous fishing, the freshwater catch data reported by Fisheries and Oceans Canada does not provide an accurate representation of the actual scope of freshwater fisheries in Quebec. More comprehensive catch reporting would help to better understand the fisheries and manage freshwater fish populations.

Introduction

According to the Food and Agriculture Organisation of the United Nations (FAO), inland freshwaters represent 12% of the reported global fisheries catch (FAO 2020). Fishing in inland waters is an activity which includes several sectors, commonly identified as industrial (or large- scale commercial), artisanal (or small-scale commercial), recreational (or ‘sport fishing’) and subsistence (Pauly and Zeller 2016). However, these sector definitions must be modified in Canada, where aboriginal fisheries are recognized in federal and provincial law. Here, we combine aboriginal fisheries with subsistence fisheries into a sector that we call ‘indigenous/subsistence,’ while cognizant of the fact that many aboriginal fisheries can be ‘commercial’ in that the fish caught can be legitimately sold (which is not the case for recreational fisheries).

People in numerous countries, e.g., in sub-Saharan Africa, rely on freshwater fishes as a non-negligible part of their animal protein intake. However, in wealthier countries, a great part of freshwater catch can be attributed to recreational fishing. This is especially the case for Canada, which is also rich country, in that it contains 20% of the world’s freshwater. With such wealth comes the responsibility of managing and taking account of the existing fisheries in numerous bodies of water. Unfortunately, Canadian freshwater fisheries suffer from a lack of accessible and accessible data.

Canadian freshwaters are home to multiple fish species with various morphological and ecological characteristics (Coker *et al.* 2001), and Quebec is no exception to this. Freshwater covers 10% of the province’s territory and makes up 3% of the world’s non-marine water reserve. Quebec’s freshwater

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[1] Cite as: Grangy, L. and D. Pauly. 2022. A reconstruction of the freshwater catch of fisheries in Quebec (1950 to 2020), p. 16-25. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

fisheries have been the subject of many heated debates, both from social and economic points of view. First Nation and Inuit fishers frequently take part in protest movements regarding their right to fish, which is currently regulated under federal laws, and regulation issued by the Department of Fisheries and Oceans (DFO/MPO).

However, inland fisheries tend to not get as much attention as marine fisheries for a number of reasons, including the fact that most of Canadian fish sales revenue is generated by marine fisheries (Cooke and Murchie 2015). The need to gain a better understanding of global catch to assess the impact of fisheries on marine wildlife was unambiguously stated by Kleisner *et al.* (2013), and their arguments also apply to freshwater fisheries. It is important to be able to rely on trustworthy freshwater catch statistics when devising management policies for the conservation of freshwater ecosystems and to allow for sustainable of freshwater fish populations (Cooke *et al.* 2016).

Here, we present a reconstruction of the total freshwater catch in Quebec based on analysis of literature and datasets published online about the artisanal, recreational and indigenous/subsistence freshwater fisheries of Quebec from 1950 to 2020. This study will thus provide an idea of the quality (or not) of the data available on Quebec's freshwater fisheries. Also, it will contribute to a reconstruction of the freshwater catch of the whole of Canada by the *Sea Around Us* that will be assembled by summing the results of province- and territory-specific reconstructions. Eventually, this will contribute to global freshwater fisheries catch, as was also done for marine fisheries (Pauly and Zeller 2016).

Material and methods

Commercial fisheries: using the reported data as a baseline

In Quebec, there is apparently no explicit legal difference between industrial and artisanal fisheries, and artisanal fisheries are only described as fisheries which catch, land, and transform their product all by themselves. Moreover, commercial freshwater fisheries in Quebec are almost exclusively familial enterprises, including the eel and Atlantic sturgeon fisheries (Saint-Pierre and Bournival 2016). Therefore, it was decided to refer to 'commercial' fisheries as artisanal, even if a very small fraction of the catch might be taken by larger-scale operations.

The MAPAQ (*Ministère de l'Agriculture, des Pêches et de l'Alimentation du Québec*) oversees the reporting of freshwater landings in collaboration with the DFO (Fisheries and Oceans Canada, or also in French MPO: Pêches et Océans Canada). As FAO does not provide the reported Canadian freshwater catch by province/territory, but only does for Canada as a whole, the MAPAQ and DFO database, which cover only the commercial sector, was used as the baseline for reported freshwater catch (MPO 1990 - 2020).

Data was available from 1990 to 2020 on the MAPAQ and DFO websites. To estimate catches before 1990, the well documented landing data disclosed by the BSQ (*Bureau Fédéral de la Statistique* 1962, 1970) were used, which covered a 19-year long period from 1950 to 1969. In the absence of a better alternative, a linear interpolation was performed for the 20 years from 1969 to 1990, except for the catch of striped bass (*Morone saxatillis*), because catching this species was prohibited for every fishing sector since 1973 by Quebec's *Loi de 2002 sur la conservation et la mise en valeur de la faune* (Légis Québec 2002).

Recreational fisheries

The available data on recreational catch by species are of very variable reliability, possibly due, among other things, to anglers not distinguishing between closely related species, as suggested by the authors of the Quebec fishing survey of 1975 (Cluzeau and Pelletier 1978). Fishing surveys were also found that were clearly overestimating the recreational catch (MPO 1986). However, from 1990 on, the catch data by species became more reliable, as a result of questionnaire-based surveys conducted every 5 years (Gouvernement du Québec Faune et Parcs 1996 and MPO 1994, 2003, 2007, 2012).

However, these surveys did not display the catch numbers of Atlantic salmon; this information was found from 1984 to 2020 in a specific document about salmon exploitation (MFFP 2021a). As data was mainly reported in numbers of individuals caught, the mean lengths provided by the MFFP for each species were each converted to mean weights using the Bayesian length-weight relationships (Froese *et al.* 2014; see Table 1).

Table 1. Conversion of mean length at capture (in cm) to weight (in g), used to re-express the recreational catch in Quebec's recreational fisheries in numbers to catch in tonnes[a)]

Species	Common name	Mean length	a	b	Mean weight
Salmo salar	Atlantic salmon	75	0.01023	3.02	4705
Micropterus dolomieu	Smallmouth bass	29	0.01096	3.05	316
Esox Lucius	Northern pike	62.5	0.00447	3.08	1519
Coregonus clupeaformis	Lake whitefish	38	0.00550	3.23	697
Sander vitreus	Walleye	40	0.00661	3.14	709
Sander canadensis	Sauger	25	0.00631	3.14	155
Osmerus mordax	Rainbow smelt	19	0.00398	3.15	42
Acipenser fulvescens	Lake sturgeon	115	0.00282	3.18	10076
Esox maskinongy	Muskellunge	95	0.00479	3.08	5912
Salvellinus fontinalis	Brook trout	25	0.00912	3.03	157
Salvellinus alpinus	Arctic char	42	0.00724	3.03	600
Salmo salar sub-species	Ouananiche	55.5	0.01023	3.02	1895
Perca flavescens	Yellow perch	17.5	0.01230	3.04	74
Salvelinus namaycush	Lake trout	45	0.00832	3.02	818
Salmo trutta	Sea trout	35	0.00851	3.02	392
Oncorhyncus mykiss	Rainbow trout	37.5	0.00955	3.03	561

a) The **a** and **b** values of length-weight relationships (LWR) in the form $\mathbf{W} = \mathbf{a} \cdot \mathbf{L}^{\mathbf{b}}$ are from the Bayesian LWR routine of Froese *et al.* (2014) implemented in FishBase (www.fishbase.org)

Thus, the number of fishing permits delivered per year (most of which were available from the MPO's fishing surveys as well) were multiplied by the catch limit (or 'quota') associated which each permit, with the resulting catch estimate used as 'anchor points' (Zeller *et al.* 2007). For the years for which the number of fishing permits was not found, linear interpolations were applied. Total catch weight was then calculated for each year assuming that it was directly linked to the number of active fishermen.

Thanks to the MPO surveys and to the associated anchor points, it was possible to associate each taxonomic group to an approximate mean percentage of catch, i.e., trout and salmon (40%), walleye (31%), pike and bass (23%), perch (4%), and 'other species' (2%). The total catch weight found earlier was multiplied by those percentages. This method was then used for each species reported in the surveys.

Indigenous/subsistence fisheries

Ten First Nations and one Inuit community in Quebec (Anishinabeg, Atikamekw, Nehirowisiwok, Eeyou and Eenou, Hurons-Wendats, Innus, Inuits, Kanien'keha:ka, Mi'gmag, Naskapis and W8banakiak) accounted for 2% of Quebec's population in 2020. Fishing and fish products are very important part of the culture of First Nations (Marushka *et al.* 2021), and fishing gears and techniques are as diverse as the groups deploying them (Assembly of First Nations 2007). Fishing is an important part of ancestral cultures and rituals that are passed from elders to the following generations, and it is also a vital activity contributing to food supply.

First, the number of people who identify as belonging to First Nation or Inuit communities were gathered from the website of Government du Québec (2022). In years when demographic data were lacking, linear interpolations were performed. It was then noted that 35% of First Nation or Inuit community members declared to be engaging in fishing activities in 2017 (Kumar *et al.* 2019); this number doesn't seem to have changed between 2001 and 2017, and was 38% in the middle of the 1980s (Berkes 1990). However, based on literature, it was assumed that this percentage was somewhat higher in the 1950s and then decreased linearly. The fishing quotas for each species of the Ministère des Forêts, de la Faune et des Parcs (MFFP 2021b) were then used, and it was assumed that each fisher would fill the quotas each year for each species. In doing so, this method assumes that the number of fishes caught directly depends on the number of active fishers each year. Finally, the number of fishes for each species was converted to weight using the data in Table 1.

Fish species and taxonomic breakdown

There were many anadromous species such as trout, salmon, and eel in the fisheries catch of Quebec, and these species were added to the freshwater catch when they were clearly described as being fished in freshwater. For example, it was clearly stated in previous ethnological literature that the American eel was mostly, if not almost entirely caught in freshwaters on tidal shores along the tributaries of the Saint Lawrence River (Saint-Pierre and Bournival 2016). The 24 species found and the other unidentified taxa were then broken down into 9 taxonomic groups (Table 2).

The name of the species was always displayed in French in official reports and documents, with the exception of older commercial fishing reports (Bureau Fédéral de la Statistique 1962, 1970), written both in English and French. The common and scientific names were then verified through FishBase (www.fishbase.org).

Table 2: Breakdown of the species important in Quebec's freshwater fisheries, with common and scientific names verified through FishBase (www.fishbase.org)

Group	English name	French name	Scientific name
Bullheads	Brown bullhead	Barbotte brune, poisson chat	*Ameiurus nebulosus* (Lesueur, 1819)
Coregonus	Lake whitefish	Grand corégone	*Coregonus clupeaformis* (Mitchill, 1818)
Eels	American eel	Anguille d'Amérique	*Anguila rostrata* (Lesueur, 1817)
Perchs and carps	American yellow perch	Perchaude	*Perca flavescens* (Mitchill, 1814)
	Common carp	Carpe	*Cyprinus carpio* Linnaeus, 1758
Pike, bass and shad	Smallmouth bass	Achigan à petite bouche	*Micropterus dolomieu* Lacepède, 1802
	Striped bass	Bar rayé	*Morone saxatilis* (Walbaum, 1792)
	Muskellunge	Maskinongé	*Esox masquinongy* Mitchill, 1824
	Northern pike	Grand brochet	*Esox lucius* Linnaeus, 1758
	American shad	Alose	*Alosa sapidissima* (Wilson, 1811)
Sturgeon	Atlantic sturgeon	Esturgeon noir	*Acipenser oxyrinchus* Mitchill, 1815
	Lake sturgeon	Esturgeon jaune	*Acipenser fulvescens* Rafinesque, 1817
Trout and salmon	Arctic char	Omble chevalier	*Salvelinus alpinus* (Linnaeus, 1758)
	Atlantic salmon	Saumon atlantique	*Salmo salar* Linnaeus 1758
	Ouananiche	Ouananiche	*Salmo salar* Linnaeus, 1758 (sub species)
	Brook trout, speckled trout	Omble de fontaine, truite mouchetée	*Salvelinus fontinalis* (Mitchill, 1814)
	Lake trout	Touladi	*Salvelinus namaycush* (Walbaum, 1792)
	Rainbow trout	Truite arc-en-ciel	*Oncorhyncus mykiss* (Walbaum, 1792)
	Sea trout	Truite brune	*Salmo trutta* Linnaeus, 1758
Walleye	Sauger	Doré noir	*Sander canadensis* (Griffith & Smith, 1834)
	Walleye	Doré jaune	*Sander vitreus* (Mitchill, 1818)
Other	Atlantic tomcod	Poulamon atlantique	*Microgadus tomcod* (Walbaum, 1792)
	Fallfish	Mulet	*Semotilus corporalis*
	Rainbow smelt	Éperlan arc-en-ciel	*Osmerus mordax* (Mitchill, 1814)
	Other species that could not be identified for each sector and year.		

Results

Commercial catch reconstruction

Figure 1 shows the reconstructed data on commercial (i.e., artisanal) freshwater catch in Quebec. On average, this catch represents 1,257 tonnes of fish per year, with a peak of 2,194 t in 1997. The catch increased from 1970 to 1997, and has decreased since 2000. When considering catch by broad taxonomic group, bullheads (20.2%), eels (17,6%), perch and carps (16.3%), and sturgeons (13.3%) accounted for the highest catch. At the species level, American eel (*Anguilla rostrata*) and brown bullhead (*Ameirus nebulosus*) account for 17.6% and 20.2% of the catch, respectively.

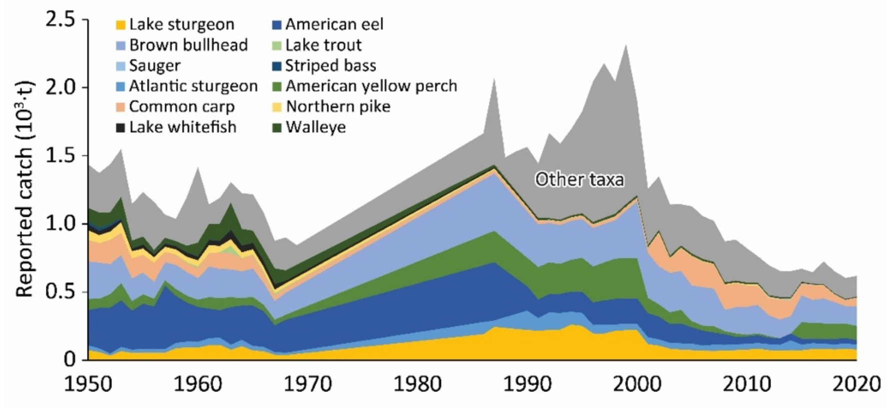

Figure 1. Reported catch in Quebec's freshwaters from 1950 to 2020 by species. This catch was assigned to the commercial (here: 'artisanal' catch as it is the only reported fishing sector in Quebec's freshwaters.

Recreational catch reconstruction

The recreational freshwater fisheries in Quebec seem to have been rather steady until the beginning of the 1990s when it started to decrease (Figure 2). The average catch weight per year is of 15,074 tonnes for the 1950-1989 period and 8,507 tonnes for the 1995 – 2020 period. Three species dominate the catch (Figure 2): brook trout (*Salvelinus fontinalis*; 24.7%), walleye (*Sander vitreus*; 31.1%) and northern pike (*Esox lucius*; 21.5%).

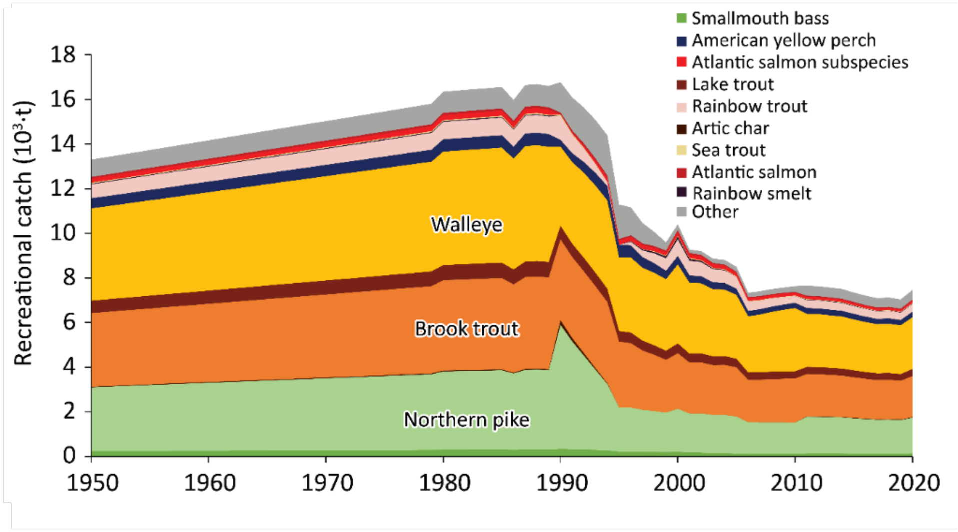

Figure 2. Reconstructed recreational catch for Quebec's freshwaters from 1950 to 2020 by species.

Indigenous/subsistence freshwater catch reconstruction

The indigenous/subsistence fisheries catch appears to have been increased by 500% between 1950 and 2020 (Figure 3). The predominant species here are northern pike (*Esox Lucius*; 13.0%), muskellunge (*Esox masquinongy*;12.6%) and lake sturgeon (*Acipenser fulvescens*;14.3%).

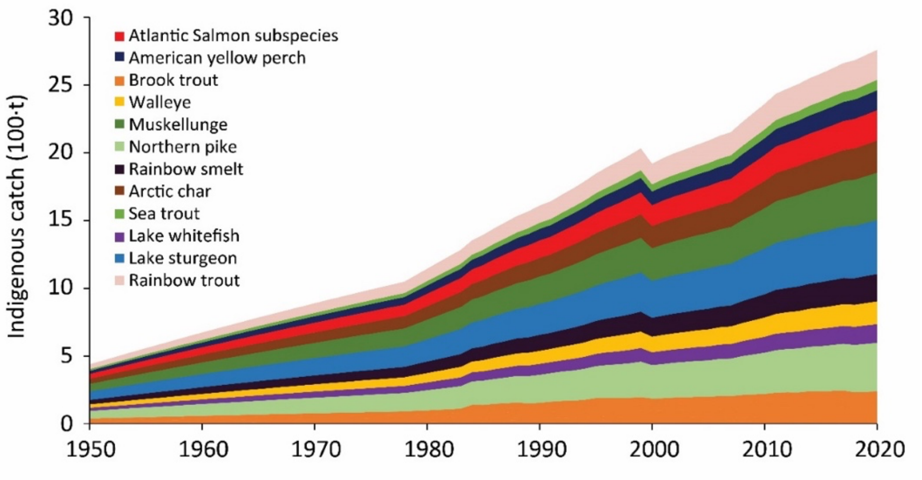

Figure 3. Reconstructed indigenous catch for Quebec's freshwaters from 1950 to 2020, by species.

Total freshwater catch reconstruction

Overall, the total catch reconstruction of Quebec is largely dominated by the recreational catch, accounting for 81% of the reconstructed catch on average (Figure 4). Accordingly, the same average dominance of trout and salmon (36%), walleye (26.5%), and pike and bass (21.8%) can be observed (Figure 5). The total catch in freshwater seems to be increasing slightly until the early 1990s, when it starts to decrease from a peak of 20,000 tonnes.

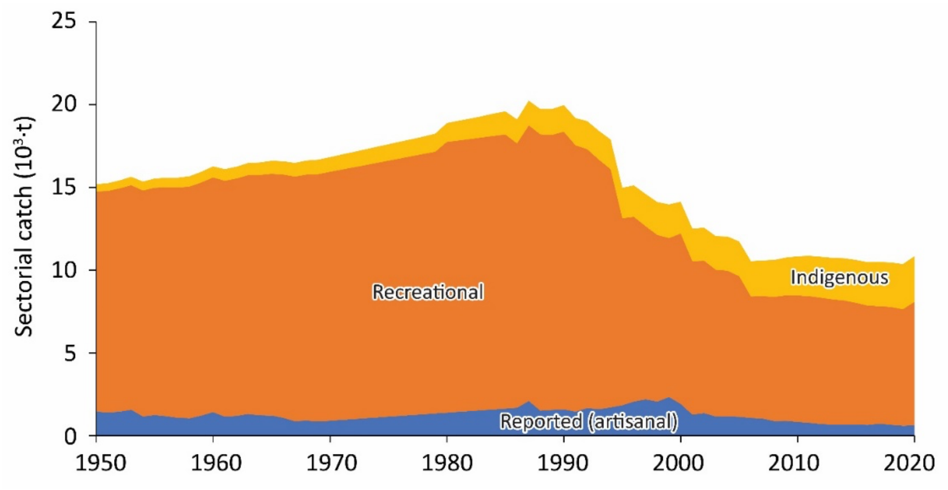

Figure 4. Total reconstructed freshwater catches for Quebec from 1950 to 2020, by fishing sector (in tonnes)

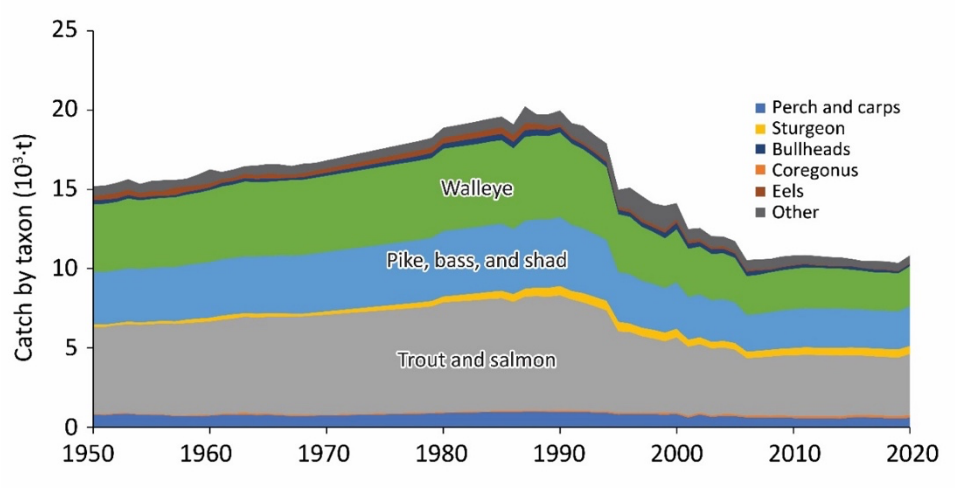

Figure 5. Total reconstructed freshwater catches for Quebec from 1950 to 2020 by major taxonomic group.

Discussion

Overall, the freshwater catch in Quebec has decreased since the early 1990s. While this is probably due to overfishing in the case of sea American eel, sturgeons, and striped bass, it is also likely due to a lower number of recreational fishers, combined with effects of climate change, particularly the warming of freshwater bodies (Lynch *et al.* 2016). Its consequences on marine ecosystems in the Northern hemisphere were already well demonstrated (Möllmann and Diekmann 2012), and so were the impacts of climate change on lakes and rivers, even though they are difficult to quantify by most current methods (Bélanger *et al.* 2013). One approach that would help in this context is the mean temperature of the catch (MTC) concept (Cheung *et al.* 2013), which has been successfully applied to a cold temperate lake in Europe (Kangur *et al.* 2022) and which would be ideally suited for application in Quebec.

One key result of this analysis is that the likely total freshwater catch in Quebec (Figures 4 and 5) is, over the 1950-2020 period, approximately 12 times higher than the reported catch on Figure 1. The catch reported by the DFO accounts only for the artisanal sector, which clearly leads to a huge underestimation of the total freshwater catch. Quebec is widely known for offering high-quality recreational fishing; it is very important to include the recreative sector in any attempt to report total freshwater catches.

Regarding the recreational catch, it must also be noted that there are 29 recreative fishing zones in Quebec. A search for data on these zones was undertaken, but no reliable information was found. An observation of a different kind was noted when trying to find data for various areas: there is a trustworthy database (covering the years 1989 to 2020) of catch in controlled exploitation zones (ZEC) to which we were graciously given access to after contacting their managers via an online form, but as this catch only represents 3% of the total recreational catch, the usefulness of including these data in this study is debatable.

The '*Société des établissements de plein air du Québec*' (SEPAQ), the organisation responsible for monitoring wildlife reserves and regional parks in Quebec, also displayed catches from 2017 to 2020, but they also covered a minuscule fraction of the estimated recreational catch (~2%). Therefore, we opted for concentrating on the big picture, i.e., the overall provincial catch.

Although the increase of indigenous catch may have a demographical and ethnological explanation, there may be some doubts about the results of this fishing sector's reconstruction. The indigenous population in Quebec has indeed been increasing since the 1950s (Bouchard *et al.* 1989); but there is still very little detailed information on the species and weight of fishes caught by the indigenous people of Quebec. It is also possible that the quotas used in this study are not representative of their fisheries.

In conclusion, the key result of this study is that that the actual reported freshwater catch in Quebec is strongly underestimated due to the exclusion of two important fishing sectors. This result is robust, even if the many uncertainties inherent to this study are considered. It will be very interesting to know if this also applies to the inland waters of Canada as a whole.

Acknowledgements

Most of study was produced during a 2-month stage the first author spent as a volunteer to the *Sea Around Us*; she takes this opportunity to thank the team and particularly Dr. M.L. 'Deng' Palomares for making her feel welcome and supporting her work.

References

Assembly of First Nations. 2007. Traditional foods: Are they safe for First Nations consumption? *Assembly of First Nations*, Ottawa.

Bélanger, C., D. Huard, Y. Gratton, D.I. Jeong, A. St-Hilaire, J.C. Auclair and I. Laurion. 2013. *Impacts des changements climatiques sur l'habitat des salmonidés dans les lacs nordiques du Québec*. Université du Québec, Institut National de la Recherche Scientifique, Eau, Terre et Environnement, Montréal. 167 p.

Berkes, F. 1990. Native subsistence fisheries: a synthesis of harvest studies in Canada. *Arctic*, 43(1): 35-42.

Bouchard, S., S. Vincent and J. Mailhot. 1989. *Peuples autochtones de l'Amérique du Nord : de la réduction à la coexistence*. Télé-Université, Sainte-Foy, Canada. 367 p.

Bureau Fédéral de la Statistique. 1962. *La statistique des pêches Québec 1962*. Ottawa, Canada. 36 p.

Bureau Fédéral de la Statistique. 1970. *La statistique des pêches Québec 1970*. Ottawa, Canada. 34 p.

Cheung, W.W.L., R. Watson and D. Pauly. 2013. Signature of ocean warming in global fisheries catch. *Nature,* 497: 365-368.

Cluzeau, P. and J. Pelletier. 1978. *Étude sur la pêche sportive au Québec en 1975*. La pression de pêche sportive en 1975 Volume III. Ministère du Tourisme, de la Chasse et de la Pêche, Quebec, Canada.

Coker, G.A., C.B. Portt and C.K. Minns. 2001. Morphological and Ecological Characteristics of Canadian Freshwater Fishes. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2554. Department of Fisheries and Oceans, Canada. iv + 89 p.

Cooke, S.J., and K.J. Murchie. 2015. Status of aboriginal, commercial and recreational inland fisheries in North America: past, present and future. *Fisheries Management and Ecology*, 22(1): 1-13.

Cooke, S. J., E.H. Allison, T.D. Beard, R. Arlinghaus, A.H. Arthington, D.M. Bartley, I.G. Cowx, C. Fuentevilla, N.J. Leonard, K. Lorenzen, A.J. Lynch, V.M. Nguyen, S.-J. Youn, W.W. Taylor and R.L. Welcomme. 2016. On the sustainability of inland fisheries: finding a future for the forgotten. *Ambio,* 45(7): 753–764.

Food and Agriculture Organization of the United Nations. 2020. Fishery statistical collections: global capture production (1950–2015). FAO, Rome.

Froese, R., J.T. Thorson and R.B. Reyes Jr. 2014. A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, 30(1): 78-85.

Gouvernement du Québec Faune et Parcs. 1996. *La pêche récréative en 1995*. Gouvernement du Québec, Montréal.

Government du Québec. 2022. Populations autochtones du Québec. Available at: www.quebec.ca/gouvernement/portrait-quebec/premieres-nations-inuits/profil-des-nations/populations-autochtones-du-quebec

Griffith, E. and C.H. Smith. 1834. The class Pisces, arranged by the Baron Cuvier, with supplementary additions. *In*: B. Cuvier (ed) *The animal kingdom, arranged in conformity with its organization, with supplementary additions to each order (2nd ed.)* Whittaker & Co., London. 680 p., 1-62 pls. + 3.

Kangur, K., E. Tammiksaar and D. Pauly. 2022. Using the "mean temperature of the catch" to assess fish community responses to warming in a temperate lake. *Environmental Biology of Fishes,* 105: 1405-1413. doi.org/10.1007/s10641-021-01114-7

Kleisner, K., D. Zeller, R. Froese and D. Pauly. 2013. Using global catch data for inferences on the world's marine fisheries. *Fish and Fisheries,* 14: 293–311.

Kumar, M.B., C. Furgal, P. Hutchinson, W. Roseborough and S. Kootoo-Chiarello. 2019. *Activités de récolte chez les Premières Nations vivant hors réserve, les Métis et les Inuits: évolution dans le temps, obstacles et facteurs associés*. Catalogue 89-653-X2019001. Statistique Canada, Ottawa. 65 p.

Lacepède, B.G.E. 1802. *Histoire naturelle des poissons: IV*. Chez Plassan, Paris, France. i-xliv 728 p., Pl. 1-16.

Lesueur, C.A. 1817. A short description of five (supposed) new species of the genus Muraena, discovered by Mr. Le Sueur, in the year 1816. *Journal of the Academy of Natural Sciences*, *Philadelphia,* 1(5): 81-83.

Lesueur, C.A. 1819. Notice de quelques poissons découverts dans les lacs du Haut-Canada, durant l'été de 1816. *Mémoires du Muséum National d'Histoire Naturelle*, 5: 148-161, 2 pls.

Légis Québec. 2002. Loi de 2002 sur la conservation et la mise en valeur de la faune, chapitre C-61.1, a. 110 et 162. Available at: www.legisquebec.gouv.qc.ca/fr/document/lc/c-61.1

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata [10th revised edition], volume 1. Vienna, Austria. 824 p.

Lynch, A.J., B.J. Myers, C. Chu, L.A. Eby, J.A. Falke, R.P. Kovach, T. Krabbenhoft, T. Kwak, J. Lyons, C. Paukert and J.E. Whitney. 2016. Climate change effects on North American inland fish populations and assemblages. *Fisheries*, 41(7): 346-361.

Marushka, L., M. Batal, C. Tikhonov, T. Sadik, H. Schwartz, K. Fediuk and H.M. Chan. 2021. Importance of fish for food and nutrition security among First Nations in Canada. *Canadian Journal of Public Health*, 112(1): 64-80.

Ministère des Forêts, de la Faune et des Parcs. 2021a. *Bilan de l'exploitation du saumon au Québec en 2020*. Gouvernement du Québec, Canada. 302 p. Available at: mffp.gouv.qc.ca/nos-publications/bilan-exploitation-saumon-2020/

Ministère des Forêts, de la Faune et des Parcs. 2021b. *Code de pratique relatif à la pratique des activités de pêche des Abénakis d'Odanak et de Wôlinak, saison de pêche 2022-2023*. Grand Conseil de la Nation Wabanaki, Canada. 13 p. Available at: gcnwa.com/wp-content/uploads/2022/04/CODE-PECHE-2022-2023_VF_SOB.pdf

Ministère Pêches et Océans Canada. 1986. *La pêche récréative du Québec en 1985*. Gouvernement du Québec, Ministère du Loisir, de la Chasse et de la Pêche, Montréal.

Ministère Pêches et Océans Canada. 1994. *Enquête sur la pêche récréative au Canada, 1990*. Série de publications de l'analyse économique et commerciale, rapport n°148. Ottawa, Canada.

Ministère Pêches et Océans Canada. 2003. *Enquête sur la pêche récréative au Canada, 2000*. Série de publications de l'analyse économique et commerciale, rapport n°165. Ottawa, Canada.

Ministère Pêches et Océans Canada. 2007. *Enquête sur la pêche récréative au Canada, 2005. Analyses économiques et statistiques*. Ottawa, Canada.

Ministère Pêches et Océans Canada. 2012. *Enquête sur la pêche récréative au Canada, 2010. Analyses économiques et statistiques*. Ottawa, Canada.

Mitchill, S. L. 1814. Report, in part, of Samuel L. Mitchill, M. D., Professor of Natural History, &c, on the fishes of New-York. D. Carlisle, New York. 28 p.

Mitchill, S. L. 1815. The fishes of New York, described and arranged. *Transactions of the Literary and Philosophical Society of New-York,* 1(5): 355-492, 1-6 pls.

Mitchill, S. L. 1818. Memoir on ichthyology. The fishes of New York, described and arranged. In a supplement to the Memoir... (continued). *American Monthly Magazine and Critical Review,* 2(5): 321-328.

Mitchill, S.L. 1824. Masquinongy of the Great Lakes. *Minerva, New York*, 1(16): 297.

Möllmann, C. and R. Diekmann. 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the Northern Hemisphere. *Advances in Ecological Research*, 47: 303-347.

Pauly, D. and D. Zeller. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications,* 7: 10244.

Rafinesque, C.S. 1817. Additions to the observations on the sturgeons of North America. *American Monthly Magazine and Critical Review,* 1: 288.

Saint-Pierre, L. and M.-T. Bournival. 2016. *État de situation sur les pratiques traditionnelles ou artisanales de pêche et de transformation de ses produits au Québec*. Direction du patrimoine et de la muséologie, Ministère de la Culture des Communications, Quebec. 195 p.

Walbaum, J.J. 1792. Petri Artedi Sueci Genera piscium: in quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis : redactis speciebus 242 ad genera 52 : Ichthyologiae.

Wilson, A. 1811. Clupea, in ichthyology, ... The Cyclopedia; or, universal dictionary of arts, sciences, and letters v. 9: 3 unnumbered pp.

Zeller, D., S. Booth, G. Davis and D. Pauly. 2007. Re-estimation of small-scale fishery catches for U.S. flag-associated island areas in the westernPacific: the last 50 years. *U.S. Fisheries Bulletin* 105: 266-277.

Websites:

www.dfo-mpo.gc.ca/stats/commercial/fresh-yrlist-eng.htm (accessed April 24, 2022)

Comparing assessments of sardinella stocks in Senegal and Northwest Africa[1]

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Abstract

This contribution compares stock assessment2 of sardinella species (*Sardinella aurita* and *S. maderensis*) off Senegal and neighboring countries performed from 2011 to 2013 using a now dated approach, i.e., surplus-production modelling (with and without considering environmental variability), with an assessment performed with the CMSY method. The results are similar and suggest that the fishery was near MSY in the 1990s, thus validating earlier suggestions that fishing effort should not have been allowed to increase beyond its 1990s level.

Introduction

This contribution compares stock assessments of sardinella species (*Sardinella aurita* and *S. maderensis*) performed by the first 3 authors a decade ago in the context of a consultancy for the Centre de Recherche Océanographique de Dakar-Thiaroye (CRODT) and the USAID-supported COMFISH Project, to the results that would have been obtained had the same data been analyzed with the recently-developed CMSY++ method (see oceanrep.geomar.de/id/eprint/52147/), which is improved over the CMSY method of Froese *et al.* (2017).

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[1] Cite as: Mathews, C.P., N. Lazar, V. Ndiaye, S. Baxter and D. Pauly. 2022. Comparing assessments of sardinella stocks in Senegal and Northwest Africa, p. 26-42. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

In the following sections, a summary of the approaches and findings of the CRODT-COMFISH Project are presented, which jointly provide a context for the comparison with the CMSY++ method.

Assessments by the CRODT/COMFISH Project (2011-2013)

Catch and biomass estimates

A review of all catch and effort data available from the CRODT and Senegal's DPM (Bureau of Statistics), the Food and Agriculture Organization (FAO) and fisheries projects and organizations covering the Region[2] encompassing The Gambia, Senegal, Mauritania and Morocco was carried out. Contradictions between data sets were resolved wherever possible.

In the process, a new abundance index for sardinella was developed, i.e., the mean CPUE at the Senegalese ports of Joal and Mbour, normalized for changes in fishing power of the standard fishing unit (two pirogues operating one *seine tournante*). The new abundance index uses artisanal data and includes the effects of technical change on the fishery from 1980-2011.

Well-fitted and robust Schaefer-type surplus-production models (Schaefer 1954, 1957; Ricker 1975; Pauly 1984) were constructed, and two variants, based on the CLIMPROD software (Fréon 1993), took explicit account of environmental changes.

The results of the project were strong enough to be used to inform decision makers and could have been safely included in Participatory Management Plans then (in 2013) being prepared to inform the CLPAs (Local Artisanal Fisheries Councils, to which management decisions are partially devolved under Senegal's fishing laws) and other entities. Note that CLPAs cover areas much smaller than the sardinella stock(s), and thus must coordinate their action for positive results.

The Senegalese sardinella fishery was found to be overfished: an average artisanal Maximum Sustainable Yield (MSY) of 250,000 t·year^{-1} could be taken with an effort of 115,000 *pirogue* (= canoe) trips per year instead of the then (2011) current 220,000 t·year^{-1} at 155,000 trips·year^{-1}. CPUE was around 1.4 t·trip^{-1} and would have increased to an average of 2.2 t·trip^{-1} at MSY if effort were to be successfully reduced. Fishers operating *pirogues* would have received comparably higher incomes while the processing sectors (employing mainly women) would have handled around 20% more fish, making more available for local consumption.

The regional sardinella fishery (i.e., combining the sardinella fisheries of The Gambia, Senegal, Mauritania and Morocco) was also overfished: MSY of around 580,000 t·year^{-1} occurred at effort which was then equivalent to 350,000 t·trip^{-1} with a mean CPUE of 1.78 t·trip^{-1}. The actual average effort was then 28% higher at around 415,000 t·trip^{-1} so the fishery produced only 500,000 t·year^{-1} at CPUE of 1.2 t·trip^{-1}, around 48% lower than it could get (at MSY). These assessments, however, assumed that available official data on landings and effort are complete. However, a (then) recent report on Illegal, Unreported and Undocumented (IUU) fishing (Koutob *et al.* 2013) shows that:

(i) very large amounts of unrecorded fish – around 450,000 t·year^{-1} have been taken since around 2005, in addition to the official landings reported in these assessments;

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[2] In Northwest Africa, the 4 countries listed are considered to form a "Sub-Region." Here, this will be referred to as a 'Region,' with the corresponding adjective being 'regional.'

(ii) around 250,000 t·year^{-1} of these IUU landings were probably sardinella;

(iii) this gap in the landings and effort statistics is a serious obstacle to making comprehensive sardinella assessments.

In spite of these issues, it may be possible to provide a reasonably accurate picture of the sardinella fishery in 2011, based on the following information:

- Official (artisanal) sardinella landings in Senegal were around 225,000 to 250,000 t·year^{-1} taken at around 155,000 standard artisanal trips·year^{-1};
- Another 200,000-250,000 t·year^{-1} of invisible sardinella landings were taken by industrial IUU boats at an effort equivalent to or greater than 155,000 standard artisanal trips·year^{-1};
- Real sardinella landings are probably around 500,000 t·year^{-1}, taken at an effort equivalent to or greater than 310,000 trips·year^{-1}, with a total biomass of less than 500,000 t;
- Thus, IUU catches will keep CPUE in the artisanal fishery low;
- In the absence of IUU fishing, the artisanal fleet would take much higher landings and CPUE than it does now.

Any attempt to increase artisanal CPUE without reducing or eliminating IUU fishing of sardinella would only increase artisanal effort at the cost of reducing artisanal CPUE and landings. Thus, sustainable fishing of Senegalese sardinella depends firstly on reducing or eliminating IUU fishing of sardinella: this is a necessary enabling condition, but is not a sufficient condition for achieving sustainability. The same reasoning is applied in this report to the regional sardinella stock: a second necessary, but not sufficient enabling condition for achieving sustainability is likely to be the reduction or removal of IUU fishing for sardinella in the entire Region.

A third necessary, but not sufficient enabling condition for sustainable sardinella fishing is the creation and implementation of a government unit for managing the sardinella fisheries that would coordinate the work of the CLPAs from Dakar Ouest to the Siné Saloum. A fourth necessary, but not sufficient condition for sustainable sardinella fishing in Senegal is a transparent and efficient regional strategy and a regional fishery management plan for sardinella, including strategies for locally appropriate management units in each country which will manage locally available resources.

Current work on how climate change impacts landings is not yet sufficiently advanced for results to be fully integrated into sardinella management. However, it is now clear that climate change does impact stocks. Managers now need to include this fact in assessments as a fifth necessary, but still not sufficient enabling condition needed to attain sustainable management.

Comprehensive bio-economic modeling carried out by CRODT/COMFISH Project (Dème *et al.* 2012) shows that Senegalese and regional sardinella fisheries were fished at or near the Open Access Equilibrium (i.e., generate zero net profits) in 2011. The strategy of aiming at MSY suggested above will increase profits, reduce costs and increase total and spawning biomass, and will probably be sufficient to ensure sustainable fishing (but will not secure MSY or a positive rent). More robust bio-economic modelling including for studies of fishing capacity management are needed to address the sixth and final necessary condition for achieving sustainable sardinella management in both Senegal and the regional context.

Dème *et al.* (2012) summarized all available estimates of sardinella biomass. These estimates are very useful for identifying the key sardinella spawning, nursery and grow out areas; notably, the review showed a marked northward shift of sardinella grounds during the last few decades. This northward shift was related to higher sea temperatures in Senegalese waters and perhaps to a stronger upwelling, associated with intensifying coastal wind (Bakun 1990).

Modelling presented here shows that from 2008-2011 sea temperatures increased by around 2°C, and suggested that this may have increased (i) the Senegalese sardinella stocks (ii) regional landings. However, further temperature increases are likely to reduce regional and Senegalese landings of sardinella, e.g., over the next 1-2 decades because sardinella may migrate northwards to maintain itself in the water temperatures that they prefer (Cheung *et al.* 2009).

Addressing these six necessary conditions may be sufficient to achieve sustainable sardinella fishing. All enabling conditions must eventually be fulfilled for sustainable fishing to be achieved.

An informal review by the first author of biomass estimates from surveys in the Region carried out by European fisheries research vessels (e.g., the Norwegian *R/V Fridtjoft Nansen*; Samb and Pauly 2000) suggests that several of their short-term surveys were conducted during periods or seasons of low stock biomass, thus giving misleading results. Available annual plots of biomass are therefore inaccurate representations of stock abundance and were ignored in this study. Regional vessels could provide spatially and temporally better resource coverage, leading to realistic biomass estimates which could be used to assess stocks more accurately than can be done currently.

By definition, fishing mortality (F) in a given year can be estimated from the catch (C) and the biomass (B) in that year (Sekharan 1974). Here combining echo-acoustic estimates of biomass (from the Norwegian *R/V Fridtjoft Nansen*) and catches led to F values of 0.68 year^{-1} for *S. aurita* and 0.34 year^{-1} for *S. maderensis*. Combining these with natural mortality (M) estimates of 0.66 year^{-1} and 0.65 year^{-1} (From Pauly 1980), respectively gives exploitation rates $E = F/(M+F)$ of 0.51 for *S. aurita* and 0.34 for *S. maderensis*. These results suggest that the stocks are heavily exploited, which is congruent with all the evidence available.

Standardization of effort

Because anecdotal evidence indicated that the fishing power of the sardinella fleet increased over time (see also Fitzpatrick 1996), we decided to carry out a first estimate of the changes in the fishing power of the standard sardinella fishing unit. CPUE and thus effort should be measured in a standardised way over time so that one unit of effort means the same for all boats and for different gear during the whole time series. We used CPUE data for the Senegalese ports of Joal and Mbour for this because:

- The fleets located in Joal and Mbour are relatively stable;
- These fleets generate around 80% of Senegal's sardinella catch;
- None of the catch landed in these two ports originate from outside Senegalese waters;
- These fleets have access to many other species, e.g., *Ethmalosa fimbriata* and many other small pelagic fish species, and demersal fish and shrimp; thus, they do not need to follow sardinella schools as they migrate northwards.

Changing technology in Senegal could have biased estimates of CPUE, as it improved over the years and decades because of:

- increasing engine power which allows access to more distant and less heavily fished areas;
- increasing length and depth of nets;

- increasing numbers of fishers per fishing unit;
- use of larger boats/pirogues;
- use of echosounders and cell phones by fishers to improve the detection of fish schools;
- increasing fisher knowledge of fish and schooling behaviour, leading to new fishing strategies;
- other technical changes, many of which are peculiar to each fishery/gear/species.

These changes all tend to increase the fishing power of the standard fishing unit (i.e., the nominal effort), so that the effective effort has been underestimated in recent years. Such underestimates can lead to serious biases in assessments which risk misleading managers; notably, they can fail to detect reduced stock productivity, leading to optimistic management decisions which push the stock further towards reduced biomass, and eventual depletion.

Therefore, we used the cumulative effort and mean catch per unit of effort (CPUE) data from the artisanal fisheries, based in the ports of Joal and Mbour, to provide an assessment of the stock and of biomass trends for sardinella in Senegal and in the northwest Africa.

We used a qualitative method based on local knowledge to characterize the evolution of fishing power over time by interviews with fishermen and processors to reconstruct the history of fishing power in the artisanal seine fisheries in Senegal. The required questionnaire was developed and used in Joal, Mbour and St Louis in April 2013.

The standard fishing unit over the whole time series was:

- a large pirogue used for taking the fish;
- a smaller pirogue used for laying the net;
- a purse seine net (*seine tournante*) ;
- three outboard engines, one for each pirogue and one spare so that engine maintenance would not reduce fishing time.

Questions about the nature of a standard fishing unit were addressed to experienced fishers who had fished from the 1970s to 2011. Characteristics measured in this way included pirogue size (LOA), net size, number of crew, engine horsepower, number of engines, search time, and capacity for holding the sardinella catch. A summary of these interviews is presented Table 1, which allowed the estimation of an increase of power of 5.8% per year. Also, it appeared that the fishing power in the artisanal seine fisheries of the “Grande Côte” and the “Petite Côte” varied in the same way. Data shown in Table 1 were combined with data on number of trips to obtain the total standardised effort expended in each year. Figure 1 shows the observed and the adjusted effort obtained. The data in Table 1 were then combined with nominal effort (number of artisanal boats deployed in a given year (flatter, blue line in Figure 1) to obtain effective effort (ascending, red line in Figure 1).

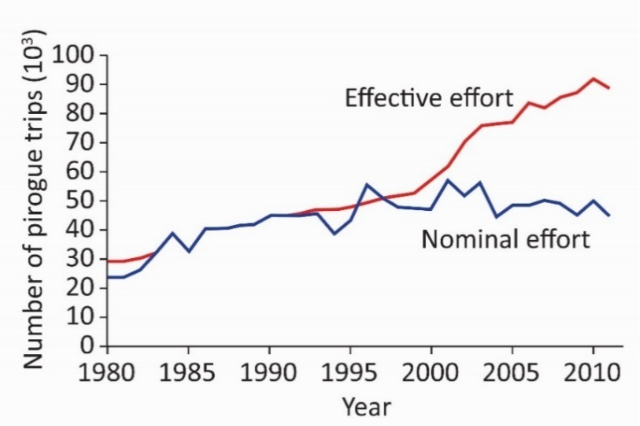

Figure 1. Nominal vs. effective effort in the Senegalese artisanal fishery for sardinella, 1980 to 2011. Based on CRODT/DPM data, with corrections based on 'a' at the bottom of Table 1

Table 1. Summary of fishers' responses regarding their perception of the past fishing power of *pirogues* (= canoes performing day trips) targeting sardinella and belonging to artisanal seine fisheries in St Louis and Mbour/Joal, in Senegal (May 2013)

Item	**'73 – '80**	**'80 – '90**	**'90 – '00**	**2011**
LOA (m)-setting unit (SM = small pirogue)	10	12	15	15
LOA (m)-carrying unit (large pirogue)	10	17	21	25
Horsepower (hp)	25	40	60	60
kW (hp/1.34)	19	30	45	45
Vessel Capacity Unit = (LOA·BR) + (0.45·kW)	168	390	725	806
Crew-setting unit	3	3	4	5
Crew-carrying unit	10	12	15	25
Net-length (m)	300	500	600	800
Net-depth (m)	30	30	35	40
Capacity of pirogue (m)	230	551	1008	1350
CPUE (# of boxes = 45 kg per pirogue)	--	--	100	600
Power of pirogue (LOW·kW)/1000	373	866	1612	1791
Power of seine (L·D·Crew size)/1000	117,000	225,000	399,000	960,000
Total power per unit	117,373	225,866	400,612	961,791

a) The numbers in this row in the original (2013) version of this table were erroneous function, and generated an estimate of fishing power of 719% in 2011 (instead of the correct 819%), corresponding in an annual increase of fishing power of about 5.5% (instead of 5.8%). However, as even 5.5% is an extremely high estimate compared to the catchability increase data in Palomares and Pauly (2019), the original conversion from nominal to effective fishing effort is retained here, along with the various plots and parameter estimates based thereon.

Fitting surplus-yield models to the available catch and effort data

Catch of sardinella (in t wet weight) and effective effort data for three areas were analysed:

(i) The Joal/Mbour area where sardinella landings are less likely to contain landings taken outside Senegalese waters; these include around 80% of all sardinella landings made into Senegalese ports;

(ii) All catches landed into Senegalese ports; these include substantial catches taken in southern Mauritania and The Gambia since around 2000, so that the fishery assessed includes fish taken from the margins of neighbouring countries from around 2000 onwards;

(iii) All 'regional' sardinella catches, i.e., originating from The Gambia, Senegal, Mauritania and Morocco.

The catch (C) and effort (f) data for the 3 areas were first plotted as C/f (or CPUE) vs effort, and the intercept (a) and slope (b) of the resulting linear were regressions used to compute Schaefer-type parabola of ('equilibrium') catch or 'yield' vs effort from $Y = a \cdot f - bf^2$, with $MSY = a^2/2b - b \cdot (a/2b)^2$, and $f_{MSY} = a/2b$. Figure 2 shows a pair of plots for each of the 3 geographical areas, with the plots on the left displaying the catch/effort vs effort from which the Schaefer-type plots on the right were derived. Note, however, that no adjustments were made to account for the fact that the catch data, given the rapid increase of effort, were not 'equilibrium' catches. The absence of such adjustment, e.g., through a method proposed by Gulland (1969), should have led to overestimation of MSY and the effort level that leads to MSY (Pauly 1984).

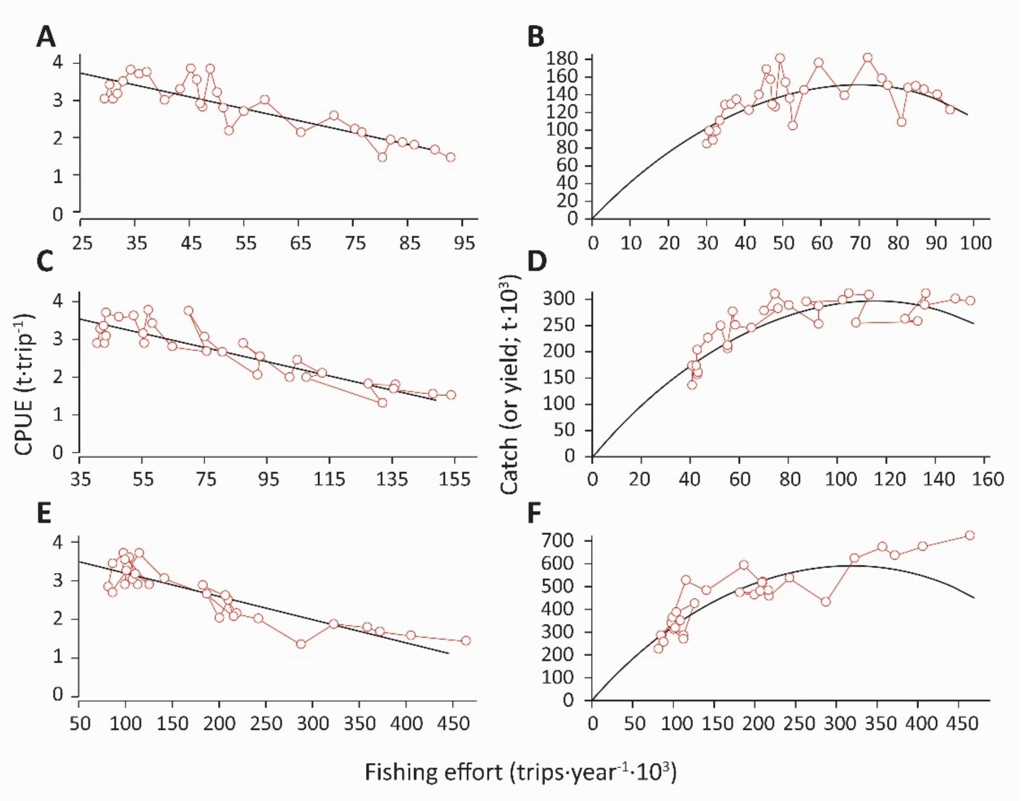

Figure 2. Surplus-yield modelling of the sardinella fisheries at 3 geographic scales in Northwest Africa. **A**: CPUE vs effort and **B**: surplus-yield model in Joal/Mbour area of Senegal; **C**: CPUE vs effort and **D**: surplus-yield model of sardinella landed in Senegal's ports; **E**: CPUE vs effort and **F**: surplus-yield model in the Region covering The Gambia, Senegal, Mauritania and Morocco. Note that no adjustments were made to account for the fact that the catch data, given the rapid increase of effort, were not 'equilibrium' catches.

All three assessments show that the sardinella stocks around Joal/Mbour, the whole of Senegal and the entire Region are fished at effort levels beyond the level of effort required to take MSY. The results suggest that there is an excess of capacity in the Senegalese artisanal fishery so that effort/capacity reduction of around 35% will be needed to return to MSY in Senegal. The corresponding regional figure is 28%.

Figures 2D and 2F show that MSY and E_{MSY} were reached from around 2003 for the Senegalese and regional fisheries respectively. However, Figure 2F also suggests that overfishing of the regional stock did not start until around 2008. Large-scale fishing by Senegalese boats in neighbouring EEZs is believed to have started around 2003 or a little later: such fishing may have been motivated by falling CPUE (Figure 2C) in the Senegalese artisanal fishery which fell from an average of around 3.4 $t \cdot trip^{-1}$ in the early 1980s to around 2.2 $t \cdot trip^{-1}$ around 2001, corresponding to a decline of 1.2 $t \cdot trip^{-1}$. This fall will probably have reduced fisher incomes in a similar fashion.

Surplus-yield modelling with environmental variables

The potential impact of two environmental factors, increasing sea surface temperatures (SST) due to global warming and the intensification of the upwelling off Northwest Africa due to the intensification of coastal winds (Bakun 1990) were studied using the CLIMPROD software of Fréon (1993).

CLIMPROD can handle over 30 different surplus production curves based on underlying models including: (i) the standard Schaefer, Fox and Pella and Tomlinson models which assume that CPUE is influenced only by effort (ii) eight of models based on the assumption that CPUE is influenced by effort and that only catchability is influenced by an environmental variable (V) (iii) twelve models which assume that CPUE is influenced by effort and that only abundance is influenced by V (iv) four models for which it is assumed that CPUE is influenced by effort and that both abundance and catchability are influenced by V.

These models allow inclusion of biologically realistic assumptions about the number of exploited year classes (N_{yr}); the age at recruitment of the exploited species (t_r, years) and the incidence and ending of the effects of the environmental variable V. Based on the knowledge of sardinella life cycles in Senegal and the Region documented here, we assumed that:

(i) N_{yr} = 3-4 for the Joal/Mbour catches where the population is often dominated by juveniles;
(ii) N_{yr} = 4 years for the whole of Senegal and the whole region where adults are more abundant (we also found that assuming $N_{yr} \leq 2$ and ≥ 5 led to inferior fits rejected them for these reasons);
(iii) t_r = 1 year for all cases;
(iv) V affects abundance and/or catchability from age 0 to age 1 for all cases.

Two environmental variables were used with the corresponding landings and effort data:

a. the CRODT Temperature Index (TI); and
b. the CRODT Upwelling Index (UI), both of which are specific to Senegalese waters.

Because UI and TI are specific to Senegal, they were used only to model the Joal/Mbour and the Senegalese fisheries.

Data were also available which reflected Atlantic Oscillation Index (AMO), but as this represents a large part of the Atlantic, it provided only a very poor fit for all data sets. This was probably because the AMO has a long cycle of around 25 years while landings and effort data were only available from 1980-2011. During preliminary fitting, we found that all models which assumed that V affects catchability, or both catchability and abundance, either gave bad fits or provided no significant improvements over models which assumed that V affected abundance only, or that V had no effect. Therefore, we assumed that V could affect abundance, but did not affect catchability.

During preliminary fitting we also found that models for *S. maderensis* did not fit as well and/or were biologically less likely than those for *S. aurita*. Thus, given the smaller catches for *S. maderensis* and its biological similarity with *S. aurita*, we pooled the data for both species. It may be appropriate to revisit this decision when more comprehensive data are available.

The Schaefer-type models identified above, which describe the relations between catch and effort are robust enough to be used to identify management options. However, CLIMPROD may also be used to identify effects of environmental variables on C and CPUE, as well as effort. Various fits were made to data for the Joal/Mbour segment, and to the data for the whole of Senegal, using both the temperature index (V = TI) and the upwelling index (V = UI) available for Senegal (Figure 3).

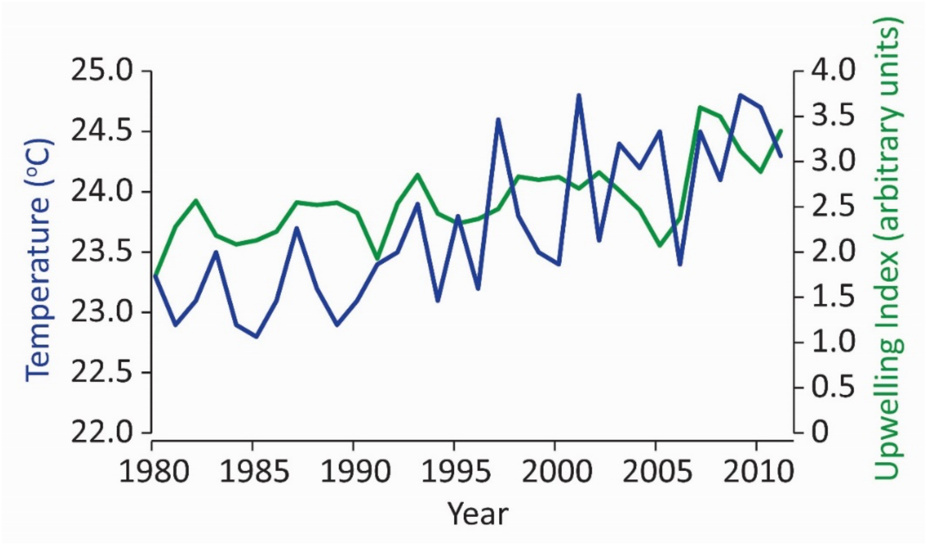

Figure 3. Sea Surface Temperature (blue) and upwelling intensity off Senegal as used for the surplus-yield models in Figure 4.

With temperature, the best fit was obtained with the model CPUE = a(TI)+bf, where a and b are constants and CPUE and f are measured in $t \cdot trip^{-1}$ and $trips \cdot year^{-1}$ respectively.

Cury and Roy (1989) showed that intermediate levels of upwelling were associated with a high productivity of small pelagic fishes in upwelling systems, whereas weak and strong upwelling were associated with low productivity. This suggests a parabolic fit of the UI variable, and we found indeed that this formulation was optimal. Thus, the CLIMPROD presented here had the form $CPUE = a + b \cdot (UI) + c \cdot (UI)^2 + d \cdot f$, where a is the intercept, and b, c and d are partial regression coefficient (slopes), and CPUE and f are measured in $t \cdot trip^{-1}$ and $trips \cdot year^{-1}$ respectively.

Figure 3 shows the temperature trend of off Senegal which, if it can be extended to the rest of the stock, especially Mauritania and The Gambia, may explain (at least in part), why both Senegalese landings (Figure 2D) and regional landings (Figure 2F) in the late 2000s and early 2010s years are higher than the equilibrium curves suggest, as illustrated in Figure 4B (though this is also explained by the simple fact that effort increased).

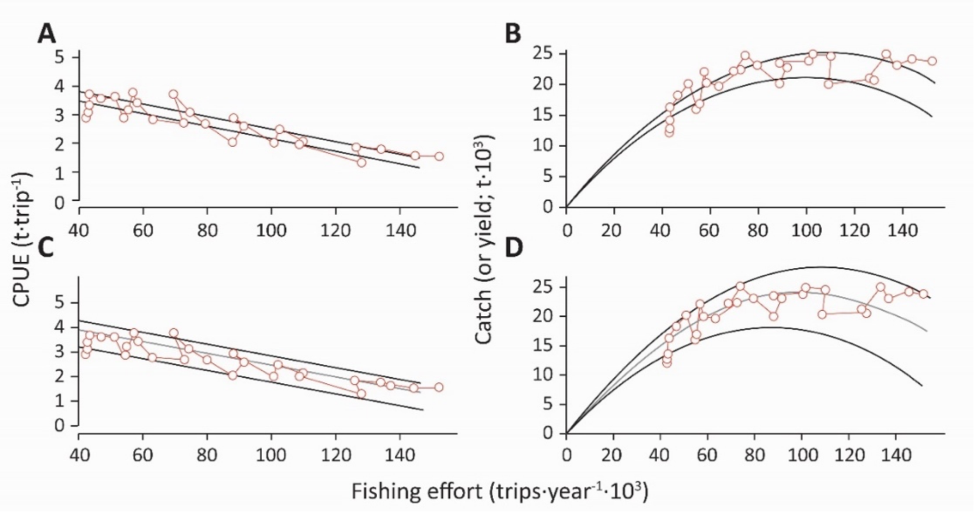

Figure 4: CPUE vs effort (left) and surplus-yield models of the Senegalese sardinella fisheries accounting for environmental variables. **A&B**: Accounting for temperature, with the upper lines corresponding to 24.8 °C and the lower lines to 24.8 °C. **C&D**: Accounting for upwelling intensity (UI), with the upper lines corresponding to 1.9 UI units and the lower lines to 3.8 UI units (see also Figure 3).

This model in Figure 4B suggests that MSY is 50,000 t higher at 24.8 °C than at 22.8 °C (Table 2). A prudent fishing strategy could take 50,000 t·year^{-1} less than suggested by the surplus-yield model for Senegal (Figure 2D), and 20,000 t·year^{-1} t less than the current 'equilibrium' landings. Although less fish would be landed, implementation of such a policy would increase the mean CPUE from around 1.6 t·trip^{-1} to around 2.6 t·trip^{-1}.

Table 2. Temperature dependant estimates of MSY, f_{MSY} and CPUE at MSY for the Senegalese sardinella fishery

Temp. (°C)	**MSY (t·yr^{-1})**	**f_{MSY} (trips·yr^{-1})**	**t·trip^{-1} at f_{MSY}**	**2013 catch (t)**
22.8	200,000	100,000	2.00	150,000
24.8	250,000	110,000	2.27	230,000

The CLIMPROD model also suggests that stock productivity is low for values of UI < 1.9, intermediate at values near 2.8 and highest for values of UI ± 3.8 (Figure 4C and D).

Overall results of the CRODT/COMFISH Project

Assuming that all landings and effort data about the Senegalese and the Regional fishery are included in the data sets used here, the following conclusions can be made:

The new abundance index based on CPUE at Joal and Mbour, which accounts for the technological changes of the standard fishing units (*seine tournante*), can be combined with nominal effort data to produce robust and reliable Schaefer-type surplus-production models. These can be used to identify management options for decision makers.

Our analysis shows that the Senegalese fishery is overfished. The stock produced MSY of 250,000 t at 115,000 trips·year^{-1} in 2003. In 2011, the fishery had landings of only 220,000 t at a much higher effort of 155,000 trips, i.e., 34% higher than the effort needed to take MSY.

CPUE fell in Senegal from around 3.4 t·trip^{-1} in the early 1980s to around 2.2 t·trip^{-1} in 2003, and to around 1.5 t·trip^{-1} in 2011. Senegalese artisanal fishers' complaints about "*la rarefaction de la resource*" (i.e., the fish resource becoming rare) are entirely justified. If fishing effort in the fishery were to be reduced so as to produce MSY, CPUE would increase from current levels of 1.5t t·trip^{-1} to around 2.2 t·trip^{-1}, i.e., by around 47%.

The regional model using the new measure of effective effort also shows that the sardinella fishery suffers from overfishing: MSY occurred at around 580,000 t and 325,000 effective artisanal trips per day, in around 2007 instead of the 2011 equilibrium yield of 500,000 t at around nominal 425,000 trips·year^{-1}. The fishery landed 80,000 t less and fished at 90,000 trips·year^{-1} more than it would at MSY, so that it is heavily overfished with an excess capacity which is around 30% too high.

CPUE fell in the Region from around 3.25 t·trips^{-1} in the early 1980s to around 1.08 t·trips^{-1} in 2011, i.e., to around 33% of values in the 1980s, also confirming fishers' complaints about "*rarefaction de la resource*". If the fishery is returned to MSY, the CPUE would rise to 1.78 t·trips^{-1}, i.e., it would increase by around 48%. (Note that most of the sardinella catch from outside but landed in Senegal are taken by industrial boats).

CPUE at MSY in the Senegalese fishery would be around 2.2 t·trips^{-1} while regional CPUE in 2011 would be around 1.8 t·trips^{-1}. The Senegalese fishery is more productive, perhaps because Senegal's EEZ has one of the most important nursery areas and juvenile grow-out areas for sardinella in the Region.

Mean water temperatures have increased during the study period and probably caused unusually high landings of Senegalese and regional landings since 2008. Higher temperature (a change in mean sea temperature from 22.8 ^{o}C to 24.8 ^{o}C) increased MSY from 200,000 to 250,000 t·year^{-1} of sardinella.

Environmental surplus-production modelling showed that landings are influenced by both of the temperature and upwelling intensity. Models with good fits were obtained, but a more critical review of how these temperature and upwelling indices affect landings is needed before environmentally sensitive modelling can be fully integrated into fisheries management plans.

CMSY sardinella assessments (2022)

Principle of CMSY

The CMSY method of Froese *et al.* (2017), strongly improved from the Catch-MSY method of Martell, is, as the Maximum Sustainable Yield (MSY) concept, is based on an approach to fish population dynamics formulated by Schaefer (1954, 1957; see above). This approach, known as 'surplus-production' modelling, is based on the idea that a given ecosystem has, for any population, a distinct carrying capacity (k). If this population is diminished by external event (e.g., fishing), the population will grow back toward its carrying capacity. This growth depends on its intrinsic growth rate (r; here expressed in year^{-1}), which depends on the biological traits of the individuals of that population growth rate, size at first maturity, natural mortality, fecundity, etc.; see FishBase; www.fishbase.org), and by its current biomass (B).

Thus, fishing can maintain a population at any biomass level by withdrawing, each year, the biomass equivalent to the growth of that population. Because the production of new biomass is maximal when carrying capacity is halved (i.e., at k/2), MSY is produced when the unexploited biomass (B_0) is halved, and $B_0 \approx$ k.

The CMSY method relies on this framework, and basically consist of tracing thousands of trajectories of the biomass of a stock and identifying the trajectories that are viable while compatible with the catches taken from this stock and some other constraints, or 'priors' (here 'viable' means not going extinct). The constraints are assumptions relating to the biomass reductions due to fishing, a range of possible estimates of carrying capacity (k) for the stock in the ecosystem in question, and a range of possible values of intrinsic rate of population growth (r).

Given a time series of catches, prior ranges of r and k values, thousands of biomass trajectories can be produced, of which very few can be viable. Moreover, the number of acceptable r-k data pairs is further reduced by reduced by the constraints relating to the biomass reductions due to fishing, expressed as fractions such as B_{end}/k, B_{start}/k or B_{int}/k, relating to the 'biomass left' at the end of the available catch time series, at its start, or some intermediate value. Here, information from the first part of this contribution is used as priors (see Table 2).

Finally, the CMSY model can be turned into a Bayesian version of the full Schaefer model (BSM), by using CPUE data from other stock assessments, which usually results in reducing the uncertainty around estimates of MSY and related parameter estimates (see Froese *et al.* 2017).

The CMSY approach assumes that from one year (t) to the next (t+1), the biomass (B_t) follows the equation:

$$B_{t+1} = B_t + r(1 - B_t/k)B_t - C_t \qquad \text{...1)}$$

where r is the intrinsic rate of population growth, k the carrying capacity ($\approx B_0$), and C_t the catch in year t. When the biomass (B_t) declines below 0.25·k, Equation (1) is modified to allow reduced recruitment (≈ 'depensation'):

$$B_{t+1} = B_t + (4\mathrm{r}\,B_t/k)(1 - B_t/k)B_t - C_t \mid B_t/k < 0.25 \qquad \text{...2)}$$

where $4r \cdot B_t/k$ induces a linear reduction of population growth below $B_{MSY}/2$, i.e., half of the biomass capable of generating maximum sustainable yield (MSY).

The R software that implements the CMSY method (or more precisely CMSY++, the version used here; see oceanrep.geomar.de/id/eprint/52147/) includes a routine that produces priors for k (Froese *et al.* 2017), whose output were accepted as defaults

$$k_{low} = \max(C)/r_{high}\,;\ k_{high} = 4\max(C)/r_{low} \qquad \text{...3)}$$

where k_{low} and k_{high} are the default lower and upper limits of k, max(C) is the maximum catch in the time series, and r_{low} and r_{high} are the lower and upper limits of r-range, which is explored by the CMSY. Thus, we have:

$$k_{low} = 2max(C)/r_{high}\,;\ k_{high} = 12max(C)/r_{low} \qquad \text{...4)}$$

with variables as in Equation (3).

Froese *et al.* (2017) formulated the BSM method such that the standard deviation of r in log-space is described by a uniform distribution (ranging between 0.001 irf and 0.02 irf), i.e.,

$$irf = 3/(r_{high} - r_{low}) \qquad \text{...5)}$$

where *irf* is an inverse range factor to infer the r-range, with r_{high} and r_{low} usually provided by FishBase (www.fishbase.org) for fishes (Table 1), and SeaLifeBase (www.sealifebase.org) for invertebrates.

The k estimation by BSM also assumes that k has a log-normal distribution, with the mean of k providing a credible estimate.

The BSM method allows the estimation of a catchability coefficient (q) that relates CPUE (when available) to biomass. Here, priors are given by:

$$q_{low} = 0.25 r_{pgm} CPUE_{mean}/C_{mean};\ q_{high} = 0.5 r_{high}/CPUE_{mean} \qquad \ldots 6)$$

where q_{low} and q_{high} define a (uniform) range of prior for the catchability coefficient; r_{pgm} is the geometric mean of the prior range for r; $CPUE_{mean}$ is the mean CPUE over the last few years, and C_{mean} is the mean catch over the same few years.

Finally, gradual improvements of the fishing boats, and of their gear, rigging, and instrumentation, which can be substantial, can be (and was) considered in BSM analyses, particularly when using industrial CPUE data, by including a technological 'creep' factor (Palomares and Pauly 2019). However, the recommended creep factor for periods around 30 years is about 3% per year.

The CMSY/BSM method has been applied to hundreds of 'data-rich' stocks, which enabled comparisons with the results of models requiring more data. It has also been applied successfully to multiple stocks in countries and regions with few 'classical' assessments, notably in Turkey (Demirel *et al.* 2020) and Northeast Asia (Liang *et al.* 2020; Zhai *et al.* 2020), with Palomares *et al.* (2020) representing a global application.

CMSY application to sardinella catch data

Samb and Pauly (2000) showed that the seasonal latitudinal migrations of sardinella from The Gambia and the South to Morocco in the North and back (see also Pauly 1994) preclude a real understanding of stock dynamics based exclusively on sub-national and even national data. Thus, CMSY++ (oceanrep.geomar.de/id/eprint/52147/10/CMSYUserGuideMarch2021.pdf) is here applied to the data in Table 3, pertaining to sardinella (mainly to *S. aurita*, combined with smaller catches of *S. maderensis*) for the Northwest African Region, i.e., The Gambia, Senegal, Mauritania and Morocco.

The CMSY++ was run with a prior range for r of 0.5 to 1.2 $year^{-1}$ from FishBase (www.fishbase.org) for *Sardinella aurita* and *S. maderensis* and the following relative biomass priors: B_{start}/k = 0.3-0.7 and B_{end}/k = 0.1-0.5. Also, given the high estimate of 5.8% per year increase of gear efficiency, CMSY was run with a high estimate of technological 'creep' of 3% (Palomares *et al.* 2019).

Table 3. Catch and effort data. *Sardinella* spp. from Northwest Africa as used for the surplus-yield (Figure 2A&B) and CMSY++ assessments (Figure 5D-E)

Year and catch, effort and CPUE from Joal/Mbour (Senegal)				Sum of catches from The Gambia, Senegal, Mauritania and Morocco
Year	Catch (t)	Effort	CPUE	Catch (t) used for assessment
1990	125,208	43,584	2.87	399,885
1991	142,069	44,953	3.16	320,320
1992	172,083	45,964	3.74	340,829
1993	160,386	47,026	3.41	267,900
1994	131,530	47,041	2.80	256,830
1995	128,788	47,962	2.68	287,930
1996	185,748	49,752	3.73	545,390
1997	156,853	51,031	3.07	525,760
1998	138,519	51,915	2.67	586,230
1999	107,644	52,800	2.04	487,020
2000	147,620	57,251	2.58	462,650
2001	179,054	61,921	2.89	461,650
2002	140,712	70,412	2.00	460,650
2003	185,993	75,579	2.46	538,239
2004	161,375	76,694	2.10	512,450
2005	153,733	77,023	1.99	557,829
2006	110,738	83,643	1.32	467,320
2007	150,085	82,123	1.83	612,900
2008	152,158	85,690	1.77	676,110
2009	148,227	87,904	1.69	654,870
2010	143,446	92,318	1.55	679,800
2011	125,782	94,612	1.33	712,345

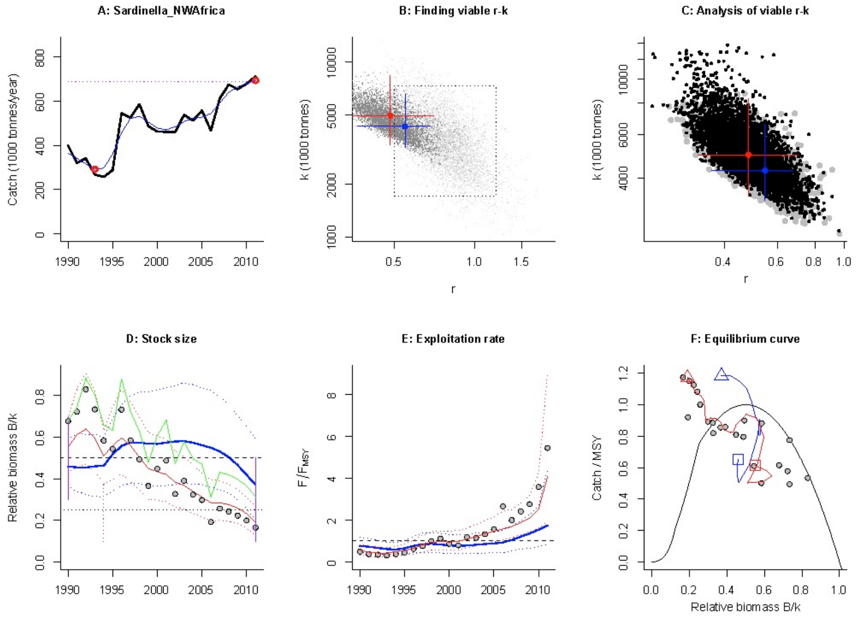

Figure 5. Output of the CMSY++ software running with catches of *Sardinella aurita* + S. *maderensis* from The Gambia, Senegal, Mauritania and Morocco for the years 1990 to 2011, and the priors mentioned in the text above. **A:** Catch (from Table X); **B:** viable combinations of r and k, with the blue cross referring to the most likely r-k pair compatible with the catches and prior information (see Table X), and the red cross to most likely r-k combination that also used the CPUE data in Table 3, thus leading to the BSM model in panel F; **C:** Narrower view of the viable runs. **D:** Stock biomass (blue line) and its (wide) 95% confidence interval, along with the CPUE series (dots), the corresponding trend line (red) and the green documenting the effect of the improvements, i.e., technological 'creep'); **E:** Exploitation rate (F/F_{MSY}) and its confidence interval, with the blue representing the median F/F_{MSY} and the red line representing the trend of the CPUE (dots) converted into F/F_{MSY} via $F = f \cdot q$, where q is catchability. **F:** Equilibrium curve of the Schaefer-type model, showing that the high catches (blue line) and high CPUE (red line) of later years were not sustainable.

The results of the CMSY++ application to the data in Table 3 are shown in Figures 5 and 6. Figure 5A recalls the catch data used for this exercise (see Table 3, rightmost column), which were analyzed *without* (blue crosses in Figures 5B and 5C) and *with* the CPUE data from Joal/Mbour (see Table 3).
Figures 5A, B, and C show the blue and red crosses to be close to each other, suggesting that the CPUE data and the regional catch data in Table 3 relate to similar biomass trends. Figure 5D, although slightly confusing, illustrates the same concept, i.e., that the biomass and the CPUE series have similar trends. Figure 5E illustrates the same notion, but in terms of F/F_{MSY}, while 5F, using a Bayesian surplus-production model, documents that the sardinella fisheries in Joal/Mbour and along the NW African coast were rarely in equilibrium, thus failing to meet fundamental assumptions of surplus-production modelling. Finally, Figure 6 shows the trajectory of the sardinella stock off NW Africa from high abundance and low fishing mortality (green panel) in the periods preceding the 1990s to the low abundance and overfishing status (red panel) in the 1990s, where they would remain despite various efforts to 'manage' the fishery.

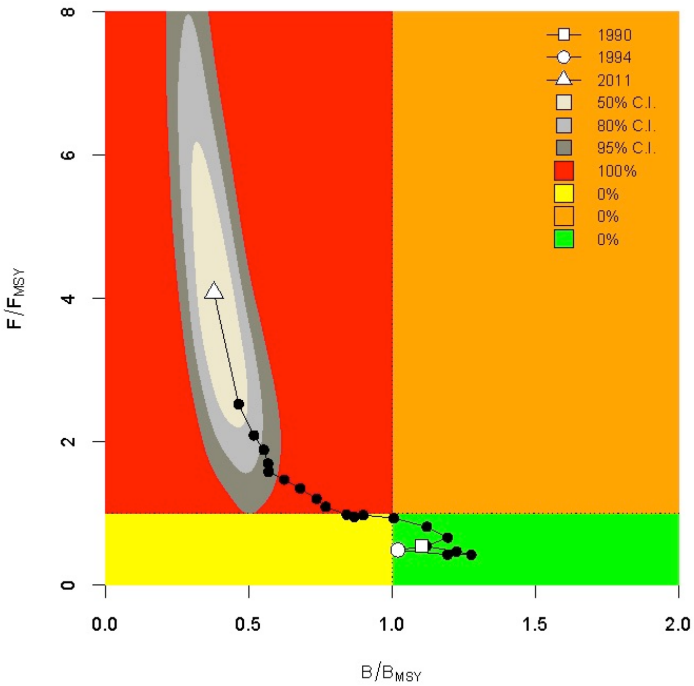

Figure 6. Kobe plot illustrating the trajectory from under- to overfishing in the sardinella fisheries of N.W. Africa (see text).

Discussion and Conclusions

The exercise performed here comparing the results of an earlier approach with those obtained using a recently updated methodology leads to similar conclusions with both approaches: the sardinella stock(s) off NW Africa were at or near MSY in the 1990s, and the increase of effort that occurred in the 21st Century was excessive (see also Palomares *et al.* 2021).

This suggests that the modelling effort performed a decade ago led to management advice that was essentially correct, even if various assumptions of the surplus-yield models that were then used (notably the equilibrium assumption) were not met.

This, if anything, suggests that current debates about details of various stock assessment models may not matter when they are robust enough to point to the *direction* of the intervention(s) required to put a fishery on a sustainable path. In the case of the Senegalese and NW African sardinella fisheries, the intervention that would have mattered is stopping the increase of, then reducing the effort expended by the fishery. However, this was not done.

The waste of resources that this implies is heightened by the recent development in NW Africa of using sardinella to produce animal feed for export (Pauly 2019). As a much-appreciated food for people, the Senegalese and others in the Region are deprived of nutritious, healthy food.

Acknowledgements

The surplus-yield assessments presented in the first part of this contribution are based on data and previous studies presented in spring 2013 to the CRODT and USAID COMFISH PENCOO GEJ in a consultant report funded by USAID as part of its support for developing marine fisheries management in Senegal. C.M. thanks his colleagues in Senegal who provided data and information that helped with the completion of this work. The second part of this contribution, was written in August 2022 by S.B. and D.P., who, together with CM, thank Elaine Chu for re-drafting all figures.

References

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science*, 247: 198-201.

Cheung, W.W.L., V.W.Y. Lam, J.L. Sarmiento, K. Kearney R. Watson and D. Pauly. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries,* 10: 235-251. doi.org/10.1111/j.1467-2979.2008.00315.x

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46(4): 670-680.

Dème. M., D. Thiao, F.M. Sow, A. Sarre and H.D. Diadhiou, 2012. *Dynamique des populations de sardinelles en Afrique du nord-ouest: contraintes environnementales, biologiques et socio-économiques*. USAID COMFISH Project. University of Rhode Island, Narragansett, R.I. 125 p. www.crc.uri.edu/download/Sardinella-Rapport_FR_508.pdf

Demirel, N., M. Zengin and A. Ulman. 2020. First large-scale eastern Mediterranean and Black Sea stock assessment reveals a dramatic decline. *Frontiers in Marine Science*, 7(103):1-13. doi.org/10.3389/fmars.2020.00103

Fitzpatrick, J. 1996. Technology and fisheries legislation, p. 191-199 In: *Precautionary Approach to Fisheries. Part 2: Scientific Papers*. Prepared for the Technical Consultation on the Precautionary Approach to Capture Fisheries (Including Species Introductions), Lysekil, Sweden, 6-13 June 1995. FAO Fisheries Technical Paper 350, part 2. FAO, Rome, Italy. 210 p. Available at: www.fao.org/3/w1238e/W1238E09.htm#ch7

Fréon, A.O. 1993. *CLIMPROD Experimental interactive software for fitting surplus production models including environmental variables*. Computerized Information Series (Fisheries) No. 5. FAO, Rome, Italy. 76 p.

Froese, R., N. Demirel, G. Coro, K.M. Kleisner and H. Winker. 2017. Estimating fisheries reference points from catch and resilience. *Fish and Fisheries*, 18(3): 506-526. doi.org/10.1111/faf.12190

Gulland, J.A. 1969. *Manual of methods for fish stock assessment. Part I. Fish population analysis*. FAO Manuals in Fisheries Science 4. FAO, Rome, Italy. 154 p.

Koutob, V., D. Belhabib, C. Mathews, V. Ndiaye and N. Lazar. 2013. *Gestion concertée pour une pêche durable au Sénégal, Evaluation préliminaire des captures de la pêche Illicite, non-déclarée et non règlementée au Sénégal, sources de Journal du Conseil données, logique et conclusions*. USAID and CRC/URI, Senegal. 72 p.

Liang, C., W. Xian and D. Pauly. 2020. Assessments of 15 exploited fish stocks in Chinese, South Korean and Japanese waters using the CMSY and BSM methods. *Frontiers in Marine Science,* 7(298). doi.org/10.3389/fmars.2020.00298

Palomares, M.L.D and D. Pauly. 2019. On the creeping increase of vessels' fishing power. Special issue on "Managing local and global fisheries inthe Anthropocene". *Ecology and Society,* 24(3): 31. Available at: www.ecologyandsociety.org/vol24/iss3/art31/

Palomares, M.L.D., M. Khalfallah, J. Woroniak and D. Pauly. 2020. Assessment of 14 species of small pelagic fish caught along the coast of Northwest African countries, p. 77-108. *In:* M.L.D. Palomares, M. Khalfallah, J. Woroniak and D. Pauly D (eds.) *Assessments of marinefisheries resources in West Africa with emphasis on small pelagics*. Fisheries Centre Research Report 28(4).

Pauly, D. 1994. Un mécanisme explicatif des migrations des poissons le long des côtes du Nord-Quest africain, p. 235-244. *In:* M. Barry-Gérard, T. Diouf and A. Fonteneau (eds.) *L'évaluation des ressources exploitables par la pêche artisanale sénégalaise – Documents scientifiques présentés lors du Symposium, 8-13 février 1993, Dakar, Sénégal*. Tome 2. ORSTOM Éditions, Paris.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *Conseil international pour l'Exploration de la Mer,* 39(3): 175-192.

Pauly, D. 1984. *Fish Population Dynamics in Tropical Waters: a manual for use with programmable calculators*. ICLARM Studies and Reviews 8. ICLARM, Manila, Philippines. 325 p.

Pauly, D. 2019. How the global fish market contributes to human micronutrient deficiencies. *Nature, News and Views*, 25 September 2019. doi.org/10.1038/d41586-019-02810-2

Sekharan, K.V. 1974. Estimates of the stock of oil sardine and mackerel in the present fishing grounds off the west coast of India. *Indian Journal of Fisheries,* 21(1): 177-182.

Ricker, W. 1975. *Computation and interpretation of biological statistics of fish populations.* Bulletin of the Fisheries Research Board of Canada. Bulletin 191. Environment Canada, Ottawa, Canada. 382 p.

Samb, B. and D. Pauly. 2000. On 'variability' as a sampling artefact: the case of Sardinella in North-western Africa. *Fish and Fisheries,* 1: 206-210. doi.org/10.1046/j.1467-2979.2000.00016.x

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Bulletin of the Inter-American Tropical Tuna Commission*, 1: 27-56.

Schaefer, M.B. 1957. A study of the dynamics of populations of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Bulletin of the Inter-American Tropical Tuna Commission,* 2: 227-268.

Zhai, L. C. Liang and D. Pauly. 2020. Assessments of 15 exploited fish stocks in Chinese waters using the CMSY and BSM methods. *Frontiers inMarine Science,* 7(623): 1-11. doi.org/10.3389/fmars.2020.00623

Plugging life-history gaps in FishBase with data on sharks and rays [1]

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Abstract

Length-weight relationships (LWR) and parameter estimates of the von Bertalanffy growth function (VBGF) are important life history traits that are essential for fishery stock assessment and management. The aim of this study is to fill gaps in LWR and VBGF parameters of species of sharks and rays included in the *Sea Around Us* database of marine fisheries catches (www.seaaroundus.org), but which lack these key parameters in FishBase, the global online encyclopedia of fishes (www.fishbase.org). We found in the literature or estimated LWR parameters for all the 21 species of shark and rays that we selected, along with VBGF parameters. The results of the study indicate that most of these exploited species grow slowly, and thus are at risk from fisheries pressure and ocean warming.

Introduction

Although length-weight relationships (LWR) and the parameters of the von Bertalanffy growth function (VBGF) are important for fisheries management, this information is still missing for many exploited species. For instance, sharks and rays have been fished heavily for their fins and their populations are declining worldwide (Clarke *et al.* 2013). Yet, some heavily exploited sharks and rays still lack these data in FishBase (www.fishbase.org), the online encyclopedia of fishes. One such case is *Rhizoprionodon longurio* (Jordan & Gilbert 1882), considered 'Vulnerable' in IUCN's Redlist (see www.iucnredlist.org/).

LWR are important to the study of fishes and their populations (Abdurahiman *et al.* 2004; Froese 2006) as they allow for the conversion of growth in length to growth in weight, which is a basic information for fish stock assessments; also, LWR allow comparisons between the life histories of species of various shapes (Froese 2006).

Similarly, the growth of individual fish is what ensures the maintenance of a population's biomass over time, and its replenishment following declines due to environmental fluctuations of fisheries extractions (Pauly 1984). Growth thus determines an exploited population's vulnerability to overfishing (Musick *et al.* 2000).

There are three general types of data needed to find the growth parameters of the VBGF (Pauly 1984): (1) periodic markings on skeletal parts, e.g., otoliths, or other bones, (2) tagging-recapture data, and (3) size frequency data, i.e., generally the easiest type of data to collect and analyze (see Pauly 1998).

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[1] Cite as: McRae, T.M., S. Tong and M.L.D. Palomares. 2022. Plugging life history gaps in FishBase with data on sharks and rays, p.43-51. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

Thus, to fill the gaps for shark and rays, especially those that occur in the catch statistics reported by fishing countries to the Food and Agriculture Organization of the United Nations (FAO), and which the *Sea Around Us* builds upon (Palomares *et al.* 2016), we assembled here the parameters of length-weight relationships (LWR) of 21 species of shark and rays. Also, published parameters of the VBGF were assembled and standardized for 20 species of shark and rays, and a set of growth parameters was estimated based on the growth parameters of morphologically similar species. The data obtained in this study will be encoded in FishBase.

Materials and Methods

Species included

The 21 shark and ray species included here are of interest to the *Sea Around Us* (www.seaaroundus.org), as they are species that are now strongly exploited, but data deficient (Table 1).

Length-weight relationships

The length-weight relationships (LWR) we use are of the form $W = a \cdot L^b$ where α is a multiplicative term, generally obtained as the antilog of the y-intercept of the log-log regression

$$log(W) = \alpha + b \cdot log(L) \qquad ...1)$$

where *W* and *L* are weight and length pairs (here in g and cm, respectively), *b* is the slope of the regression, equivalent to the exponent of the LWR and α the intercept, whose antilog is an estimate of *a,* the multiplicative term (Froese 2006).

The parameters of LWR were sourced through a literature search; in cases where no such parameters were found, length/weight data pairs representative of the population were fitted with Equation 1. Where suitable data were available, separate LWR for females and males were calculated. If FishBase was used to obtain the LWR, the Bayesian length-weight parameters were based on the methods of Froese *et al.* (2014).

Growth parameters

The VBGF for length has the form:

$$L_t = L_\infty(1 - \mathrm{e}^{-K \cdot (t - t_0)}) \qquad ...2)$$

where L_t is the length at age *t*, L_∞ is the asymptotic length, *K* is a coefficient of dimension time^{-1} expressing how fast L_∞ is approached, and t_0 is a parameter setting the origin of the curve on the age-axis. The VBGF for weight has the form

$$W_t = W_\infty(1 - e^{-K \cdot (t - t_0)})^b \qquad ...3)$$

where W_∞ is the weight corresponding to L_∞, b the exponent of the LWR and the other parameters are the same as in the VBGF for length.

For comparisons of growth performance within and between different species, one can use the index

$$Ø' = \log(K) + 2 \cdot \log(L_\infty) \qquad ...4)$$

which is relatively constant within species (and higher taxa with similar shapes), as assessed by studying and relating hundreds of L_∞-K data pairs (Pauly 2019).

Length growth parameter estimates, most separated by sex, were either found in various publications or estimated using non-linear regression from published data for 20 of our 21 species. Growth parameters were inferred using *Ø'* only for scalloped bonnethead (*Sphyrna corona*), which is similar in shape and likely growth performance of other hammerhead of the genus *Sphyrna,* and for which growth parameters are available in FishBase.

Conversion of TL to DW for rays

Table 1. Summary of the length-weight relationships of 21 species of sharks and rays. For sharks, 'length' (in cm) corresponds to total length (TL); for rays, it corresponds to disk width (DW).

Species	**Sex**	**a**	**b**	**Source**
Sharks				
Callorhinchus callorynchus	Unsexed	0.00457	3.13	FishBase/Froese *et al.* (2014)
Carcharhinus amblyrhynchoides	Female Male Unsexed	0.00933 0.0117 0.0107	2.923 2.868 2.891	Najmudeen *et al.* (2019) Najmudeen *et al.* (2019) Najmudeen *et al.* (2019)
Carcharhinus signatus	Unsexed	0.00457	3.08	FishBase/Froese *et al.* (2014)
Etmopterus pusillus	Unsexed	0.00355	3.05	FishBase/Froese *et al.* (2014)
Hemitriakis japanica	Female Male	0.0197 0.00636	2.595 2.849	Kamura *et al.* (2000) Kamura *et al.* (2000)
Mustelus griseus	Female Male	0.00344 0.00363	2.968 2.948	Wang and Chen (1982) Wang and Chen (1982)
Mustelus lunulatus	Unsexed	0.005	2.92	Navia *et al.* (2006)
Nasolamia velox	Female Male Unsexed	0.000068 0.000068 0.000068	3.91 3.9 3.9	Guzman *et al.* (2020) Guzman *et al.* (2020) Guzman *et al.* (2020)
Pristiophorus cirratus	Unsexed	0.00389	3.12	FishBase/Froese *et al.* (2014)
Rhizoprionodon longurio	Unsexed	0.00035	3.539	Márquez-Farias *et al.* (2005)
Sphyrna corona	Unsexed	0.000015	3.75	Guzman *et al.* (2020)
Squatina australis	Unsexed	0.0162	2.908	Raoult *et al.* (2016)
Squatina guggenheim	Female Male	0.00492 0.0124	3.13 2.89	Awruch *et al.* (2008) Awruch *et al.* (2008)
Squatina tergocellata	Unsexed	0.00399	3.16	Bridge *et al.* (1998)
Rhinobatos annandalei	Unsexed	0.00178	3.10	FishBase/Froese *et al.* (2014)
Rhinobatos rhinobatos	Unsexed	0.00204	3.08	FishBase/Froese *et al.* (2014)
Rays				
Amblyraja radiata	Unsexed	0.00199	3.22	FishBase/Froese *et al.* (2014) & this study
Bathyraja griseocauda	Female Male	0.0021 0.0053	3.22 3.01	Arkhipkin *et al.* (2008) Arkhipkin *et al.* (2008)
Bathyraja scaphiops	Unsexed	0.0037	3.12	FishBase/Froese *et al.* (2014)
Dasyatis marmorata	Unsexed	0.048	2.94	Yeldan and Gundogdu (2018)
Myliobatis californica	Unsexed	0.013	3.00	Ehemann *et al.* (2017)

For several species of rays in our study (*Amblyraja radiata, Bathyraja griseocauda, Bathyraja scaphiops),* LWR parameters or VBGF parameters could only be found that involved total length (TL) instead of disc width (DW). To convert these parameters into DW for these species, conversion equations were found either through searching the literature for the equation itself or estimating a TL/DW ratio via an image of the species. For *Bathyraja griseocauda,* a conversion equation was found directly through Arkhipkin *et al.* (2008). For *Amblyraja radiata* and *Bathyraja scaphiops*, images of the species were used from FishBase with a known total length to calculate the ratio between total length and disc width. The conversion ratios were then applied to the LWR and VBGF parameters measured in TL to obtain the parameters in DW.

Validation of the estimated parameters

Plots of log(a) vs b were generated either for populations of the same species, or, in cases where FishBase did not have data for that species, the plots were created for species of the same genus or of the same family. If the newly estimated parameters followed the trend of available data points, the estimate was accepted as valid.

The VBGF parameters obtained from the literature were plotted in an auximetric plot (i.e., graphs with log(K) as Y-axis and log(L_∞) as X-axis, with each dot representing a set of growth parameters) jointly with those available in FishBase for populations of the same species. In monospecific genera and/or family, the estimated VBGF parameters were plotted for species in the same genera and/or family.

If the estimated parameters followed the trend of the ellipsoid cloud for that species group, the estimates were validated and accepted; otherwise, they will be tagged as 'doubtful' in FishBase). When growth parameters were available for females and males separately, the parameters estimated for both sexes were ignored, because L_∞ tends to be biased upward and K downward when a single growth curve is estimated in species with sexually dimorphic growth (D. Pauly, pers. comm., February 2022).

Results and Discussion

There were 21 species of sharks and rays selected for this study; we obtained LWR parameters for them either from the literature (including that covered in FishBase) or by estimating these parameters by fitting length-weight data pairs in various publication with Equation 1 (see Table 1 and Figure 1).

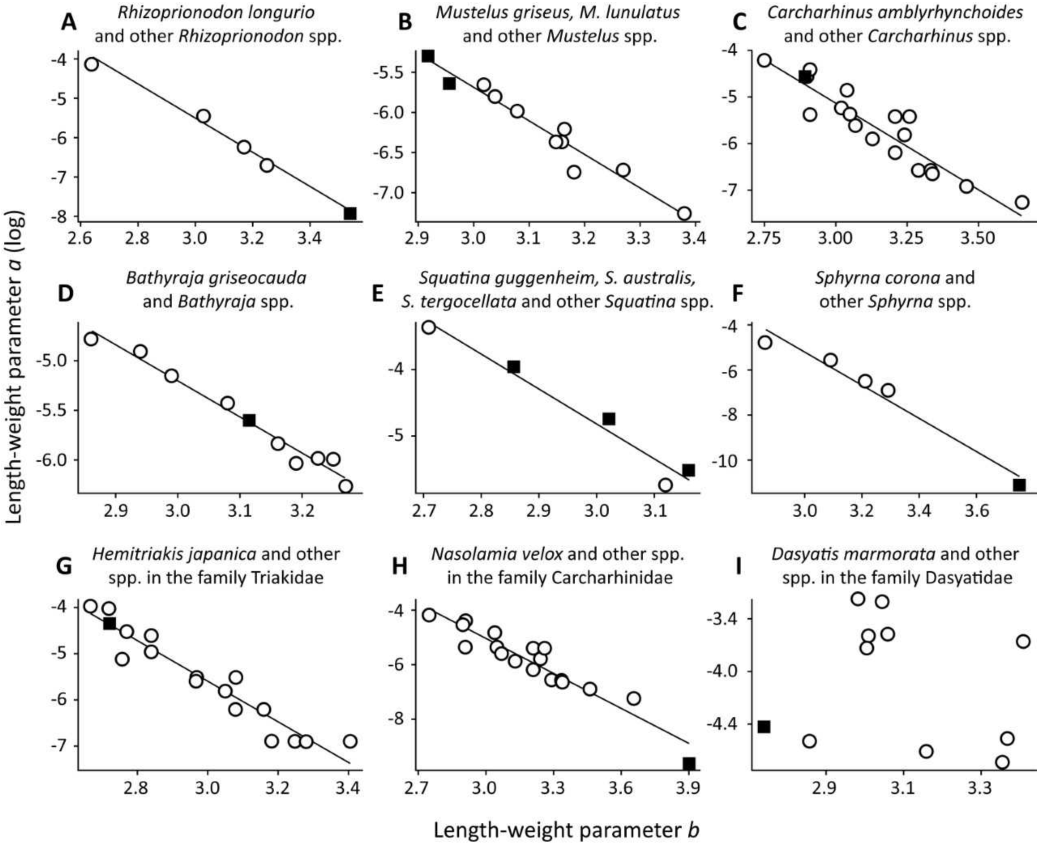

Figure 1. Plot of length-weight parameters (log(a) vs b in shark and ray taxa in FishBase as of the end of December 2021 (dots) and those newly estimated (black squares). The lengths for sharks are total length in cm, and disk width for rays.

The plots in Figure 1 do not imply vast differences in the length-to-weight relationships of the taxa in question, despite the wide ranges of the a and b values that they cover, because high values of a compensates for low values of b, and vice-versa. What such plots reflect, rather (particularly when they refer to a single species, as do such plots in FishBase), are cyclical variations of the parameters of LWR due to different patterns of seasonal oscillations in length (whose increase slows down, but hardly reverses in winter) and weight growth (which usually becomes negative in winter). Indeed, these oscillations, as shown by simulations performed by one of the authors (M.L.D. Palomares) documented on p. 53-54 of Pauly (2019), cause LWR parameters to oscillate seasonally from the upper right corner of the graphs in summer to its lower right corner in winter, in a fashion similar to the plots in Figures 1A to H.

This implies that, ideally, LWR should be computed from L-W data pair samples covering all seasons equally, and/or that care must be taken, when using LWR, to account for their seasonal oscillations. Table 2 presents the VBGF parameters for our 21 species of sharks and rays, while Figure 2 shows that most of the L_∞ and K values obtained fit within an ellipsoid encompassing most of the data for a family. One exception is *Bathyraja griseocauda* whose K value is similar to those in other species within the family, while its asymptotic length is much higher than other species. Also, the species of interest in the genus *Squatina*, i.e., *S. guggenheim*, *S. tergocellata* and *S. australis*, do not have much family data available, and it is difficult to judge how well these data fit into that family.

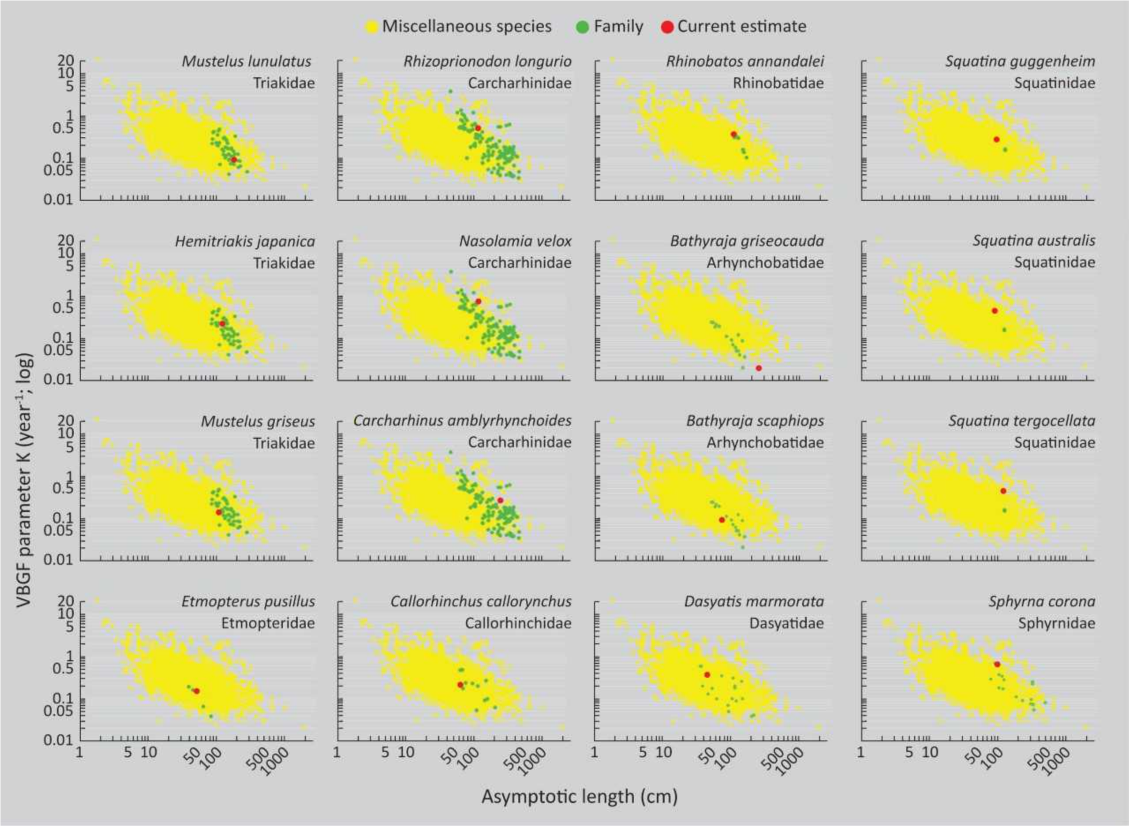

Figure 2. Auximetric plots (log(K) vs. log(L_∞) for sharks and ray taxa (see text).

While some of the data in Figure 2 suggest that the growth performance of shark and rays is not lower than that of bony fish of similar sizes, it is also the case that sharks and rays have low absolute values of K, implying that they require a long time to approach the adult sizes (Smith *et al.* 1998). Thus, populations cannot quickly replace themselves, and cannot resist a strong fishing pressure (Pauly 1984). Indeed, sharks and rays are known to be susceptible to over-exploitation (Stevens et al. 2000) also due to their low fecundity (Stevens et al. 2000).

Although the importance of obtaining length-weight relationships and growth parameters of exploited species is known to be vital for fisheries management, there are still many exploited species for which this information is lacking. This study, which helps fill this knowledge gap for different exploited species of sharks and rays, may serve to illustrate how such gaps can and should be filled, to assist in fisheries management and conservation efforts.

Table 2. Summary of the von Bertalanffy growth parameters of 20 species of sharks and rays; lengths or width are in cm, weight in g and K are in $year^{-1}$. The method (Meth.) used are analysis of length-frequency data (L/F), or marking on skeletal parts (SP).

Species	**Meth.**	**Sex**	**L_∞**	**L-type**	**W_∞**	**K**	**Ø’**	**Source**
Sharks								
Callorhinchus callorynchus	L/F	F	71	TL	2815	0.17	2.93	Bernasconi *et al.* (2015)
		M	563	TL	1363	0.26	2.91	Bernasconi *et al.* (2015)
Carcharhinus amblyrhynchoides	L/F	F	255	TL	100652	0.29	4.27	Najmudeen *et al.* (2019)
		M	237	TL	74538	0.23	4.11	Najmudeen *et al.* (2019)
Carcharhinus signatus	SP	U	270	TL	140772	0.11	3.91	Santana and Lessa (2004)
Etmopterus pusillus	SP	F	54	TL	684	0.13	2.58	Coelho and Erzini (2007)
		M	49	TL	508	0.17	2.61	Coelho and Erzini (2007)
Hemitriakis japanica	SP	F	132	TL	6276	0.20	3.54	Tanaka *et al.* (1978)
		M	111	TL	4280	0.24	3.48	Tanaka *et al.* (1978)
Mustelus griseus	SP	F	125	TL	5721	0.11	3.23	Wang and Chen (1982)
		M	94	TL	2346	0.18	3.201	Wang and Chen (1982)
Mustelus lunulatus	L/F	U	176	TL	18024	0.09	3.46	Olvera (2006)
Nasolamia velox	L/F	F	121	TL	9470	0.66	3.98	Bizarro *et al.* (2009)
		M	111	TL	6564	0.79	3.99	Bizarro *et al.* (2009)
Pristiophorus cirratus	SP	F	TL	TL	24052	0.15	3.53	Walker and Hudson (2005)
		M	TL	TL	10886	0.31	3.62	Walker and Hudson (2005)
Rhizoprionodon longurio	SP	F	124	TL	9104	0.46	3.85	Espinosa (2011)
		M	110	TL	5983	0.58	3.85	Espinosa (2011)
Sphyrna corona	Ø’a)	U	97	TL	423	0.64	3.78	This study
Squatina australis	L/F	F	97	TL	9548	0.45	3.62	Jones *et al.* (2010)
		M	86	TL	6759	0.42	3.49	Jones *et al.* (2010)
Squatina guggenheim	L/F	U	95	TL	6980	0.27	3.39	Vooren and Klippel (2005)
Squatina tergocellata	L/F	F	138	TL	22925	0.27	3.71	Bridge *et al.* (1998)
		M	103	TL	9195	0.77	3.91	Bridge *et al.* (1998)
Rhinobatos annandalei	L/F	F	91	TL	2169	0.57	3.67	Purushottama *et al.* (2020)
		M	99	TL	2817	0.43	3.62	Purushottama *et al.* (2020)
Rhinobatos rhinobatos	SP	U	150	TL	10404	0.2	3.54	Başusta *et al.* (2008)
Rays								
Amblyraja radiata	SP	F	60	DW	1058	0.10	2.56	McPhie and Campana (2009) & this study
Bathyraja griseocauda	SP	F	270	DW	141648	0.02	3.16	Arkhipkin *et al.* (2008)
		M	266	DW	105479	0.02	3.15	Arkhipkin *et al.* (2008)
Bathyraja scaphiops	SP	F	88	DW	4315	0.06	2.69	Bücker (2006)
		M	59	DW	1239	0.13	2.68	Bücker (2006)
Dasyatis marmorata	L/F	U	46	DW	3713	0.36	2.88	Yeldan and Gundogdu (2018)
Myliobatis californica	SP	F	157	DW	50309	0.10	3.39	Martin and Caillet (1988)
		M	152	DW	45653	0.08	3.27	Martin and Caillet (1988)

a) The growth parameter L_∞ was inferred from the maximum length for this species and *K* via the mean *Ø’* of the genus *Sphyrna*, whose species have very similar shapes.

Acknowledgements

We thank Daniel Pauly for editing our draft and Elaine Chu for Figures 1 and 2.

References

Abdurahiman, K.P., T.H. Nayak, P.U. Zacharia, K.S. Mohamed. 2004. Length-weight relationship of commercially important marine fishes and shellfishes of the southern coast of Karnataka, India. *NAGA, World Fish Centre Quarterly,* 27: 9-14.

Arkhipkin, A.I., N. Baumgartner, P. Brickle, V.V. Laptikhovsky, J.H.W. Pompert, Z.N. Shcherbich. 2008. Biology of the skates *Bathyraja brachyurops* and *B. griseocauda* in waters around the Falkland Islands, Southwest Atlantic. *ICES Journal of Marine Science*, 65: 560–570.

Awruch, C., F. Lo Nostro, G. Somoza, E. Di Giacomo. 2008. Reproductive biology of the angular angel shark *Squatina guggenheim* (Chondrichthyes: Squatinidae) off Patagonia (Argentina, southwestern Atlantic). *Ciencias Marinas*, 34(1): 17–28.

Başusta, N., S. Demirhan, E. Çiçek, A. Başusta and T. Kuleli. 2008. Age and growth of the common guitarfish, *Rhinobatos rhinobatos*, in Iskenderun Bay (north-eastern Mediterranean, Turkey). *Journal of the Marine Biological Association of the UK,* 88(4): 837-842. doi.org/10.1017/S0025315408001124

Bernasconi, J., L. Cubillos, E. Acuña, R. Perier and E. Di Giácomo. 2015. Growth, maturity and mortality of cockfish, *Callorhinchus callorynchus*, in San Matías Gulf, Northern Patagonia, Argentina. *Revista de Biologia Marina Y Oceanografia*, 50(2): 283-298.

Bizzarro, J.J., W.D. Smith, R.E. Hueter and C.J. Villavicencio–Garayzar. 2009. Activities and Catch Composition of Artisanal Elasmobranch Fishing Sites on the Eastern Coast of Baja California Sur, Mexico. *Bulletin Southern California Acadmey of Sciences*, 108(3): 137-151.

Bridge, N.F., D. Mackay and G. Newton. 1998. Biology of the ornate angel shark (*Squatina tergocellata*) from the Great Australian Bight. *Marine and Freshwater Research*, 49: 679-686.

Bücker, A. 2006. Age and growth of skates of the genus *Bathyraja* in Argentina. Master's thesis, University of Bremen, Bremen, Germany. 56 p. Available at: epic.awi.de/id/eprint/30907/

Clarke, S.C., S.J. Harley, S.D. Hoyle and J.S. Rice. 2013. Population Trends in Pacific Oceanic Sharks and the Utility of Regulations on Shark Finning. *Conservation Biology*, 27: 197-209.

Coelho, R. and K. Erzini. 2007. Population parameters of the smooth lantern shark, *Etmopterus pusillus*, in southern Portugal (NE Atlantic). *Fisheries Research*, 86(1): 42-57.

Ehemann, N.R., X.A. Pérez-Palafox, P. Mora-Zamacona, M.I. Burgos-Vázquez, A.F. Navia, P.A. Mejía-Falla and V.H. Cruz-Escalona, 2017. Size-weight relationships of batoids captured by artisanal fishery in the southern Gulf of California, Mexico. *Journal of Applied Ichthyology,* 33: 1051-1054.

Espinosa, D.C. 2011. Population dynamics of the bironche shark, *Rhizoprionodon longurio* (Jordan and Gilbert 1882), in the Gulf of California. PhD thesis, Centro de Investigaciones Biologicas del Noroeste, La Paza, Mexico. 131 p. Available at: cibnor.repositorioinstitucional.mx/jspui/handle/1001/249

Froese, R., 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology,* 22: 241–253.

Froese, R., J. Thorson and R.B. Jr. Reyes. 2014. A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology,* 30(1): 78-85.

Guzman, H.M., R. Cipriani, A.J. Vega and J.M. Morales-Saldaña. 2020. Fisheries and conservation assessment of sharks in Pacific Panama. *Aquatic Conservation Marine and Freshwater Ecosystems,* 30: 315– 330.

Jones, A.A., N.G. Hall and I.C. Potter. 2010. Species compositions of elasmobranchs caught by three different commercial fishing methods off southwestern Australia, and biological data for four abundant bycatch species. Fisheries Bulletin, 108: 365-381.

Jordan, D.S. and C.H. Gilbert. 1882. Synopsis of the fishes of North America. No. 16, US Government Printing Office, Washington, D.C. 1018 p.

Kamura, S., H. Hashimoto and K. Gushima. 2000. The second record, tendency of occurrences and food habit of eiraku shark Hemitriakis japonica (Müller et Henle) in the Seto Inland Sea. Journal of the Faculty of Applied Biological Science, Hiroshima University, 39: 1-7.

Márquez-Farias, J. F., D. Corro-Espinosa and J.L. Castillo-Géniz. 2005. Observations on the Biology of the Pacific Sharpnose Shark (*Rhizoprionodon longurio*, Jordan and Gilbert, 1882), Captured in Southern Sinaloa, México. *Journal of Northwest Atlantic Fishery Science,* 35: 107-114.

Martin, L.K. and G.M. Cailliet. 1988. Age and growth determination of the bat ray, *Myliobatis californica* Gill in central California. *Copeia*, 1988(3): 762–773.

McPhie, R.P. and S.E. Campana. 2009. Bomb dating and age determination of skates (family Rajidae) off the eastern coast of Canada. *ICES Journal of Marine Sciecne*, 66(3): 546-560.

Musick, J.A., G. Burgess, G. Cailliet, M. Camhi and S. Fordham. 2000. Management of Sharks and Their Relatives (Elasmobranchii). *Fisheries,* 25: 9-13.

Najmudeen, T.M., P.U. Zacharia, P.K. Seetha, K.T.S. Sunil, M. Radhakrishnan, S. Akhildev and A. Sipson. 2019. Length–weight relationships of three species of pelagic sharks from southeastern Arabian Sea. *Regional Studies in Marine Science*, 29: 100647.

Navia, A.F., A. Giraldo and P. Mejia-Falla. 2006. Notes on the biology and diet of *Mustelus lunulatus* in the central fishing zone in the Pacific Ocean off Colombia. *Investigaciones Marinas,* 34(2): 217-222.

Olvera, M.A.E. 2006. Determination of age and growth of the Gray Musola Shark (*Mustelus lunulatus*, Jordan and Gilbert 1882) in the northern region of the Gulf of California by means of vertebral rings Bachelor's thesis, University of Guadalajara, Mexico. 45 p. Available at: repositorio.cucba.udg.mx:8080/xmlui/bitstream/handle/123456789/4890/Gonzalez_Alcaraz_Espiridion.pdf?sequence=1

Palomares, M.L.D., W.W.L. Cheung, V.W.Y. Lam and D. Pauly. 2016. The distribution of exploited marine biodiversity, p. 46-58. *In*: D. Pauly and D. Zeller (eds.) *Global Atlas of Marine Fisheries: A critical appraisal of catches and ecosystem impacts*. Island Press, Washington D.C.

Pauly, D. 1984. *Fish Population Dynamics in Tropical Waters: a manual for use with programmable calculators*. ICLARM Studies and Reviews 8. ICLARM, Manila, Philippines. 325 p.

Pauly, D. 1998. Beyond Our Original Horizons: The Tropicalization of Beverton and Holt. *Reviews in Fish Biology and Fisheries,* 8: 307–334.

Pauly, D. 2019. *Gasping Fish and Panting Squids: Oxygen, Temperature, and the Growth of Water-Breathing Animals – 2nd Edition*. Excellence in Ecology (22). International Ecology Institute, Oldendorf/Luhe, Germany. 279 p.

Purushottama, G.B., V. Ramasubramanian, K.V. Akhilesh, S.G. Raje Thakurdas, S.J. Kizhakudan and P.U. Zacharia. 2020. Biological observations on the Bengal guitarfish *Rhinobatos annandalei* Norman, 1926 from the eastern Arabian sea, India. *Indian Journal of Fisheries,* 67(2): 23-34.

Raoult, V., V. Peddemors and J.E. Williamson. 2016. Biology of angel sharks (*Squatina* sp.) and sawsharks (*Pristiophorus* sp.) caught in south-eastern Australian trawl fisheries and the New South Wales shark-meshing (bather-protection) program. *Marine and Freshwater Research,* 68: 207-212.

Santana, F.M. and R. Lessa. 2004. Age determination and growth of the night shark (*Carcharhinus signatus*) off the northeast Brazilian coast. *Fisheries Bulletin,* 102: 156-167.

Smith, S.E., D.W. Au and C. Show. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research,* 49: 663-678.

Stevens, J.D., R. Bonfil, N.K. Dulvy and P.A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57: 476–494.

Tanaka, S., C. Chen and K. Mizue. 1978. Shark Studies-16: Age and Growth of Japanese Tope Sharks. *Nagasaki University Faculty of Fisheries Research Report*, 45: 19-28.

Vooren, C.M. and S. Klippel. 2005. Diretrizes para a conservação de espécies ameaçadas de elasmobrânquios, p. 213-228. In: V.M. Vooren and S. Klippel (eds.) Ações para a conservação de tubarões e raias no sul do Brasil. Igaré, Porto Alegre.

Walker, T.I. and R.J. Hudson. 2005. Sawshark and elephant fish assessment and bycatch evaluation in the southern shark fishery. FRDC Report 1999/103. Primary Industries Research Victoria, Marine and Freshwater Systems, Department of Primary Industries, Queenscliff, Victoria, Australia. 34 p.

Wang, T. and C. Chen. 1982. Age and Growth of Smooth Dogfish, *Mustelus griseus* in Northwestern Taiwan waters. *Journal of the Taiwan Fisheries Society,* 9: 1-12.

Yeldan, H. and S. Gundogdu. 2018. Morphometric relationships and growth of common stingray, *Dasyatis pastinaca* (Linnaeus, 1758) and marbled stingray, *Dasyatis marmorata* (Steindachner, 1892) in the northeastern Levantine Basin. Journal of the Black Sea/ Mediterranean Environment, 24(1): 10-27.

Reply to the Comment on "Masking and unmasking fishing down effects: The Bohai Sea (China) as a case study" [1,2]

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Abstract

This rebuttal to comments by Guan *et al.* (2020; *Ocean & Coastal Management*) points out that the mean trophic levels (here referred to as MTI) of the fishable biomass in the Bohai Sea they present for the 2010s does not contradict earlier demonstrations of the fishing down phenomenon having occurred in that sea. Their alternative estimates of trophic levels correlate strongly with those they suggest were erroneous, and their questioning of 1959 biomass estimates is moot because MTI is determined by the taxonomic composition of the biomass, not its absolute level. In summary, the comment was beside the point.

Introduction

The long-lived, larger fish on top of marine food webs, when exploited by multispecies industrial fisheries, tend to decline faster than the short-lived, smaller fish with lower trophic levels. One result is that the mean trophic level of exploited fish assemblages gradually decline, as does the mean trophic level of catches from an ecosystem exploited in this manner. This phenomenon, now known as 'Fishing Down Marine Food Webs' (Pauly *et al.*, 1998), has been documented through detailed analyses of fisheries catch data from a wide range of ecosystems all over the world (Santos and Vianna 2020; see also www.fishingdown.org).

The article by Liang and Pauly (2020) that Guan *et al.* (2020) commented on is part of a series of articles demonstrating – against specious claims to the contrary – that the 'fishing down' phenomenon can indeed be shown to occur in the waters around all continents (Table 1), even if limiting oneself to a subset of articles published from 2012 on, and with neither of us as coauthors. However, the fishing down phenomenon is frequently masked by various effects that have now been identified (Liang and Pauly 2017, 2020). Thus, for Chinese waters, initial demonstrations of the occurrence of fishing down (Pang and Pauly 2001; Du *et al.* 2014) were confirmed by Liang and Pauly (2017), who also quantified some of the masking factors that have prevented previous authors from appreciating the ubiquity and intensity of this phenomenon.

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[1] Cite as: Liang, C. and D. Pauly. 2022. Reply to the Comment on "Masking and unmasking fishing down effects: The Bohai Sea (China) as a case study", p. 52-57. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

[2] This contribution was intended for *Ocean & Coastal Management*; however, its editor-in-chief, who shared with us the still unpublished comments on our paper, also shared our intended response to the authors of these comments, these authors then quickly corrected their comments (then 'in press') by removing their most unfounded claims. We could not respond to the unprofessional behaviour of the editor, because he then passed away. Thus, we decided to include our response in this report.

Table 1. Some of the case studies published since 2012, demonstrating the occurrence of the 'fishing down' phenomenon in Africa, Asia, Europe, Oceania, North America and South America; $\Delta\text{TL}\cdot\text{decade}^{-1}$ refers to rate of decline of the mean trophic of the catch (MTI$_c$) as assessed (sometimes approximately) from the cited figure.

Location	**Years**	**ΔTL decade^{-1}**	**Sources**
Mauritania	1990 – 2010	0.04	Meissa and Gascuel (2014, Fig. 5a)
Senegal	1990 – 2009	0.05	Ndour *et al.* (2014, Fig. 3)
Guinea	1985 – 2012	0.03	Camara *et al.* (2016, Fig. 7c)
China	1950 – 2011	0.03	Du *et al.* (2014, Fig. 1)
Oman	1995 – 2010	0.08	Abd El-Barr & El-Rahman (2014, Fig. 2)
Thailand	1988 – 2007	0.10	Juntaropakorn & Yakupitiyage (2014, Fig. 6)
Western Europe	1950 – 2010	0.01-0.05	Gascuel *et al.* (2016, Fig. 7c)
English Channel	1920 – 2010	0.10	Molfese *et al.* (2014, Fig. 2B)
Sweden	1926 – 2010	0.05	Hornborg *et al.* (2013, Fig. 1b)
Southern Australia	1936 – 2010	0.10	Alleway *et al.* (2014, Fig. 4)
California, U.S.	2003 – 2011	0.025	Tolimieri *et al.* (2013, Fig. 2)
South. Calif., U.S.	1972 – 2010	0.05	Miller and McGowan (2013, Fig. 4b)
Argentina/Uruguay	1989 – 2010	0.07	Andrés and Jaureguizar(2013, Fig. 2)
Colombia (Pacific)	1995 – 2007	0.10	Navia and Mejía-Falla (2016, Fig. 2)
Southern Brazil	2000 - 2012	0.20	Bornatowski *et al.* (2017, Fig. 4a, b)

The empirical part of the Guan *et al.* (2020) comment on (and critique of) of Liang and Pauly (2020) is summarized in their (and our) Figure 1, more specifically by the mean trophic levels (MTI$_b$) of the fishable biomass in the Bohai from 2010 on. (Here MTI$_b$ refers to the mean trophic level of the fishable biomass, in contrast to MTI$_c$, the mean trophic level of the catch).

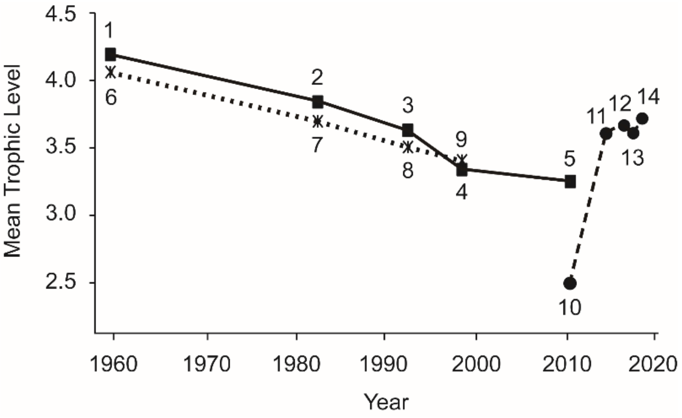

Figure 1 Mean trophic level of the fishable biomass in the Bohai Sea estimated by Liang and Pauly (2020; points 1-5), Zhang *et al.* (2007; points 6-9) and Guan *et al.* (2020; points 10-14). Note that points 10-14 are summer-only estimates, while points 1-9 are seasonaly averaged, annual estimates.

Before dealing with MTI$_b$ values from the 2010s, we note that the MTI$_b$ estimates proposed by Zhang *et al.* (2007) and by Liang and Pauly (2020) are nearly parallel over a period of 40 years and that the Liang/Pauly estimate of MTI$_b$ for 2010 is precisely where the extrapolation of the Zhang *et al.* (2007) trends would point (Figure 1). Thus, the MTI$_b$ trends of the fishable biomass of the Bohai Sea in both Zhang *et al.* (2007) and Liang and Pauly (2020) are essentially the same, and the small differences in absolute MTI$_b$ are the results of small differences in the trophic level estimates used in the two studies (Figure 2).

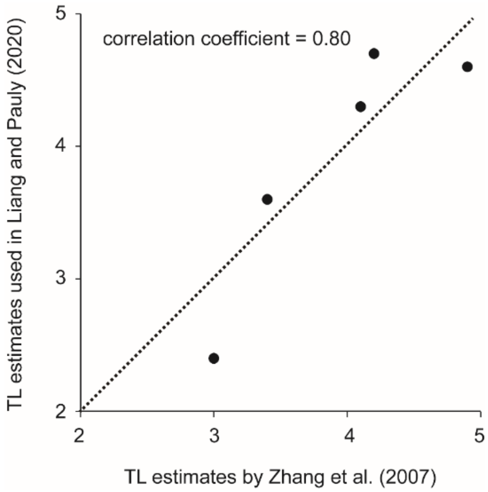

Figure 2 Comparision of trophic level estimates used by Liang and Pauly (2020) and Zhang *et al.* (2007).

Thus, the quasi-parallel MTI_b trend lines in Figure 1, which confirm that fishing down has occurred in the Bohai Sea, also makes moot their arguments for the biomass estimates from surveys performed in 1959 being erroneous. As is mentioned in Jin (2004), the research vessel and trawl used in 1959 were smaller than those used in the later years, while the cod-end mesh size used in all cruises were reported as the same, i.e., 2 cm (Jin *et al.* 2013). Thus, the biomass data in 1959 used by Liang and Pauly (2020), if no adjustment was made for area swept by the trawl net, would have underestimated its true level, while the taxonomic composition of fishable biomass in 1959 was comparable with other years. The biomass values derived by different gears in 1959 and other years did not affect our results, as MTI_b estimates are based on the taxonomic composition of the trawl hauls (from Tang *et al.* 2003). In fact, given that the survey data was scarce in early years, the fishable biomass and composition data in 1959 has been commonly used as a baseline in comparing the decadal variations of fish community structure in the Bohai Sea, notably by the very authors who criticized its use in Liang and Pauly (2020) (Zhang 2007; Jin 2004; Tang *et al.* 2003).

As for the points 10 to 14 in Figure 1, contributed by Guan *et al.* (2020), we certainly accept that variations of MTI_b could be due to extreme fluctuations of the abundance of a few small, short-lived species (including exploited zooplankton species such as *Acetes*). Indeed, this is precisely what we should expect in ecosystem with an extremely depleted biomass, and which has lost the top-down control normally exerted by large, high-trophic level, long-lived fish (Worm and Myers 2003; Cury *et al.* 2003). However, we do not agree that the high biomass of *Clupanodon punctatus* in 1998 and 2010 was the only reason that fishing down effect occurring after 1992. Based on the data provided by Guan *et al.* (2020), the current dominance of short-lived, low-trophic level species and the absence of high-trophic level species compared with 1990s (Table 1 in Liang and Pauly 2020; Table 2 in Guan *et al.* 2020), would also support the occurrence of a current fishing-down effect in the Bohai Sea.

Moreover, the decline in MTI_b from 1960 to 2010, i.e., over 5 decades, must be considered as a demonstration of the fishing down phenomenon occurring in the Bohai Sea even if we take at face value the exceptionally high estimate of Guan *et al.* (2020) for 2014-2018, who only used summer survey data for their MTI_b estimates. Their mean value is about 3.6, which is less than the value of $MTI_b \approx 4.2$ in 1959. Indeed, this would correspond to a decline of about 0.12 TL per decade, which is a high value when compared with declines in other parts of the world (Table 1), and also higher than MTI_c.

In the article by Liang and Pauly (2020), the catch composition data was obtained from successive *China Fishery Statistical Yearbooks* (Fisheries Administration of the Ministry of Agriculture 1979-2016). In these yearbooks, the catch data of each coastal province or municipality were reported by species or taxa, and the proportion of total catch in China's coastal fishing areas (the Bohai Sea, Yellow Sea, East China Sea, and South China Sea) were also available.

Thus, in our case, we assigned to the Bohai Sea the fractions of the reported catches of the 4 provinces or cities (Shandong, Hebei, Tianjin and Liaoning) that were reported to be caught in the Bohai Sea in successive *China Fishery Statistical Yearbooks*, while removing species that were not supposed to occur in the Bohai Sea. We thus created a series of catch and catch composition data which could be used to derive a series of estimated MTI_c. Meanwhile, for taxa that contain more than one species, we used the trophic level of the dominant species or the mean trophic level of main species for calculation. We think that the catch time series for the Bohai Sea represent a reasonable representation of the catches likely to have been taken there. Note that here again, it is not their absolute value in terms of tonnage which matters here; rather it is the taxonomic composition of that catch, and the trophic levels assigned to each taxon.

With the depletion of fishery resources in the Bohai Sea, fishermen will tend to retain all catches they get. This, indeed, should make the true MTI_c close to MTI_b. However, the catch data that we assembled failed to demonstrate this. This suggests a type of selection beyond the 'skipper effect': the available statistical data are more detailed for high-trophic level, high commercial value species, which thus makes the computed MTI_c diverge from MTI_b. This 'statistical selection' effect would also contribute to masking 'fishing down' when catches are available, but no biomass composition data.

Guan *et al.* (2020) suggest in their comment that Liang and Pauly (2020) have not demonstrated the fishing down to occur in the Bohai Sea based on the survey data used (1959, 1982, 1992, 1998, 2010). On the other hand, they concede a fishing down phenomenon in this area, because "it has been well proved by previous studies (Jin 2004; Zhang *et al.* 2007, 2015)", although these previous studies used the same community structure data sets that we did for 1959, 1982, 1992 and 1998.

Guan *et al.* (2020) missed a real problem with the Liang/Pauly contribution, i.e., how the small biomass reported from the mid-1990s on can support the huge large catch that we assigned to the Bohai Sea for the same period (C. Walters, Institute for the Oceans and Fisheries, University of British Columbia, pers. comm.).

The answer to this question is that the fisheries of the Bohai Sea, and by extension the fisheries along the Chinese Coast, largely catch juveniles (Zhai and Pauly 2019; Zhang *et al.* 2020), with only a few adults surviving to provide the egg production that maintains the system.

While these considerations cannot be followed upon here, we note that a transition to a fishery based predominantly on juvenile fish will increase the rate of MTI decline, because the juveniles of carnivorous fishes have lower trophic levels than the adults (Pauly *et al.* 2001; see also www.fishbase.org), and the trophic levels we used, while from a good source (Yang 2001), pertained only to the adults.

Acknowledgement

We thank Professor Carl Walters, Institute for the Oceans and Fisheries, University of British Columbia, for helpful comments on the key elements of this contribution, and Ms. Elaine Chu for assembling sources for Table 1. We also thank Lisha Guan and colleagues for helping us, if inadvertently, discover yet another effect that can cause 'fishing down' to be masked.

References

Abd El-Rahman, M.A. 2014. A bio-economic study of the trophic structure of the Omani fish catch. *Trop. Life Sci. Res.* 25: 29–40.

Alleway, H., S. Connell, T. Ward and B. Gillanders. 2014. Historical changes in mean trophic level of Southern Australian fisheries. *Mar. Freshwater Res.* 65: 884–893. doi:10.1071/MF13246.

Andrés, M.C. and A.J. Jaureguizar. 2013. Evolución temporal del nivel trófico medio de los desembarques en la zona común de pesca Argentino-Uruguaya años 1989–2010. *Frente Maritimo* 23: 83–93.

Bornatowski, H., R. Angelini, M. Coll, R.R. Barreto and A.F. Amorim. 2018. Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. *Rev. Fish Biol. Fish.* 28(1): 241–259.

Camara, M., B. Mérigot, F. Leprieur, J. Tomasini, I. Diallo, M. Diallo and D. Jouffre. 2016. Structure and dynamics of demersal fish assemblages over three decades (1985–2012) of increasing fishing pressure in guinea. *African J. Mar. Sci.* 38: 189–206.

Cury, P., L. Shannon, Y.J. Shin. 2003. The functioning of marine ecosystems: a fisheries perspective. In: M. Sinclair and G. Valdimarsson (eds.). *Responsible fisheries in the marine ecosystem.* FAO and CABI Publishing, Wallingford, UK.

Du, J., G. Ye, B. Chen and X. Zheng. 2014. Changes in the marine trophic index of Chinese marine area. *Biodiversity Sci.* 22(4), 532–538 [in Chinese with English abstract].

Fisheries Administration of the Ministry of Agriculture, 1979–2016. *China Fishery Statistical Yearbook.* Beijing: Agricultural Press of China, Beijing [in Chinese].

Gascuel, D., M. Coll, C. Fox, S. Guénette, J. Guitton, A. Kenny, L. Knittweis, J.R. Nielsen, G. Piet, T. Raid, M. Travers-Trolet, M. and S. Shephard. 2016. Fishing impact and environmental status in European seas: A diagnosis from stock assessments and ecosystem indicators. *Fish Fish.* 17, 31–55. doi:10.1111/faf.12090.

Guan, L., X. Shan and X. Jin. 2020. Comment on "Masking and unmasking fishing down effects: The Bohai Sea (China) as a case study. *Ocean Coast. Manag.* 196, p.105282.
https://doi.org/10.1016/j.ocecoaman.2019.105033

Hornborg, S., A. Belgrano, V. Bartolino, D. Valentinsson, D and F. Ziegler. 2013. Trophic indicators in fisheries: A call for re-evaluation. Biol. Lett. 9(1): 1050.

Jin, X. 2004. Long-term changes in fish community structure in the Bohai Sea, China. *Estuarine, Coastal Shelf Sci.* 59: 163–171.

Jin, X., X. Shan, X. Li, X., J. Wang, Y. Cui and T. Zuo. 2013. Long-term changes in the fishery ecosystem structure of Laizhou Bay, China. Sci. *China Earth Sci.* 56(3): 366–374.

Juntaropakorn, M. and A. Yakupitiyage. 2014. Phenomenon on fishing down marine food web in east coast gulf of Thailand. Asia Pac. *J. Sustainable Agric. Food Energy* 2: 1—6.

Liang, C. and D. Pauly. 2017. Fisheries impacts on China's coastal ecosystems: Unmasking a pervasive 'fishing down' effect. *PLoS ONE* 12(3), e0173296. https://doi:10.1371/journal.pone.0173296 .

Liang, C. and D. Pauly. 2020. Masking and unmasking fishing down effects: The Bohai Sea (China) as a case study. *Ocean Coast. Manag.* 184, 105033.

Meissa, B. and D. Gascuel. 2015. Overfishing of marine resources: Some lessons from the assessment of demersal stocks off Mauritania. *ICES Journal of Marine Science* 72 : 414—427. doi:10.1093/icesjms/fsu144.

Miller, E.F. and J.A. McGowan. 2013. Faunal shift in southern California's coastal fishes: A new assemblage and trophic structure takes hold. *Estuarine, Coastal Shelf Sci.* 127: 29–36. https://doi:10.1016/j.ecss.2013.04.014 .

Molfese, C., D. Beare and J. Hall-Spencer. 2014. Overfishing and the replacement of demersal finfish by shellfish: An example from the English Channel. *PLoS ONE* 9(7), e101506. https://doi:10.1371/journal.pone.0101506

Navia, A.F. and P.A. Mejía-Falla. 2016. Fishing effects on elasmobranchs from the Pacific Coast of Colombia. *Universitas Scientiarum* 21(1): 9–22.

Ndour, I., F. Le Loc'h, J. Kantoussan, M. Thiaw, H. Diadhiou, J. Ecoutin, L. Tito de Morais, and O. Thiaw. 2014. Changes in the trophic structure, abundance and species diversity of exploited fish assemblages in the artisanal fisheries of the northern coast, Senegal, West Africa. *African Journal of Marine Science* 36: 361–368. doi:10.2989/1814232X.2014.950696.

Pang, L. and D. Pauly. 2001. Part 1 - Chinese marine capture fisheries from 1950 to the late 1990s: the hopes, the plans and the data. *In:* R. Watson, L. Pang and D. Pauly (eds.). *The marine fisheries of China: development and reported catches*. Fisheries Centre Research Report 9(2).

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, F. Torres. 1998. Fishing down marine food webs. *Science 279*, 860–863.

Pauly, D., M.L. Palomares, R. Froese, P. Sa-a, M. Vakily, D. Preikshot and S. Wallace. 2001. Fishing down Canadian aquatic food webs. *Canadian Journal of Fisheries and Aquatic Sciences 58(1), 51–62.*

Santos, S. and M. Vianna. 2020. A preliminary review of the reception of 'Fishing Down Marine Food Webs'. p. 35–50 *In:* D. Pauly and V. Ruiz-Leotaud (eds.). *Marine and Freshwater Miscellanea II*. Fisheries Centre Research Reports 28(2).

Tang, Q., X. Jin, J. Wang, Z. Zhuang, Y. Cui and T. Meng. 2003. Decadal-scale variations of ecosystem productivity and control mechanisms in the Bohai Sea. *Fisheries. Oceanography* 12 (4/5), 223–233.

Tolimieri, N., J.F. Samhouri, V. Simon, B.E. Feist and P.S. Levin. 2013. Linking the trophic fingerprint of groundfishes to ecosystem structure and function in the California current. *Ecosystems* 16, 1216–1229. doi:10.1007/s10021-013-9680-1.

Worm, B. and R.A. Myers. 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84(1),162–173.

Yang, J. 2001. A study on food and trophic levels of Bohai Sea fish. *Modern Fish. Infor.* 16(10), 10–19 [in Chinese].

Zhai, L. and D. Pauly. 2019. Yield-per-recruit, utility-per-recruit, and relative biomass of 21 exploited fish species in China's coastal seas. *Froniers of Marine Science* 6: 724, doi:10.3389/fmars.2019.00724.

Zhang, B., Q. Tang and X. Jin. 2007. Decadal-scale variations of trophic levels at high trophic levels in the Yellow Sea and the Bohai Sea ecosystem. *Journal of Marine Systems* 67(3–4): 304–311.

Zhang, B., Q. Wu and X. Jin. 2015. Interannual Variation in the food web of commercially harvested species in Laizhou Bay from 1959 to 2011. *J. Fish. Sci. China* 22(2): 278–287.

Zhang, W., M. Liu, Y. Sadovy de Mitcheson, L. Cao, D. Leadbitter, R. Newton, D.C. Little, S. Li, Y. Yang, X. Chen and W. Zhou. 2020. Fishing for feed in China: Facts, impacts and implications. *Fish Fish.* 21(1): 47–62

Key information on 25 species of sturgeon; Family Acipenseridae[1]

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Abstract

Key information was compiled from the literature on the 25 species of sturgeons; i.e., of members of the Family Acipenseridae (genera *Acipenser*, *Huso, Pseudoscaphirhynchus* and *Scaphirhynchus*), of which the Yangtze sturgeon (*Acipenser dabryanus*) was declared extinct in July 2022 by the IUCN, and another, the Syr Darya sturgeon (*Pseudoscaphirhynchus fedtschenkoi*), is likely extinct. This included maximum length; mean length at first maturity, growth parameters and maximum ages (by sex when available, but mostly missing for Syr Darya sturgeon), main countries of occurrence, status and key references, including the original species descriptions. These variables yielded interesting relationships when plotted against each other.

Introduction

The fishes of the Family Acipenseridae, the sturgeon, belonging to the genera *Acipenser* (17 species), *Huso,* (2 spp.), *Pseudoscaphirhynchus* (2 spp.) and *Scaphirhynchus* (3 spp.), occurring in Eurasia and North America, have been used by people for thousands of years for their flesh and more recently for their eggs, i.e., for 'caviar.'

The large size and slow lifestyle of most sturgeon coupled with the high value of caviar make them very susceptible to overfishing, while the diadromous habits of most species endanger them in rivers that are dammed, or polluted. Thus, of their species, the Yangtze sturgeon (*Acipenser dabryanus*) was declared extinct on July 21, 2022 (en.wikipedia.org/wiki/Dabry's_sturgeon), while another species the Syr Darya sturgeon (*Pseudoscaphirhynchus fedtschenkoi*) is likely extinct. In fact, the latter, has apparently never been studied in terms of its life-history, as is evident from reviewing the sturgeon literature of Imperial Russia (see Pauly and Pauly 2022, this vol.), translations of the ichthyological literature of the ex-Soviet Union (e.g., Berg 1962; Nikolsky 1961; Suworow 1959), and recent sources (en.wikipedia.org/wiki/Syr_Darya_sturgeon).

Here, we present, as a complement to Pikitch *et al.* (2005), key biological traits of the 24 species of sturgeons (for which such data exist) mainly to facilitate subsequent studies on these fishes.

Material and Methods

For each member of the Family Acipenseridae in FishBase (www.fishbase.org), the following was sought (by sex if available):

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[1] Cite as: Chu, E. and D. Pauly. 2022. Key information on 25 species of sturgeon; Family Acipenseridae, p. 57-68. *In:* Pauly, D and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

- Maximum reported length (total length, or TL, as provided by the original authors, or derived from the ratio of the original length to total length, obtained from anatomically correct drawings; cm);
- Mean length at first maturity (L_m; in cm TL);
- Mean age (or range) at first maturity (t_m; years), maximum reported age (in years);
- The 3 parameters of the von Bertalanffy growth function (VBGF), i.e., L_{inf} (TL; cm), K ($year^{-1}$) and t_o (year), and
- The 2 parameters of length-weight relationships (a, b) of the form $W = a \cdot L^b$, with weight in g and total length in cm.

References are provided, included the reference of the original description of each species.

We plotted K vs T_{max} to test the relationship $T_{max} \approx 3/K$, with T_{max} being the longevity (i.e., the maximum age reported from the wild and K a parameter of the von Bertanlanffy growth equation, as proposed by Taylor (1958).

Also, the data that we gathered were used to test for sturgeons the hypothesis of Pauly (1984, 2022) that the length at first maturity of teleosts can be predicted from the maximum length they can reach (L_{max}). This hypothesis relies on the fact that the the ratio $L_{max}{}^D/L_m{}^D$ is mathematically equivalent to Q_m/Q_{maint}, i.e., the ratio of the metabolic rate of an individual fish at first maturity to its metabolic rate at its maximum length, at which it doesn't grow and only maintains itself.

The exponent D is defined by $D = 3(1\text{-}d)$, with d being the exponent of relationship linking the respiratory surface are of gills (S) and body weight (W) such that $S \propto W^d$, with d ranging between 0.6 and 0.9 in fishes (Pauly and Cheung 2017), and around 0.80 in sturgeon in Winberg (1960, p. 86), who included 5 sturgeon species in his review.

Pauly (1984, 2022) suggested that, as individual fish grow, they ogygen suppy per unit weigth declines (because $d < 1$), and hence their ratio Q/Q_{maint} also declines. When a critical ratio, i.e., Q_m/Q_{maint}, corresponding to $L_{max}{}^D/L_m{}^D$ is reached, a trigger is set for the fish to consider - previously ignored - environmental and social clues for spawning (Pauly 2022).

Also, we tested, for $D = 0.6$ whether the ratio $L_{max}{}^D/L_m{}^D$ was near 1.35 (95% confidence intervals 1.22-1.52) as estimated for other teleosts (Pauly 2022). The value of $D = 0.6$ implies that the gill surface area and the oxygen consumption of sturgeon are proportional to their weight raised to a power $d = 0.8$, and $D = 3(1\text{-}d)$.

Results and Discussion

Table 1 presents the traits that were compiled, which are complete except for one species, the Syr Darya sturgeon (*Pseudoscaphirhynchus fedtschenkoi*), which is probably extinct, and for which - despite a thourough scanning of the literature, including in Russian - no information on age, growth and reproduction was found.

The results of the first hypothesis to be tested (i.e., that $T_{max} \approx 3/K$) are shown on Figure 1, which shows two regression lines, a standard one (dotted), with $3/K = 7.59 + 0.75 \cdot T_{max}$, the other forced through a zero intercept (solid), with $3/K = 0.84 \cdot T_{max}$. As identifying the 'best' of these two regressions is not obvious, we suggest using the mean of their two slopes, which leads to $T_{max} / 2.4 \approx K$, as an empirical model to predict K ($year^{-1}$) from longevity (years) in sturgeons and possibly in related and/or similar fishes.

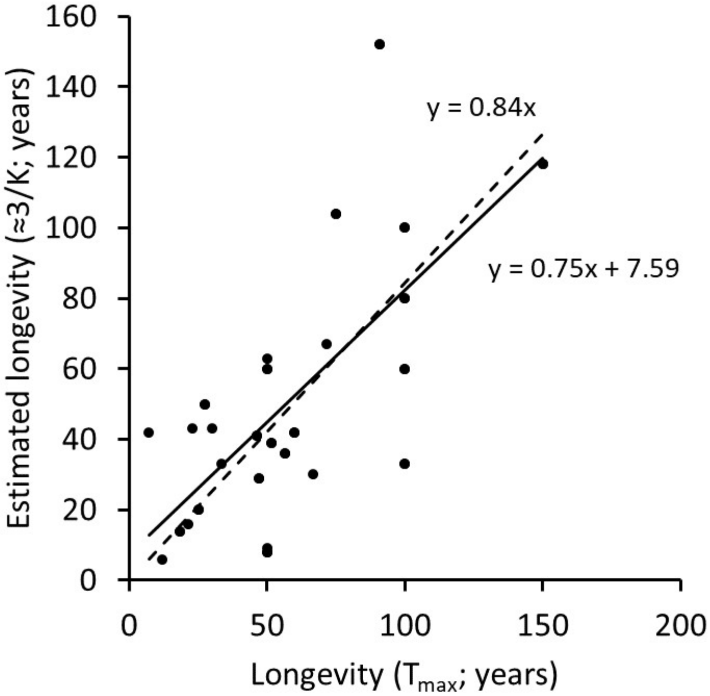

Figure 1. Plot of estimated longevity obtained by 3/K, where K is a parameter of the von Bertalanffy growth equation vs. observed longevity (T_{max}), both from Table 1 (n = 44). The values of r^2 are 0.48 for the regression with a zero intercept (dotted line) and 0.83 for that with a non-zero intercept.

Figure 2 shows a plot of L_{max}^D vs. L_m^D for values of D = 0.6 for linear regressions with and intercept assumed to be zero. As might be seen, the slope is 1.35, i.e., the very value that has been estimated for other teleosts (Pauly 2022). Note however, that the data in Table 1 for beluga (*Huso huso*) were not used, as they produced an outlier, which, because of the huge size of beluga, also had an undue 'lever' effect on the plot in Figure 2.

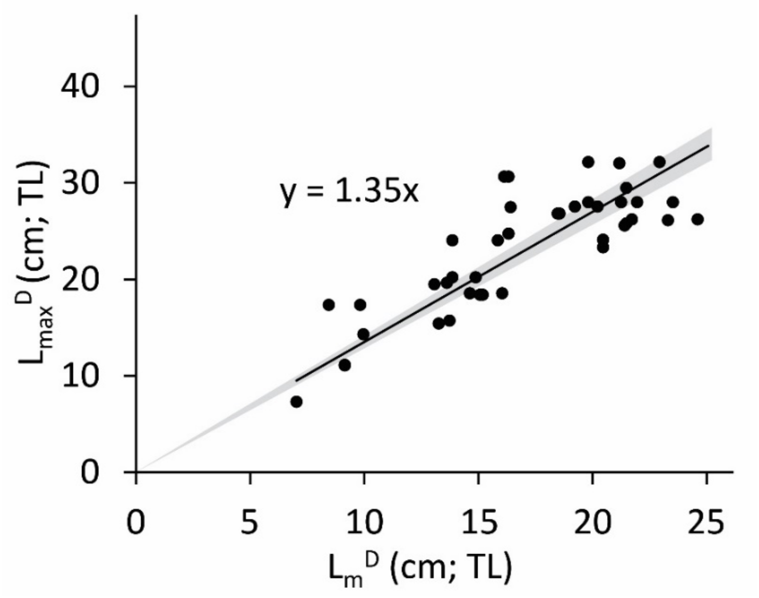

Figure 2. Plot of the maximum length of sturgeons of various species vs. their mean length at first maturity (from Table 1, but excluding *H. huso*, see text) raised to a power D = 0.6, with n = 41, r^2 = 0.977 (and a 95% confidence interval in grey).

This is consistent with the hypothesis that the size at first reproduction of sturgeons is determined by the interaction of their growth and respiration, as suggested for fish in general by Pauly (1984), and as subsequently demonstrated in a large number of teleost species (Pauly 2022).

The plot illustrating the positive correlation between spawning periodicity and age at first maturity in the females in 16 species of sturgeon in Pikitch *et al*. (2005, their Figure 3) can also be considered evidence for this hypothesis, as the slow growth of sturgeons (as expressed by the low values of their growth parameter K) implies that after spawning (which reduces their weight and thus their respiratory requirements), several years of growth are needed for them to get back in the weight-induced respiratory stess that triggers (re-)maturation and spawning (Pauly and Liang 2022a, 2022b).

Table 1. Key traits of 25 species of sturgeon (Family Acipenseridae); note that the Yangtze sturgeon is extinct and the Syr Darya sturgeon likely extinct, with the latter lacking all traits except for maximum length.

Common name	**Species**	**Location**	L_{inf}	**K**	t_o	L_m	L_{max}	**Sex**	***a***	***b***	t_m	t_{max}	**References**
Siberian sturgeon	*Acipenser baerii*	Indigirka	149	0.06	-2.59	72.5	141	Female	0.0015	3.26	11.75	63	Ruban and Akimova 1991; Ruban 2005; Pordlesnyi 1958
Shortnose sturgeon	*Acipenser brevirostrum*	St John River; Canada	144	0.042	-1.96	77.7	143	Female	0.0035	3.21	17.2	67	Dadswell 1979
Yangtze sturgeon	*Acipenser dabryanus*	Yangtze River	250	0.06	-2.14	87.5	130	Male	0.0028	3.29	4 to 7	8	Changjiang Aquatic Resources Survey Group, Sichuan Province 1988
Yangtze sturgeon	*Acipenser dabryanus*	Yangtze River	250	0.06	-2.14	102	130	Female	0.0028	3.29	6 to 8	8	Changjiang Aquatic Resources Survey Group, Sichuan Province 1988
Yangtze sturgeon	*Acipenser dabryanus*	Yangtze River	263	0.06		106	250	Female	0.0028	3.29	8 to 10	9	Froese 2022; Chen 2007
Lake sturgeon	*Acipenser fulvescens*	Nottaway River	156	0.033	-5.59	80	150	Female	0.0049	2.99	20	152	Magnin 1966; Anderson 1954; Magnin 1964; Pauly 1978
Lake sturgeon	*Acipenser fulvescens*	Nottaway River	156	0.033	-5.59	90	150	Male	0.0049	2.99	18	152	Magnin 1966; Anderson 1954; Magnin 1964; Pauly 1978
Danube sturgeon	*Acipenser gueldenstaedtii*	Black sea and azov sea	253	0.045	-3.5	105	210	Unsex	0.0039	3.06	9 to 10	30	Fischer *et al*. 1987; Lagutov and Lagutov 2008; Ambroz 1964; Pauly 1978
Green sturgeon	*Acipenser medirostris*	Rouge River Oregon	238	0.05	-2	166	225	Female	0.033	2.72	17	42	Erickson and Webb 2007; Adams *et al* 2002; Nakamoto 1995; Van eenennaam *et al* 2006; Adair *et al*. 1982
Green sturgeon	*Acipenser medirostris*	Rouge River Oregon	238	0.05	-2	153	201	Male	0.004	3.11	15	42	Erickson and Webb 2007; Adams *et al* 2002; Nakamoto 1995; Van eenennaam *et al* 2006; Adair *et al*. 1982
Sakhalin sturgeon	*Acipenser mikadoi*	Tumnin River and Datta Bay	197	0.42	--	153[a]	190	Unsex	0.0045	3.16	8 to 10	42[b]	Koshelev *et al* 2012; Mugue 2010a; Nakamoto 1995; Koshelev and Kolpalov 2020
Adriatic sturgeon	*Acipenser naccarii*	Adriatic Sea	200	0.11	-1.3	80	200	Male	0.0014	3.29	7	50	Arlati 1996; Fischer *et al* 1987; Kottelat and Freyhof 2007; Congiu *et al* 2011; Garcia-Gallego *et al* 2009
Adriatic sturgeon	*Acipenser naccarii*	Adriatic Sea	200	0.11	-1.3	100	200	Female	0.0014	3.29	10	50	Arlati 1996; Fischer *et al* 1987; Kottelat and Freyhof 2007; Congiu *et al* 2011; Garcia-Gallego *et al* 2009
Fringebarbel sturgeon	*Acipenser nudiventris*	Caspian Sea	276	0.053	-3.36	163	258	Female	0.0068	2.97	17	36	Fazli *et al*. 2020a; Mousavi and Ghafor 2014; CITES 2000
Fringebarbel sturgeon	*Acipenser nudiventris*	Caspian Sea	276	0.053	-3.36	145	258	Male	0.0068	2.97	13	36	Fazli *et al*. 2020a; Mousavi and Ghafor 2014; CITES 2000
Atlantic sturgeon	*Acipenser oxyrinchus*	St. Lawrence River	315	0.03	--	165	222	Male	0.0017	3.18	22 to 24	60	Scott and Crossman 1973; Caron *et al* 2002; Magnin 1964; Carlander 1969; Stevenson and Secor 1999
Atlantic sturgeon	*Acipenser oxyrinchus*	St. Lawrence River	315	0.03	--	190	230	Female	0.0017	3.18	27 to 28	60	Scott and Crossman 1973; Caron *et al* 2002; Magnin 1964; Carlander 1969; Stevenson and Secor 1999

Persian sturgeon	*Acipenser persicus*	Caspian Sea	244	0.058	-3.4	150	251	Female	0.0052	3.02	12 to 18	39	Fazli *et al* 2020b; Kottelat and Freyhof 2007; Bakhshalizadeh *et al*. 2011
Persian sturgeon	*Acipenser persicus*	Caspian Sea	244	0.058	-3.4	138	251	Male	0.0052	3.02	8 to 15	39	Fazli *et al* 2020b; Kottelat and Freyhof 2007; Bakhshalizadeh *et al*. 2011
Sterlet sturgeon	*Acipenser ruthenus*	Eastern Europe	88.2	0.12	-1.37	35	116	Male	0.0004	3.613	4 to 5	20	Muus and Dahlstrom 1968; Podlesnyi 1958
Sterlet sturgeon	*Acipenser ruthenus*	Eastern Europe	88.2	0.12	-1.37	45	116	Female	0.0004	3.613	5 to 9	20	Muus and Dahlstrom 1968; Podlesnyi 1958
Amur sturgeon	*Acipenser schrenckii*	Amur River	205	0.06	-0.92	103	300	Male	0.0028	3.17	7 to 8	60	Chen 2007; Krykhtin 1997; Chugunov and Chugunova 1964
Amur sturgeon	*Acipenser schrenckii*	Amur River	205	0.06	-0.92	105	300	Female	0.0028	3.17	9 to 10	60	Chen 2007; Krykhtin 1997; Chugunov and Chugunova 1964
Chinese sturgeon	*Acipenser sinenesis*	Yangtze river	350	0.03	-9.14	193	258	Female	0.01	2.97	17.84	33	Luo *et al* 2020; Deng *et al* 1991
Chinese sturgeon	*Acipenser sinenesis*	Yangtze river	350	0.03	-9.14	172	258	Male	0.02	2.91	14.96	33	Luo *et al* 2020; Deng *et al* 1991
Chinese sturgeon	*Acipenser sinenesis*	Yangtze River	363	0.09	--	--	346	Female	--	--	14 to 26	33	Froese 2022; Deng *et al* 1991
Starry sturgeon	*Acipenser stellatus*	Southern Caspian Sea	250	0.0064	-3.2	130	240	Female	0.0024	3.05	8.5	29	Fazli *et al* 2020c
Starry sturgeon	*Acipenser stellatus*	Southern Caspian Sea	250	0.0064	-3.2	129	240	Male	0.0024	3.05	8.5	29	Fazli *et al* 2020c
Sturgeon	*Acipenser sturio*	Atlantic coast of France	500	0.03	-2.8	145	325	Male	0.0095	2.89	13 to 15	100	Williot *et al* 2011; Letaconnoux 1961; Muus and Dahlstrom 1968; Castlenaud *et al* 1991; Froese and Binohlan 2003
Sturgeon	*Acipenser sturio*	Atlantic coast of France	500	0.03	-2.8	185	325	Female	0.0095	2.89	19 to 22	100	Williot *et al* 2011; Letaconnoux 1961; Muus and Dahlstrom 1968; Castlenaud *et al* 1991; Froese and Binohlan 2003
White sturgeon	*Acipenser transmontanus*	Fraser River, BC	350	0.04	--	169	231	Male	0.05	3.13	11 to 22	104	Semakula and Larkin 1968; Rien 1994; Brennan *et al* 1991
White sturgeon	*Acipenser transmontanus*	Fraser River, BC	350	0.04	--	208	231	Female	0.05	3.15	11 to 34	104	Semakula and Larkin 1968; Rien 1994; Brennan *et al* 1991
Kaluga	*Huso dauricus*	Amur estuary	478	0.03	-1.42	162	323	Male	0.0029	3.20	18	80	Koshelev and Ruban 2012; Mikodina *et al* 2015; Sytova *et al* 2004; Chugunov and Chugunova 1964
Kaluga	*Huso dauricus*	Amur estuary	478	0.03	-1.42	166	281	Female	0.0029	3.20	21	80	Koshelev and Ruban 2012; Mikodina *et al* 2015; Sytova *et al* 2004; Chugunov and Chugunova 1964
Beluga	*Huso huso*	Caspian; Black; Azov and Adriatic Seas	502	0.02	--	200	600	Female	0.07	3	13 to 22	118	Rochard *et al* 1991; Birstein 1993; Beverton 1987; Raischi *et al* 2020; Babushkin 1964
Beluga	*Huso huso*	Caspian; Black; Azov and Adriatic Seas	435	0.02	--	180	600	Male	0.07	3	10 to 16	118	Rochard *et al* 1991; Birstein 1993; Beverton 1987; Raischi *et al* 2020; Babushkin 1964

Syr Darya sturgeon	*Pseudoscaphirhynchus fedtschenkoi*	Syr Darya River	--	--	--	--	64	Unsex	--	--	--	--	Likely extinct; Rochard *et al* 1991
Dwarf sturgeon	*Pseudoscaphirhynchus hermanni*	Amu Darya River	31.9	0.25	-1.97	25.8	27.5	Female	0.0046	2.81	4 to 5	6	Salnikov 2003; Salnikov 1996; Ministry of Nature Protection of Turkmenistan 1999
Amu Darya sturgeon	*Pseudoscaphirhynchus kaufmanni*	Amu Darya River	65.4	0.164	-0.95	40	55.5	Male	0.002	3.15	6 to 7	14	Salnikov 1996; Mugue 2010b; Pauly 1978
Amu Darya sturgeon	*Pseudoscaphirhynchus kaufmanni*	Amu Darya River	65.4	0.164	-0.95	40	55	Female	0.002	3.15	7 to 8	14	Salnikov 1996; Mugue 2010b; Pauly 1978
Pallid sturgeon	*Scaphirhynchus albus*	Lower Missouri River	171	0.065	0.2	91.9[a]	128	Male	0.0036	3.76	5 to 7	41	Steffensen *et al* 2013; Keenlyne and Jenkins 1993; Keenlyne *et al* 1992; Keenlyne and Maxwell 1993; Bajer and Wildhaber 2007
Pallid sturgeon	*Scaphirhynchus albus*	Lower Missouri River	171	0.065	0.2	93.1[a]	128	Female	0.0036	3.76	9 to 12	41	Steffensen *et al* 2013; Keenlyne and Jenkins 1993; Keenlyne *et al* 1992; Keenlyne and Maxwell 1993; Bajer and Wildhaber 2007
Shovelnose sturgeon	*Scaphirhynchus platorynchus*	Lower Platte River	106	0.1	-4.3	78.7	98.5	Male	0.0049	3	13	43	Hamel *et al* 2015; Everett *et al* 2003; Crawford 1993
Shovelnose sturgeon	*Scaphirhynchus platorynchus*	Lower Platte River	117	0.13	-2.7	74.3	95.5	Female	0.0049	3	9	43	Hamel *et al* 2015; Everett *et al* 2003; Crawford 1993
Alabama sturgeon	*Scaphirhynchus suttkusi*	Mobile Basin	85	0.14	-2.5	46.1[a]	84.1	Female	0.0015	3.21	5 to 7	16	William and Clemmer 1991; Kuhajda and Rider 2016

a) minimum maturity length
b) maximum age is from *A. medirostris*, the 2 species are closely related and *A. mikadoi* used to be considered as the Asian type of *A. medirostris*. (Birstein 1993)

Acknowledgements

We thank Evgeny Pakhomov for checking the Russian language literature (including that from the Soviet period) for information on Syr Darya sturgeon, which confirmed that the biology of this species was either never studied, or that any study that was published appeared in an outlet too obscure to come to the attention of other authors.

References

Adair, R., W. Harper, J. Smith, S. Eggers and S. Klemp. 1982. *Annual report Klamath river fisheries investigation program*. U.S. Fish and Wildlife Service Fisheries Assistance Office. Arcata, California.153 p.

Adams, P.B., C.B. Grimes, J.E. Hightower, S.T. Lindley and M.L. Moser. 2002. *Status Review of North American Green Sturgeon, Acipenser medirostris*. National Marine Fisheries Service (NMFS), Santa Cruz. 49 p.

Ambroz, A.I. 1964. Sturgeons of the northwestern Black Sea. *Trudy VNIRO*, 51: 287-347.

Anderson, A.W. 1954. 152-year old lake sturgeon caught in Ontario. *Commercial Fisheries. Review,* 18:28.

Arlati, G. 1996. Storioni in Lombardia. *Lombardia Verde,* (2): 6–8.

Babushkin, N.Y. 1964. Biology and fisheries of Caspian beluga. *Trudy VNIRO,* 51:183–258.

Bajer, P.G. and M.L. Wildhaber. 2007. Population viability analysis of Lower Missouri River shovelnose sturgeon with initial application to the pallid sturgeon. *Journal of Applied Ichthyology,* 23:457–464.

Bakhshalizadeh, S., A. Bani, S. Abdolmalaki, R. Nahrevar and R. Rastin. 2011. Age, growth and mortality of the Persian Sturgeon, *Acipenser persicus*, in the Iranian waters of the Caspian Sea. *Caspian Journal of Environmental Sciences*, 9(2): 159–167.

Berg, L.S. 1962. *Freshwater fishes of the U.S.S.R. and adjacent countries*. Israel Program for Scientific Translations, Volume 1. Jerusalem, Israel. 493 p.

Birstein, V.J. 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. *Conservation Biology*, 7: 773–787.

Brennan, J.S. and G.M. Cailliet. 1991. Age determination and validation studies of white sturgeon, *Acipenser transmontanus*, in California, p. 209-234. *In:* P. Williot (ed). *Acipenser - Actes du Premier colloque international sur l'esturgeon, Bordeaux, 3–6 Octobre 1989*. CEMAGREF publication.

Carlander, K.D. 1969. *Handbook of freshwater fishery biology, Volume 1*. The Iowa State University Press, Ames, Iowa. 752 p.

Caron, F., D. Hatin and R. Fortin. 2002. Biological characteristics of adult Atlantic sturgeon (*Acipenser oxyrinchus*) in the St Lawrence River estuary and the effectiveness of management rules. *Journal of Applied Ichthyology*, 18: 580–585.

Castelnaud, G., E. Rochard, P. Jatteau and M. Lepage. 1991. Données actuelles sur la biologie d'*Acipenser sturio* dans l'estuaire de la Gironde, p. 251–275. *In :* P. Williot (ed). *Acipenser - Actes du Premier colloque international sur l'esturgeon, Bordeaux, 3-6 Octobre 1989*. CEMAGREF publication.

Changjiang Aquatic Resources Survey Group, Sichuan Province. 1988. *The biology of the sturgeons in Changjiang and their artificial propagation*. Sichuan Scientific and Technical Publishing House, China. 308 p.

Chen, X. 2007. *The biology and resources of Acipenseriformes*. Ocean Press, China.

Chugunov, N.L. and N.I. Chugunova, 1964. Comparative commercial and biological characteristics of sturgeons of the Azov Sea. *Trudy VNIRO,* 52:87–182.

CITES. 2000. *Acipenser nudiventris* Lovetsky, 1828. p. 43–54. *In: Convention on international trade in endangered species of wild fauna and flora. Sixteenth Meeting of the CITES animals Committee. Shepherds town (United States of America) 11-15 December 2000*. DOC. AC. 16.7.2.

Congiu, L., J.M. Pujolar, A. Forlani, S. Cenadelli, I. Dupanloup, F. Barbisan, A. Galliand and F. Fontana. 2011. Managing polyploidy in *ex situ* conservation genetics: The case of the critically endangered Adriatic Sturgeon (*Acipenser naccarii*). *PLoS ONE*, 6(3): e18249. doi.org/10.1371/journal.pone.0018249

Crawford, R. 1993. *World record game fishes 1993*. The International Game Fish Association, Pompano Beach, Florida.

Dadswell, M.J. 1979. Biology and population characteristics of the Shortnose Sturgeon, *Acipencer brevirostrum* Le Sueur, 1818 Osteichthyes: Acipenseridae) in the Saint John River estuary, New Brunswick, Canada. *Canadian Journal of Zoology,* 57: 2186–2210.

Deng, X., Z. Deng and M. Cai, 1991. Spawning population characterisitcs of *Acipenser sinensis* in Yangtze River just below Gezhouba Dam, p. 235-242. *In :* P. Williot (ed). *Acipenser -Actes du Premier colloque international sur l'esturgeon, Bordeaux, 3-6 Octobre 1989.* CEMAGREF publication.

Everett, S.R., D.L. Scarnecchia, G.J. Power and C.J. Williams, 2003. Comparison of age and growth of shovelnose sturgeon in the Missouri and Yellowstone rivers. *North American Journal of Fisheries Management*, 23: 230–240.

Fazli, H., T. Mahmoud, M.R.B. Khoshghalb and M. Moghim. 2020a. Growth, maturity and optimum yield of Ship sturgeon *Acipenser nudiventris* Lovetsky, 1828 in the Southern Caspian Sea. *Cahiers de Biologie Marine,* 61: 369–375. dx.doi.org/10.21411/CBM.A.80E090A9

Fazli, F., M. Tavakoli, M.R. Khoshghalb, M. Moghim and T. Valinasab. 2020b. Population dynamics and the risk of stock extinction of Persian sturgeon (*Acipenser persicus* Borodin) in the Caspian Sea. *Fisheries & Aquatic Life*, 28: 62–72.

Fazli, F., M. Tavakoli, M.R. Khoshghalb, M. Moghim. 2020c. Population dynamics of stellate sturgeon *Acipenser stellatus* Pallas 1771 in the southern Caspian Sea. *Iranian Journal of Fisheries Sciences,* 20(1): 45–61.

Fischer, W., M.-L. Bauchot and M. Schneider (eds). 1987. *Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de Pêche 37.* FAO, Rome. 1529 p.

Froese, R. 2022. Estimating somatic growth of fishes from maximum age or maturity. *Acta Ichthyologica et Piscatoria* 52(2): 125-133. doi.org/10.3897/aiep.52.80093

Froese, R. and C. Binohlan. 2003. Simple methods to obtain preliminary growth estimates for fishes. *Journal of Applied Ichthyology*, 19(6): 376-379.

García-Gallego, M., A. Domezain, M. de la Higuera, M.C. hidalgo, M. Furné, A.E. Morales and A. Sanz. 2009. On Nutrition and Feeding Studies as the Basis for the Culture of Different Sturgeon Species, p. 215-234. *In:* R. Carmona, A. Domezain, M. García-Gallego, J.A. Hernando, F. Rodríguez and M. Ruiz-Rejón (eds). *Biology, Conservation and Sustainable Development of Sturgeons. Fish & Fisheries Series, vol. 29.* Springer, Dordrecht. doi.org/10.1007/978-1-4020-8437-9_13

Hamel, M.J., M.L. Rugg, M.A. Pegg, R. Patiño and J.J. Hammen. 2015. Reproductive traits of shovelnose sturgeon *Scaphirhynchus platorynchus* (Rafinesque, 1820) in the lower Platte River, Nebraska. *Journal of Applied Ichthyology*, 31(4): 592-602.

Keenlyne, K.D. and L.G. Jenkins. 1993. Age at Sexual Maturity of the Pallid Sturgeon. *Transactions of the American Fisheries Society*, 122(3): 393-396. doi.org/10.1577/1548-8659(1993)122<0393:AASMOT>2.3.CO;2

Keenlyne, K.D. and S.J. Maxwell. 1993. Length conversions and length-weight relations for pallid sturgeon. *North American Journal of Fisheries Management*, 13: 395-397. doi.org/10.1577/1548-8675(1993)013<0395:LCALWR>2.3.CO;2

Keenlyne, K.D., E.M. Grossman and L.G. Jenkins. 1992. Fecundity of the pallid sturgeon. *Transactions of the American Fisheries Society*, 121(1):139-140. doi.org/10.1577/1548-8659(1992)121<0139:FOTPS>2.3.CO;2

Koshelev, V.N. and N.V. Kolpakov. 2020. Sakhalin sturgeon *Acipenser mikadoi* (Acipenseridae): results of study and proposed measures for conservation of the species. *Izv. TINRO*, 200(4): 791–808.

Koshelev, V.N., E.V. Mikodina, T.N. Mironova, A.V. Presnyakov and A.G. Novosadov. 2012. New data on biology and distribution of Sakhalin sturgeon *Acipenser mikadoi. Journal of Ichthyol*ogy, 52: 619–627. doi.org/10.1134/S0032945212050025

Koshelev, V.N. and G.I. Ruban. 2012. Maturation and fecundity of kaluga *Acipenser dauricus*. *Journal of Ichthyol*ogy, 52: 528–536. doi.org/10.1134/S0032945212040054

Kottelat, M. and J. Freyhof. 2007. *Handbook of European freshwater fishes*. Publications Kottelat, Cornol and Freyhof, Berlin. 646 p.

Krykhtin, M.L. and V.G. Svirskii. 1997. Endemic sturgeons of the Amur River: kaluga, *Huso dauricus*, and Amur sturgeon, *Acipenser schrenckii*. *Environmental Biology of Fishes,* 48(1-4): 231––239. doi.org/10.1023/A:1007358027263

Kuhajda, B.R. and S.J. Rider. 2016. Status of the imperiled Alabama Sturgeon (*Scaphirhynchus suttkusi* Williams and Clemmer, 1991). *Journal of Applied Ichthyol*ogy, 32: 15–29. doi.org/10.1111/jai.13237

Lagutov V. and V. Lagutov. 2008. The Ural River Sturgeons: Population Dynamics, Catch, Reasons for Decline and Restoration Strategies, p. 193-276. *In*: V. Lagutov (eds). *Rescue of Sturgeon Species in the Ural River Basin. NATO Science for Peace and Security Series C: Environmental Security*. Springer, Dordrecht. doi.org/10.1007/978-1-4020-8924-4_12

Letaconnoux, R. 1961. Note sur la fréquence de la distribution des captures d'esturgeons (*Acipenser sturio* L.) dans le Golfe de Gascogne. *Revue des Travaux de l' Institut des Pêches Maritimes,* 25: 253–261.

Luo, J., H. Dao, H. Zhang, X.M. Qiao, W. Xiong, Z.J. Liu, X.S. Leng, J.P. Wu, L. Shen, C.Y. Wang, J.M. Wu, S.H. Zhang, Q. Zhou, Y. Liu and K.B. Wang. 2020. Reproductive biology of an artificial population of endangered Chinese sturgeon (*Acipenser sinensis*). *Journal of Fisheries Sciences of China*, 27(3): 269–276.

Magnin, E. 1964. Croissance en longueur de trios esturgeons d'Amérique du Nord: *Acipenser oxyrhynchus* Mitchill, *Acipenser fulvescens* Rafinesque et *Acipenser brevirostris* Le Sueur. *Verhandlungen des Internationalen Verein Limnologie*, 15: 968–974.

Magnin, E. 1964. Premier inventaire ichtyologique du lac et de la rivière Waswanipi. *Naturaliste canadien*, 91(11): 273–308.

Magnin, E. 1966. Quelques données biologiques sur la reproduction des esturgeons *Acipenser fulvescens* de la rivière Nottaway, tributaire de la baie James. *Canadian Journal of Zoology*, 44: 257–263.

Mikodina, E.V., A.G. Novosadov and V.N. Koshelev. 2015. On biology of Kaluga sturgeon *Acipenser dauricus* (Acipenseridae) from the Viakhtu River (Northwestern Sakhalin). *Journal of Ichthology*, 55: 567–575. doi.org/10.1134/S0032945215040062

Ministry of Nature Protection of Turkmenistan. 1999. *The red data book of Turkmenistan. Volume 1. Invertebrate and vertebrate animals*. Second edition revised and updated. National Institute of Desert, Flora and Fauna, Ashgabat, Turkmenistan. 355 p.

Mousavi, S. and A. Ghafor. 2014. On the conditions impressing sturgeon fish. *International Journal of Advanced and Applied Sciences,* 1(4):1–5.

Mugue, N. 2010a. *Acipenser mikadoi*. The IUCN Red List of Threatened Species 2010: e.T241A13045375. dx.doi.org/10.2305/IUCN.UK.2010-1.RLTS.T241A13045375.en

Mugue, N. 2010b. *Pseudoscaphirhynchus kaufmanni*. The IUCN Red List of Threatened Species 2010: e.T18601A8498207. dx.doi.org/10.2305/IUCN.UK.2010- 1.RLTS.T18601A8498207.en

Muus, B.J. and P. Dahlström. 1968. *Süßwasserfische*. BLV Verlagsgesellschaft, München. 224 p.

Nakamoto, R.J., T.T Kisanuki and G.H. Goldsmith. 1995. *Age and growth of Klamath River green sturgeon (Acipenser medirostris)*. U.S. Fish and Wildlife Service Office, Department of the Interior, Arcata. 20 p.

Nikolsky, G.V. 1961. *Special Ichthyology*. Israel Program for Scientific Translations, Jerusalem. 552 p.

Pauly, D. 1978. A preliminary compilation of fish length growth parameters. *Berichte des Institut für Meereskunde an der Universitat Kiel,* (55): 1–200.

Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *Journal du Conseil international pour l'Exploration de la Mer* 41: 280-284.

Pauly, D. 2022. Why do fish reach first maturity when they do? *Journal of Fish Biology*, 101(2): 333-341. doi.org/10.1111/jfb.14902

Pauly, D. and C. Liang. 2022a. Temperature and the early maturation of fish: a simple sine-wave model for predicting spring spawning. *Environmental Biology of Fishes,* 105: 1481-1487. doi.org/10.1007/s10641-022-01212-0

Pauly, D. and W.W.L. Cheung. 2017. Sound physiological knowledge and principles in modelling shrinking of fishes under climate change. *Global Change Biology*, doi: 10.1111/gcb.13831 .

Pauly, D. and C. Liang. 2022a. Temperature and the early maturation of fish: a simple sine-wave model for predicting spring spawning. *Environmental Biology of Fishes,* https://doi.org/10.1007/s10641-022-01212-0

Pauly, D. and C. Liang. 2022b. A reconceptualization of the interactions between spawning and growth in bony fish. *Scientia Marina,* 84(4): doi.org/10.3989/scimar.05280.044

Pauly, D. and S.W. Pauly. 2022. The Sturgeons (Acipenseridae) in Dean's "Bibliography of Fishes", p. 69-84. *In:* Pauly, D. and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports, vol. 30 (4).

Pikitch, E.K., P. Doukakis, L. Lauk, P. Chakrabraty and D.L. Erikson. 2005. Status, trend and management of sturgeon and paddlefish fisheries. *Fish and Fisheries,* 6: 233–265

Podlesnyi, A.V. 1958. Fishes of Enisey, their environments and use. p. 97-178. *In:* I.F. Pravdin and P.L. Pirozhnikov (eds). *Commercial fishes of Ob and Enisey and their use*. Izv. VNIORH 44. Moscow, Pishchepromizdat.

Raischi, M., G. Deak, L. Oprea, N. Raischi and D. Tiberius. 2020. Age and growth determination of Lower Danube sturgeon species *Huso huso* and *Acipenser stellatus*. *IOP Conference Series: Earth and Environmental Science*, 616: 012032. doi.org/10.1088/1755-1315/616/1/012032 .

Rien, T.A. and R.C. Beamesderfer. 1994. Accuracy and precision of white sturgeon age estimates from pectoral fin rays. *Transactions of American Fisheries Society,* 123(2): 255–265.

Rochard, E., P. Williot, G. Castelnau and M. Lepage. 1991. Elements de systematique et de biologie des populations sauvages d'esturgeons, p. 475–507. *In:* P. Williot (ed). *Acipenser, Actes du Premier colloque international sur l'esturgeon, Bordeaux, 3-6 Octobre 1989*. CEMAGREF publication.

Ruban G.I. and N.V. Akimova. 1991. The ecological features of the Siberian sturgeon *Acipenser baerii* Brandt from the Indigirka River. *Journal of Ichthyology*, 31:118–129

Ruban, G.I. 2005. *The Siberian sturgeon, Acipenser baerii Brandt: species structure and ecology*. World Sturgeon Conservation Society, Special Publication No. 1. Neu Wulmstorf, Germany. 203 p.

Salnikov, V.B., N.V. Akimova, G.I. Ruban, R.L. Mayden and B.R. Kuhajda. 2003. Reproductive System of Amu-Dar Shovelnose - Big Shovelnose *Pseudoscaphirhynchus kaufmanni* and Little Shovelnose *P. hermanni* (Acipenseridae). *Voprosy Ikhtiologii*, 43(4): 499–510.

Salnikov, V.B., V.J. Birstein and R.L. Mayden. 1996. The contemporary status of the two Amu Darya River shovelnose sturgeons, *Pseudoscaphirhynchus kaufmanni* and *P. hermanni*. *The Sturgeon Quarterly*, 4(3): 10–14.

Scott, W.B. and E.J. Crossman. 1973. *Freshwater fishes of Canada. Bulletin 184.* Fisheries Research Board of Canada*,* Ottawa. xi+ 966 p.

Semakula, S.N. and P.A. Larkin. 1968. Age, Growth, Food and Yield of the White Sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. *Journal of the Fisheries Research Board of Canada*, 25(12): 2589–2602.

Steffensen, K.D., M.A. Pegg, and G.E. Mestl. 2013. Population characteristics of pallid sturgeon (*Scaphirhynchus albus* (Forbes & Richardson, 1905)) in the Lower Missouri River. *Journal of Applied Ichthyology*, 29: 687–695.

Stevenson, J.T. and D.H. Secor. 1999. Age determination and growth of Hudson River Atlantic sturgeon, *Acipenser oxyrinchus*. *Fisheries Bulletin*, 97:153–166.

Suworw, J.K. 1959. *Allgemeine Fishkunde*. VEB Deutscher Verlag de Wissenschaften, Berlin. 581 p.

Sytova, M.V., H.N. Harenko, V.A. Belyaev and A.P. Shmigirilov. 2004. The analysis of quantitative and weight parameters of sturgeons spawning groups at Amur River basin. *Vopr. Rybolovstva*, 5(3): 470–481.

Taylor 1958. Cod growth and temperature. *Journal du Conseil international pour l'Exploration de la Mer.*, 23: 366–370.

Van Eenennaam, J.P., J. Linares and S.I. Dorshov. 2006. Reproductive Conditions of the Klamath River Green Sturgeon. *Transactions of the American Fisheries Society,* 135:151–163.

Webb, M.A.H. and D.L. Erickson. 2007. Reproductive structure of the adult green sturgeon, *Acipenser medirostris*, population in the Rogue River, Oregon. *Environmental Biology of Fishes*, 79: 305–314.

Williams, J.D. and G.H. Clemmer. 1991. *Scaphirhynchus suttkusi*, a new sturgeon (Pisces: Acipenseridae) from the Mobile basin of Alabama and Mississippi. Alabama Museum of Natural History Bulletin No. 10: 17–31.

Williot P., T. Rouault, R. Brun and J. Gessner. 2011. Characteristics of the Reproductive Cycle of Wild *Acipenser sturio,* p. 165–175. *In:* P. Williot, E. Rochard, N. Desse-Berset, F. Kirschbaum and J. Gessner (eds). *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758.* Springer, Berlin, Heidelberg. doi.org/10.1007/978-3-642-20611-5_12

Winberg, G.G. 1960. *Rate of metabolism and food requirements of fishes, and New information on metabolic rate in fishes.* Translation Series No. 194. Fisheries Research Board of Canada, Dartmouth, NS. 250 p.

The Sturgeons (Acipenseridae) in Dean's "Bibliography of Fishes"[1]

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Abstract

This account presents the references pertaining to sturgeon, i.e., fishes of the Family Acipenseridae, that were included in 'A Bibliography of Fishes', published by the American Museum of Natural History in 3 volumes in 1916, 1917 and 1923 under the editorship of Bashford Dean, Charles R. Eastman, Eugene W. Gudger and Arthur W. Henn. Altogether, over five hundred references were extracted whose titles explicitly referred to sturgeon or which, in few cases, were known to contain information on sturgeon. In most cases, the names of the periodicals where articles on sturgeon appeared were expanded, such as to assist in tracing and citing them.

Introduction

The scientific literature on fishes is hugely scattered, as the literature on other widespread and culturally important organisms probably also is. This situation applies especially to the literature of the 19th and preceding centuries published in different formats and a dizzying array of European languages. Fortunately for fish, Bashford Dean's *Bibliography of Fishes* captures much of that literature, if only in the form of well-indexed titles (many translated into English or German). This bibliography is available online (see www.biodiversitylibrary.org/bibliography/11857), but its items are accessible only when the correct search term is provided.

Titles from Dean's bibliography pertaining explicitly to sturgeon are presented below to support planned biological and historical work on sturgeons worldwide. They include the 24 recognized species of the family Acipenseridae that were described at that time. Two other recognized species, *Acipenser desotoi* Vladykov 1955, and *Scaphirhynchus suttkusi* Williams & Clemmer, 1991 were described after the publication of the bibliography, for a total of 26 currently recognized species (see FishBase; www.fishbase.org).

Here, 'explicitly' refers to the publications that include sturgeon or one of its cognates (e.g., sturgeon, steur, Stör, sturio, etc.) or the common or scientific name of an acipenserid taxon (e.g., beluga, sterlet, *Scaphyrhinchus, A. ruthenus,* etc.).

References were included here if their *title* referred to sturgeon, i.e., excluding contributions which contained information on sturgeon (e.g., as element of species list) without being explicit about it. The few exceptions to this have attached to them either editor's comments mentioning '*Acipenser*' (or another relevant term), or a footnote with the reason for their inclusion (e.g., because they contained original

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[1] Cite as: Pauly, D. and S.W. Pauly. 2022. The Sturgeons (Acipenseridae) in Dean's "Bibliography of Fishes", p. 69-84. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

descriptions of sturgeon species). Two other exceptions are books by Charles Darwin, who published extensively on "ganoid" fishes, which include sturgeon[2] and which he considered to be "living fossils."

We have checked and extended the abbreviated titles using a number of online sources including the Biodiversity Library (www.biodiversitylibrary.org), the Illinois Natural History Survey - Nomenclatura Oligochaetologica (www.inhs.illinois.edu/people/mjwetzel/nomenoligo/), and the Scholarly Societies Project (www.references.net/societies/history/abbrevA.html).

The overwhelming majority of references were identified by reading through the 2162 pages (in 3 volumes) of Dean's Bibliography and verifying them with the online version, which was based on optical character recognition (OCR) and generated a very small number of reading errors. We note that the original bibliography had, in French, German and English - languages we master - few typographic errors for a work of this complexity and scope. Earlier laudatory reviews of Dean's Bibliography[3] do not mention this fact, but it is crucial in such works.

The material immediately following the acknowledgements consists of an index to the references dealing the family Acipenseridae, reproduced from volume 3 of Dean's Bibliography. The number after the date is used to distinguish between contributions by the same author in the same year. The star (*) is used to identify contributions deemed 'excellent' by the editors of Dean's Bibliography. The actual references are listed after the index. Most of the references originate from Volume 1 (A-K), or from Volume 2 (L-Z); when they originated from Volume 3, they are either labeled 'Anonymous' ('Anon.'), 'Addenda' ('Add') or 'Pre-Linnean' ('Pre-Linn.').

Acknowledgements

We thank colleagues for checking references in their mother tongue and for additional corrections and comments: Johannes Müller (Dutch), Nicolas Bailly (French), Simone Libralato (Italian), Evgeny Pakhomov and Alexei Orlov (Russian) and Villy Christensen (Danish and Swedish).

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[2] Only two books by Charles Darwin are mentioned in Dean's Bibliography ('*The Voyage of the Beagle*' and '*The Descent of Man*') despite fishes being mentioned in many more of his publications (see Pauly, D. 2004. *Darwin's Fishes: an encyclopedia of Ichthyology, Ecology and Evolution*. Cambridge University Press, Cambridge, xxv + 340 p.). *Darwin's Fishes* documents that he wrote extensively on "ganoid" fishes, which include sturgeon. However, his only explicit (and very brief) mentions of sturgeon are in his (published) marginalia.

[3] Kingsley, J.S. 1924. Dean's bibliography of fishes. *The Anatomical Record* 27(3): 175-176; Jordan, D.S. 1924. Dean's Bibliography of Fishes. *Science* 59: 17-18.

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Russian species:	Golowatschow, A. 1857.1 Lovetsky, A. 1834.1
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Synopsis-Japanese forms:	Jordan, D.S. & Snyder, J.O. 1906.4
Caucasian forms, including those from Caspian and Black Seas:	*Kavraiskiĭ T.T. 1907.1 Sodoffsky, W. 1849.1
Review-North American forms:	Kirsch, P.H. & Fordice, M.W. 1890.1
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Fossil forms from Eocene of Paris basin:	Priem, F. 1904.3

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Text in French	Duchaussoy, H. 1891.1 Roule, L. 1905.3
Text in German	Berg, P.J. 1776.1 *Ehrenbaum, E. 1896.1, Add. 1913.3 Grimm, O. 1895.1 Kornhuber, G.A. 1901.2, .3, .4 Pallas, P.S. 1776.1

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[4] 'Bohemian' is an older name for Czech, a Slavic language.

	Bergius, B. & Marwitz, Add. 1776.1
	Brandt, J.F. & Ratzburg, J.T. Add. 1831.1
Text in Russian	Borodin, N.A. 1897.1, 1901.2
	Grünberg, V. 1905.1
	*Peltzam, E.D. 1883.1
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	Kahilainen, W. 1899.1
	Katuric, M. 1903.1
	Nordqvidst, O.F. 1899.1, .3
	Schain, Z. 1883.1
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	Agassiz, J.L. 1846.2
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	Gill, T.N. Add. 1836.1
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	Forbes, S.A. & Richardson, R.E. 1905.1

Sturgeon references in Dean's Bibliography of Fishes[5]

Agassiz, J. L. 1846. [On *Huro nigricans* Cuvier; regarded as identical with *Centrarchus fasciatus* and *C. obscurus* of DeKay. — On young *Scaphirhynchus* from the Ohio river]. Proceedings of the Boston Society of Natural History, 184. [1846.2]

Agassiz, J. L. 1856. [Development of scales in garpike and sturgeon are similar; one of the points serving to indicate close relationship of the two]. Proceedings of the Boston Society of Natural History, 6: 63. [1856.1]

Aleksandrov, K. P. 1910. Das Laichen des Sterlets in der Wolga bei Simbirsk im Frühjahre 1910 [Text in Russian]. Messager Commerce de Poissons, St. Petersburg, 25: 255–258. [1910.1]

Anon. 1777. Description d'un huso monstrueux. Acta Academiae scientiarum imperialis petropolitanae, pt. 1, 80. [Anon. 665]

Anon. 1869. De steur en de steurvisscherij. Kennis en Kunst 1869, 3-6, pl. [Anon. 521].

Anslijn, N. 1838. Systematische Beschrijving der [voor ons meest belangrijke] Visschen. Leiden, 1828. 8°. [1828.1]

Antipa, G. 1906. Ueber die Störe und ihre Wanderungen in den europäischen Gewässern mit besonderer Berücksichtigung der Störe der Donau und des schwarzen Meeres. (Stenographische Protokolle) Verhandlungen des Internationalen botanischen Kongresses in Wien 1905, 134–152. Abstract in Allgemeine Fischerei Zeitung 31: 246–249. [1906.1]

Atkins, C. G. 1872. Reproduction of Sturgeon. Abstract of paper in Kowalewsky, Owsjannikow and Wagner, *q.v.,* in The American Naturalist 6: 175. [1872.3]

Ayres, W.O. 1854. Description of new fishes from California. Proc. Calif. Acad. Nat. Sci. 1854-1857, 1: 3-22. Reprinted in 2 ed. of the Academy's Proceedings. [1854.2][6]

Baer, K. E. von. 1826. Ueber den Seitencanal des Störs. Archiv für Anatomie und Physiologie (Merkel), 376–377. [1826.1]

Baer, K. E. von. 1874. Ueber das Vorkommen eines *Scaphirhynchus* in Turkestan. Sitzungsberichte der Naturforschenden Gesellschaft Dorpat 3(5): 386–387. [1874.1]

Baird, S. F. 1871. Teeth of the sturgeon. Annual Record of Science and Industry 1871–72, 213. [1871.45]

Baird, S. F. 1872. Teeth in young sturgeons. Annual Record of Science and Industry 1872–73, 264. [1872.25]

Baird, S. F. 1873. New *Scaphirhynchus* in Turkestan. Annual Record of Science and Industry 1873–75, 336. [1873.29]

Baird, S. F. 1874a. Spinal column of the sturgeon as an article of food. Annual Record of Science and Industry 1874–75, 447. [1874.22]

Baird, S. F. 1874b. Sterlet from St. Petersburg at the Brighton Aquarium. Annual Record of Science and Industry 1874–75, 428. [1874.23]

Baker, W. 1847. Large sturgeons in the Usk. The Zoologist: A Monthly Journal of Natural History, Volume 5, 1649. [1847.1]

Ball, R. 1904. On a new sturgeon (*Acipenser thompsoni*). Proceedings of the Royal Irish Academy, 1904–05, 25: 21. [1904.1]

Baženov, A. 1906. Der Stör und der Hausen in der mittleren Wolga [Text in Russian] Věst. Rybopromyšl., St. Petersburg, 1906, 21, 1-6. 3 pls. [1906.1]

Berg, L. S. 1904. Zur Systematik der Acipenseriden. Zoologischer Anzeiger 27(22): 665–557. [1904.1]

Berg, L. S. 1905. Einige Worte über den "Dick" (*Acipenser schypa, glaber, brandti*) [Text in Russian]. Trudy Saratovkogo Obchestva Jestestvoispytatelei I Liubitelei Prirody, 4, pt. 2, p. 281–283. [1905.1]

Berg, L. S. 1913. Sur un spécimen de *l'Acipenser medirostris* Ayres trouvé dans le bas Amour [Text in Russian]. Annuaire du Musée zoologique de l'Académie des sciences de St. Pétersbourg 18: 16. [1913.7]

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[5] Species names in square brackets were inserted in the titles of many references by the editors of Dean's Bibliography…. when they could ascertain their identity. They also added explanatory comments (in very small font, as reproduced here) under some references.

[6] Original description of *Acipenser medirostris* Ayres, 1854.

Berg, P. J. 1776. [Auszug eines Briefes des Banko-Kommissarius Bergius in Stockholm an den Herrn D. and Prof. Kölpin zu Stettin, die Naturgeschichte und Verpflanzung des Sterlets betreffend]. Beschäftigungen der Berlinischen Gesellschaft Naturforschender Freunde. 2: 534–535. [1776.1]

Berghaus, A. 1877. Der Sterlet [*Acipenser ruthenus*] in Pommern. Natur, n.s. 3: 673–675. [1887.1]

Bloch, M.E. 1782. Oeconomische Naturgeschichte der Fische Deutschlands. Berlin, 1782-85. 3 pts. in 1 & atlas. 108 col. pls. 4° & fol. [1782.1]

Bluntschli, H. 1903. Eisenhämatoxylin und Biondipräparate der Leber von *Ceratodus fosteri* und *Acipenser ruthenus*. Verhandlungen der Anatomischen Gesellschaft 17: 198–199. fig. [1903.1]

Boettger, O. 1871. Ueber den Fang von Stören im Main. 12. *Berichte* des Offenbacher Vereins für Naturkunde, p. 12–13. [1871.1]

Borodin, N. A. 1885. An attempt to impregnate artificially the eggs of *Acipenser stellatus* Bulletin of the United States Fish Commission 5: 275–276. [1885.1]

Borodin, N. A. 1897. Materials for the biology of sturgeons. [Text in Russian] Moscow, 1897. 5 p. pl. 8°. [1897.1]

Borodin, N. A. 1899. Die künstliche Verbreitung des russischen Stör (*Acipenser güldenstädtii*) in Uralfluss. Allgemeine Fischerei Zeitung. 24: 337–338. [1899.1]

Borodin, N. A. 1901. Zur Biologie der Acipenseriden. [Text in Russian] Dnevnik XI-go Siezda Russkih Jestestvoispytatelei I Vrachei St. Petersburg, 20-30 dekabria 1901, 12: 301–302. [1901.2]

Borodin, N. A. 1902. Kurze Anleitung zur Befruchtung von Störeiern und zur Erbrütung von Jungen daraus [Text in Russian] St. Petersburg, 3 p. [1902.1]

Brandt, J. F. 1831a. Bemerkungen über die Störarten, welche Hausenblase liefern. Berlinisches Jahrbuch der Pharmacie 32: 48–59. [1831.1]

Brandt, J. F. 1831b. Nachträgliche Bemerkungen über die Störarten, welche Hausenblase liefern. Berlinisches Jahrbuch der Pharmacie 32: 317–320. [1831.2]

Brandt, J. F. 1850. Ueber Albinismus und eine abweichende Farbenspielart des Sterläd (*Acipenser ruthenus*). Bulletin de l'Académie des sciences de St.-Pétersbourg 10: 13–16. [1850.1]

Brandt, J. F. 1869. Einige Worte über die europäisch-asiatischen Störarten (Sturionides) Mélanges Biol., 7:110–116. Bulletin de l'Académie des sciences de St.-Pétersbourg 9: 43–48. [1869.1][7]

Brusina, S. 1902. Nase jesetre [*Acipenser*] Rad Jugoslavenske Akademije 149: 1–69. [1902.1]

Cattaneo, G. 1886a. Note d' istologia comparata. I. Ulteriori ricerche sulla struttura delle glandule peptiche dei selaci, ganoidi e teleostei. II. Sul significato fisiologico delle glandule da me trovate nello stomaco dello storione e sul valore morfologico delle loro cellule. Bolletino Scient., Pavia, 1886, 8, nos. 3 & 4. [1886.1]

Cattaneo, G. 1886. Sull' esistenza delle glandule gastriche nell' *Acipenser sturio* e nella *Tinca vulgaris*. Rendiconti Reale Istituto lombardo di scienze e lettere. Milano, Ser. 2, 19: 676–682. [1886.3]

Chappe d'Auteroche, J. 1768. Voyage en Sibérie ... contenant ... la description géographique ... de la route de Paris à Tobolsk ; l'histoire naturelle de la même route (La description du Kamtchatka ... par M. Kracheninnikow ... traduit du Russe) 3 vols. In 4. Paris. Illust. 4°. [1768.1]

Remarques sur le sterlet, vol. i, p. 200-201. Poissons, vol. ii, p. 455-485. Charlevoix, P. F. X. 1736. Journal d'un voyage ... dans l'Amérique septentrionale, etc. (Histoire de la Nouvelle France, Vol. III.) Paris, 1744. 8°. [Pre-Linn. 1744.1]

Fishes of St. Lawrence River and Lake Champlain; fishing for gar pike and sturgeon in Lake Champlain: eel fishing in Canada. This "Histoire' as a whole or in parts passed through a number of eds.: Paris, 1749; Leyden, 1750 (Dutch); Göttingen & Amsterdam, 1750; The Hague, 1760; London, 1761; and more recently New York, 1865.

Coenen, Adriaan. 1577. Vischboek van Adriaan Coenen, zoon van Schilperoort. Dit Vis, Booc, veergadert ende gescreven van mij A. Coenen soen, geboren op de dorpe van Scheiveninghe Een visschers dorpe in de Noortsee leggende een cleijn mijlken van den vermaerden Hage in Hollant die is in veel landen wel bekent. Anno 1577 begonnen (-1578) . [Pre-Linn. 1577.1]

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[7] Includes the original description of *Acipenser baerii* Brandt 1869.

This is a MS. work cited by Bosgoed from the Koninklijke Bibliothek te 's Gravenhage (The Hague). It consists of 410 folios of colored figures.[8]

Collins, Alb. 1904. En sterlett (*Acipenser ruthenus* L.) tagen i Pythiis viken [Ein Stör in der Bucht von Pythis gefangen]. Tidskrift för Jägare och Fiskare, Helsingfors 12: 15. [1904.1]

Dean, B. 1893a. Note on the spawning conditions of the sturgeon. Zoologischer Anzeiger 16: 473–475 — Forest and Stream 41: 525 — Allgemeine Fischerei Zeitung, 388–390. [1893.3]

Dean, B. 1893b. Recent experiments in sturgeon hatching on the Delaware. [Read before the World's Fisheries Congress, Chicago] Transactions of the New York Academy of Science 13:69–74. Reprint in the Bulletin of the United States Fish Commission 13: 335–339. fig. [1893.6]

Dean, B. 1895a. The early development of garpike and sturgeon. Journal of Morphology 11: 1–62. 4 pls. & 4 figs. [1895.3]

Dean, B. 1895b. Notes on the early development of the Ganoids, *Lepidosteus*, *Acipenser*, and *Amia*. Report of the British Association for the Advancement of Science, 65th meeting, 734. [1895.6]

Dikson, B. 1912. Zur Entwicklung der Rückenplättchen und der Rückenflosse bei dem Sterlet. [Text in Russian] Vestnik Rybopromyshlennosti St. Petersburg, 27: 363–371. [1910.1]

Drzewina, A. 1904. Sur la non-spécificité des cellules granuleuses du rein de l'*Acipenser sturio* L. (note préliminaire). Comptes rendus des séances et mémoires de la Société de Biologie. Paris 56, pt. 1, p. 957–959. [1904.2]

Duchaussoy, H. 1891. Notes recueillies dans les archives. II. "Ung gros esturgeon pesché à Amyens." Bulletin de la Société linnéenne du nord de la France, Amiens 10: 118–119. [1891.1]

Duméril, A. H. A. 1867. Prodrome d'une monographie des esturgeons et description des espèces de l'Amérique du Nord qui appartiennent au sous-genre *Antaceus*. Nouvelles Archives du Muséum d'Histoire Naturelle de Paris 3: 131–188. 6 pls. [1867.2]

Duméril, A. H. A. 1868. Note sur trois poissons: *Acipenser dabryanus*[9]*, Polyodon gladius* et *Peristethidion prionocephalum*, accompagnée de quelques considérations générales sur les groupes auxquels ces espèces appartiennent. Nouvelles Archives du Muséum d'Histoire Naturelle de Paris 4: 93–116. [1868.1]

Ebner, Victor von. K1896. Ueber den feineren Bau der Chorda dorsalis von *Acipenser*. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse Abteilung I, Biologie, Mineralogie, Erdkunde 104, pt. 3, p. 149–159. [186.4]

Ehrenbaum, E. 1896. Beiträge zur Naturgeschichte einiger Elbfische [*Osmerus eperlanus* L., *Clupea finta* Cuv., *Acerina cerua* L., *Acipenser sturio* L.] Wissenschaftliche Meeresuntersuchungen Kiel (Abteilung Helgoland), n.s.1, Heft 1: 35–79. 3 pls. [1896.1]

Ehrenbaum, B. 1913. Ueber die Stör[10]. Centralfischerei Verein für Schleswig-Holstein, Rendsburg, 36. Jahresbericht, p. 173–176. [Add. 1913.3]

Ergomyöev, N. 1914. Ein Beitrag zur Fütterung und zum Wachstum der Sterlet-Brut. [Text in Russian] Rybopromyshlennaja Zhizn', Petrograd, 3: 224–230. [Add. 1914.1]

Evermann, B.W. 1898. Note on the Columbia sturgeon. Recreation 8: 465. [1898.4]

Forbes, S. A. and Richardson, R. E. 1905. On the shovel-nose sturgeon [*Parascaphirhynchus albus*] from the Mississippi river. *Bulletin* of the *Illinois State Laboratory* of Natural *History* 7: 37–44. 3 pls. [1905.1][11]

Fulton, T. W. 1903. Ichthyological notes. 21st Annual Report of the Fisheries Board of Scotland i. Sturgeons, p. 228–231. [1903.2]

Gesner, C. 1563. Fischbuch, das ist ein kurtze doch vollkomne Beschreybung aller Fischen so in dem Meer unnd süssen Wassern, Seen, Flüssen oder anderen Bächen jr Wonung habend, sampt jrer waaren Conterfactur: zu Nutz und Gütem allen Artezen etc. gestelt, insonders aber denen so ein Lust habend zü erfaren und betrachten Gottes wunderbare Werck in seinem Geschöpften. Erstlich in Latein durch Cünradt Gässner beschriben yetz neüwlich aber durch

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[8] There is a modern facsimile edition of this manuscript by Florike Egmond: Egmont, F. Het Visboek. De wereld volgens Adriaen Coenen 1514 – 1587 (Amsterdam: Walburg Pers: 2005).

[9] This species, known as Yangtze sturgeon was declared extinct by the IUCN as of July 21, 2022; en.wikipedia.org/wiki/Dabry%27s_sturgeon

[10] This was a transcription error; the original reads correctly 'Über den Stör'.

[11] Original description of *Scaphirhynchus albus* (Forbes & Richardson, 1905).

Cünradt Forer etc, in das Teütsch gebracht. Zürych, 1563. Ix. 404 p. woodcuts. fol. [Pre-Linn. 1563.1][12]

First ed. of Forer's version of the "De piscium." Others are: Zurich, 1563 (a separate issue) & 1575; Frankfort, 1598; & Heidelberg, 1606).

Golowatschow, A. 1857. Notice sur quelques espèces de poissons du genre *Acipenser*. Bulletin de la Société impériale des naturalistes de Moscou 30 pt. 3: 530–548. [1857.1]

Goronowitsch, N. 1888. Das Gehirn und die Cranialnerven von *Acipenser ruthenus*. Ein Beitrag sur Morphologie des Wirbelthierkopfes. Morphologische Jahrbuch 13: 427–514. 12 pls. [1888.1]

Gray, J. E. 1834. Characters of two new species of sturgeon (*Acipenser*, Linn.) Proceedings of the Zoological Society of London. 2: 122–123. Archiv für Naturgeschichte (Weigmann) p. 272. — Isis (Oken) 1835, p. 1050–1051. [1834.1][13]

Green, S. 1883. Hatching striped bass, sturgeon and trout. Transactions of the American Fisheries Society 1882 (1883): 37–40. [1883.1]

Greve, C. H. 1896. Ueber die Lebensweise der central-asiatischen Arten der Gattung *Scaphirhynchus*. Sitzungsberichte der Gesellschaft Naturforschender der *Univ*ersität *Dorpat*. 11: 137–144. [1896.1]

Grevé, C. H. 1897. An old record of the occurrence of the sturgeon (*Acipenser sturio* L.) in the Clyde. Transactions of the Natural History Society of Glasgow, n.s. 4: 385. [1897.1]

Grimm, O. 1872. Ueber das Geruchsorgan der Störe. Vorläufige Mittheilung. Göttingen Nachrichten, p. 537–539. [1872.1]

Grimm, O. 1895. Ueber der Sterlet. Allgemeine Fischerie Zeitung 20(8):145–146. [1895.1]

Grimm, O. 1906. Ein Stör mit drei Rogensäcken [Text in Russian] Vestnik Rybopromyshlennosti, St. Petersburg, 21: 287. [1906.2]

Grimm, O. 1910. Zur Fortpflanzung des Sterlets [Text in Russian] Vestnik Rybopromyshlennosti, St. Petersburg, 25: 325–324. [1910.1]

Grünberg, V. 1905. Notizen über das Leben des Aral-Störs im Syr-Darja [Text in Russian], Russkoe Sudochodstvo, St. Petersburg, 20, pt. 7, p. 86–91. [1905.1]

Guicciardini, L. 1648. Belgium, dat is: Nederlandt, ofte beschryvinge derselviger provincien ende steden. Amstelodami, 1648. figs. maps. fol. [Pre-Linn. 1648.1]

"Visschen van de Mase, p. 13; van de Schelde, p. 14. Haringhen, cabeljau, salmen, steuren, p. 20-21. Grousame visschen, p. 264." Bosgoed.

Other eds.: 1st., Antwerp, 1567 (in French & Italian); 1580 & 1588 (both in Dutch); Basel, 1580 (German); & Amsterdam, 1613 (Latin).

Gunn, T. E. 1865. The sturgeon off Yarmouth. The Zoologist: A Monthly Journal of Natural History, 23: 9470. [1865.1]

Gunn, T. E. 1866. Sturgeons off the coast of Norfolk and Suffolk. The Zoologist: A Monthly Journal of Natural History 2. Ser. 1: 311–312; 510. [1886.3]

Günther, A.1873. Note on *Scaphirhynchus fedtschenkoi*[14]. The Annals and Magazine of Natural History; Zoology, Botany, and Geology 12: 239–250. [1873.5]

Harting, P. 1875. Ingewanden-stehen van een steur. Album der Natuur. (Wetensch. bijblad.), 78 [1875.3]

Heckel, J. J. 1836. *Scaphirhynchus*, eine neue Fischgattung aus der Ordnung der Chondropterygier mit freien Kiemen. Annalen des Wiener Museums der Naturgeschichte 1:68–78. — Archiv für Naturgeschichte 2. Jahrgang, 241. [1836.2]

Heckel, J. J. 1851. Stör-Arten der Lagunen bei Venedig. Sitzungsberichte der Akademie der Wissenschaften in Wien 6, 2. Abth., p. 547–563. [1851.3]

Heckel, J. J. and Fitzinger, L. J. 1836. Monographische Darstellung der Gattung *Acipenser*. Annalen des Wiener Museums der Naturgeschichte 1: 261–326. Notice in Archiv für Naturgeschichte (Wiegmann), 1837, 2. Jahrgang, p. 239. [1836.1]

Herrick, C. J. 1902. [Review of] Johnston on the brain of *Acipenser,* etc. Science, n.s. 14: 930– 931. [1902.3]

Hildegarde de Pinguia (also styled Saint Hildegard. Abbess of Bingen). 1895. For accounts of the life and natural history observations of this remarkable personage, *see* Jessen, Carl. "Ausgabe der Hss. der medic.-naturhistor. Werke der heiligen Hildegard." Sitzungsberichte der Akademie der

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[12] The authors own a facsimile edition of this work, which includes woodcuts and text pertaining to sturgeon.

[13] Original description of *Acipenser sinensis* Gray, 1835. Note partly divergent dates.

[14] See reference to Kessler (1878).

Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse Abteilung I, Biologie, Mineralogie, Erdkunde 45, 1. Abtheilung p. 97–116. [Pre-linn 1533.1][15]

Hilgendorf, F. M. 1892. Eine neue Stör-Art von Nord-Japan, *Acipenser mikadoi*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, p. 3–4. [1892.1][16].

Hovey, H. C. 1884. The sturgeon fishery. Bulletin of the United States Fishery Commission 4: 346–348. [1884.1]

Ionescu, C. N. 1905. Les pores abdominaux des Acipensérides. Annales scientifiques de l'Université de Jassy 3: 167–168. [1905.1]

Ivanzov, N. 1887. Der *Scaphirhynchus*. Vergleichend-anatomisches Beschreibung. Bulletin de la Société impériale des naturalistes de Moscou, , p. 1–41, 2 pls. [1887.1]

Jaquet, M. 1897. Anomalie du museau chez un *Acipenser ruthenus*. Archives des sciences médicales de Bucarest 2: 358–359. [1897.1]

Jaquet, M. 1899. Ligne latérale supplémentaire chez un *Acipenser ruthenus*. Bulletin de la Société des sciences de Bucarest 8: 791–792. [1899.2]

Johnston, J. B. 1898a. Hind brain and cranial nerves of *Acipenser*. Anatomischer Anzeiger 28: 580–602, 13 figs. [1898.1]

Johnston, J. B. 1898b. The olfactory lobes, fore-brain and habenular tracts of *Acipenser*; a summary of work on their minute structure. Zoological Bulletin, Boston 1: 221–241. [1898.2]

Johnston, J. B. 1901. Some points in the brain of lower invertebrates. Biological Bulletin, Woods Hole 2: 356–357. [1901.1]

Johnston, J. B. 1902. The brain of *Acipenser*. A contribution to the morphology of the vertebrate brain. Zoologische Jahrbücher /Abteilung für Anatomie 15: 59–260. 11 pls. & 33 figs. [1902.2]

Jordan, D. S. and Snyder, J. O. 1906. List of fishes recorded from Okinawa or the Riu Kiu islands of Japan. Proceedings of the United States National Museum 32: 491–504. [1907.1]

Jourdain, S. 1877. Recherches sur la trompe buccale de l'esturgeon. Paris, pl. 8° [1887.1]

Jungersen, H. F. E. 1894. Om embryonalnyren hos støren (*Acipencer sturio*). Videnskabelige. Meddelelser fra den Naturhistoriske forening i Kjöbenhavn, 1893, 188-203. — Zoologischer Anzeiger 16th Jahr. 464–467; 469–472. Also separate; Kjøbenhavn, 1894. 8°. [1894.2]

Kahilainen, W. 1899. Amerikkalainen jarvisampi eli-saita (*Ascipenser rubicundus*). Suomen Urheilu 2: 322–323. pl. [1899.1]

Kammerer, P. 1907. Der Sterlett (*Acipenser ruthenus* L.). Blatter für Aquarien – und Terrarienkunde. 18. Jahrgang, no. 18. [1907.7]

Katuric, M. 1903. Novo nalazište jesetre atlantske, *Acipenser sturio* L. Rad JugoslavenskeAkademije Znanosti i Umjetnosti 154:1–6. [1903.1]

Kavraiskiĭ, T. T. 1907. Die Störarten der Kaukasusländer und ihrer angrenzenden Meere [Text inRussian and German]. Tiflis, xii, 78 p. 14 pls 8°. The final portion of this indicated: "Lieferung 5 und Schluss des Werkes: Die Fische der Kaukasus." [1907.1]

Kessler, K. T. 1873. (first account) On a remarkable fish of the family of sturgeons discoveredby M.A.P. Fedtschenko in the river Suirdar (*Scaphirhychus fedtschenkoi*). The Annals and Magazine of Natural History; Zoology, Botany, and Geology 4. ser. 12: 269–276. [1873.2][17]

Kessler, K.T. 1874. Fishes of the Black and Caspian Seas compared and described [Text in Russian] Bulletin the Society of Naturalists, St. Petersburg, 132 p., 8 pl. [1874.1]

Kessler, K. F. 1877. Fishes of the Aralo-Caspio-Pontine region (in his The Aralo-Caspian expedition). St. Petersburg, 360 p., 26 figs). [1877.1][18]

Kirsch, P.H. and M. W. Fordice. 1890. A review of the sturgeons (Acipenseridae) of North America. Proceedings of the Academy of Natural Science of Philadelphia 1899, 245–257. [1890.1]

Kirtland, J. P. 1844a. Descriptions of *Acipenser rubicundus*, *A. platyrhynchus* and *Rutilus storerianus*. Proceedings of the Boston Society of Natural History 1841–44, 1: 71. [1844.1]

Kirtland J. P. 1844b. Remarks on *Acipenser rubicundus* and *Rutilus plagiurus*. Proceedings of the Boston Society of Natural History 1841–44, 1: 7. [1844.5]

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[15] An English translation, by P. Throop, of Hildegard von Bingen' 'Physica' is available at www.chapters.indigo.ca/fr-ca/livres/hildegard-von-bingens-physica/9781594777752-article.html. It contains half a page on sturgeon.

[16] Original description of *Acipenser mikadoi* Hilgendorf, 1892.

[17] Original description of *Pseudoscaphirhynchus fedtschenkoi* (Kessler, 1872), as species now likely to be extinct en.wikipedia.org/wiki/Syr_Darya_sturgeon.

[18] Original description of *Pseudoscaphirhynchus hermanni* (Kessler, 1877).

Kornhuber, G.A. 1901a. Vom Scherg oder Sternhausen, *Acipenser stellatus* Pallas. Verhandlungen des Vereins für Natur- und Heilkunde zu Presburg 21: 32–34. [1901.2]

Kornhuber, G. A. 1901b. Vom Stein-Schnee und vom Stör Gmelins [*Lucioperca volgensis* und *Acipenser gmelini*]. Verhandlungen des Vereins für Natur- und Heilkunde zu Presburg. 21: 39–41. [1901.3]

Kornhuber, G. A. 1901c. Vom Waxdick, *Acipenser gludenstädti* Brandt. Verhandlungen des Vereins für Natur- und Heilkunde zu Presburg 21: 30–32. [1901.4]

Kosmak, G. W. 1895. Dermal armor of the sturgeon. Journal of the New York Microscopical Society 11: 1–21. 3 pls. [1895.1]

Kuchin, I. B. 1910. Essai de fécondation artificielle du frai de *Stenodus leucichthys* et de sterlet, et plan des travaux subséquents en vue de développer la pisciculture dans la région des monts Ouraliens. [Text in Russian] Bulletin de la Société ouralienne d' Amateurs des Sciences naturelles Ekaterinburg 30: 29–47. [1910.1]

Kupffer, C. W. 1893. Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Kranioten. 5 Hefte. 1893–1900. [1893.1] i. Die Entwicklung des Kopfes von *Acipenser sturio*. München & Leipzig, 1893. 95 p. 9 pls. 8˚.

Lambe, L. M. 1902. New genera and species from the Belly river series (Mid-Cretaceous). Contributions to Canadian Paleontology, Ottawa, 1902, 3: 25–82. 2 pls. [1902.1] *Myledaphus, Acipenser, Lepidotus, Rhineastes, Diphyodus.*

Lataste, F. 1894. Allures bizarres d'un esturgeon dans la Garonne. Bulletin de la Société centrale d'aquiculture de France 6. [1894.1]

Lavrov, S. 1908. Ueber die Pancreasgänge der Sterlets (*Acipenser ruthenus*). Zoologischer Anzeiger 33: 408–409. fig. [1908.2]

Leidy, J. 1873. Notice of fossil vertebrates from the Miocene of Virginia. Proceedings of the American Academy of Science of Philadelphia, 15. — American Journal of Science 3 ser. 5, p. 311––312. [1873.2] Selachian remains, *Tautoga, Acipenser*

Lesueur, C.A. 1818. Description of several species of chondropterygious fishes of North America, with their varieties. Transactions of the American Philosophical Society, n.s. 1: 383-394. pl. [1818.3][19]

Lieventhal, C. 1887. Ueber Ptomaine in giftigem Störfleische. Pharmazeutische Zeitschrift für Russland. St. Petersburg 26. [1887.1]

Linnaeus, C. 1758. Systema naturæ per regna tria naturæ, systematice proposita per classes, ordines, genera et species, cum characteribus, differentiis, synonymis, locis, etc. Tomus I. Editio decima, reformata. Holmiæ. 8°, ii + 824 p. [1758.2][20]

Linnert, K. 1909. Enthält Kaviar (Stör- resp. Hauseneier) Purinbasen? Biochemische Zeitschrift 18: 209–210. [1909.1]

Linton, E. 1893. Notes on trematode parasites of fishes. Proc. U. S. Nat. Mus., 1898, 20, 507-548. 15 pls. [1898.3] Records from freshwater fish; *Diplostomum cuticola* from various sunfish; *Distomum auriculatum* from the lake sturgeon; *D. gracile* from the bluegill; besides others from migratory and marine fishes as well as some unidentified species.

Lovetsky, A. 1830. Sur les espèces du genre esturgeon, appartenant aux eaux de l'empire Russe. Bulletin de la Société des Sciences Naturelles (Férussac). 23:131-134. — Notizen (Froriep) 30: 99–101. [1830.1]

Lovetsky, A. 1834. Diagnosis piscium ad genus Acipenerinum pertinentium, praeprimis eorum qui habitant in aquis Imperii Roici. Nouveaux mémoires de la Société impériale des naturalistes de Moscou 3: 253–264. [1834.1]

Macallum, A. B. 1886. The alimentary canal and pancreas of *Acipenser*, *Amia* and *Lepidoteus*. Journal of Anatomy and Physiology London 20:604–636. pl. Abstract in Proceedings of the Canadian Institute, Series 3, p. 271–274. [1886.1]

Maggi, L. 1899. Serie de ossicini mediani del tegmen cranii in alcuni cani (Canis) e loro omologhi ed omotipi in alcuni storini (*Acipenser*). Rendiconti Reale Istituto Lombardo di Scienze e Lettere. Milano, Ser. 2, 31: 473–1492. pl. [1899.1]

Maglio, C. 1901. Gli storioni delle acque pavesi. Rendiconti Reale Istituto Lombardo di Scienze e Lettere. Milano, Serie 2, 34: 1143–1148. [1901.1]

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[19] Original description of *Acipenser brevirostrum* Lesueur 1838.

[20] Original descriptions of *Acipenser ruthenus* Linnaeus 1758 and *Huso huso* (Linnaeus 1758)

Malenück, W. D. 1908. Zur Chemie der Protamine. I. Mitteillung. Ueber das Protamine aus den Spermatozoen des kaspischen Störs, *Acipenser guldenstädtii*. Zeitschrift für Physiologische Chemie 57: 99–112. [1908.1]

Mandelslo, J.A. 1658. Beschryving van den gedenkwaerdige zee- en landreyze deur Persien naar Oost-Indien, etc. Amsterdam, 1658. viii, 150 leaves. 4°. [Pre-Linn. 1658.1] This celebrated work, first published at Schleswig in 1645, passed through a number of editions. Some are (German) Schleswig, 1645, 1647, 1658; (Dutch) Amsterdam, 1651 & 1659; (English) London, 1696; (French) Leyden, 1719 & 1727. It was also reprinted in Arkstee & Merkus, Allg. Hist. Reisen, etc. 1753, XI, under the title "Reise nach Indostan."

Mandelslo, J.A. 1662. The voyages and travels of J. A. de Mandelslo . . . into the East Indies (In Olearus, Adam. The voyages and travels of the Ambassadors sent ... to the great duke of Muscovy, and the king of Persia, etc. London, 1662. 4°.) [Pre-Linn. 1662.1][21]

Mandelslo, J.A. 1696. Morgenlandische Reise-beschreibung, herausgegeben durch A. Olearium mitdesselben Anmerkungen. Hamburg, 1696. 174 p. fol. [Pre-Linn. 1696.1]

Mandelslo, J.A. 1713. Voyages célèbres et remarquables faits de Perse aux Indes Orientales; contenant une description nouvelle et très curieuse de l'Indostan, de l'Empire du Grand-Mogol, des îles et presqu'îles de l'Orient, des royaumes de Siam, du Japon, du Congo, de la Chine, etc. 2 vols, [in 1] Leide, 1713. pls. maps. fol. [Pre-Linn. 1713.1] Fishes, p. 88, 209, 280, 464, 559, 573, 619, 620-621, 623, 627, 634, 670, 673, 675, 684.

Matthew, G. F. 1875. Large sturgeon at Torquay. The Zoologist: A Monthly Journal of Natural History. Ser. 2 10: 4301. [1875.1]

Mearn, E. A. 1898. A study of the vertebrate fauna of the Hudson highlands. Bulletin of the American Museum of Natural History 10: 341–360. [1898.2] *Petromyzon, Carcharhinus, Acipenser, Catostomus* and various teleosts.

Mechnikov, O. 1879. Notiz über den Beckenbogen des *Scaphirhynchus hermanni*. Zoologischer Anzeiger 3: 21–23. [1880.1]

Meehan, W. E. 1910. Experiments in sturgeon culture. Transactions of the American Fisheries Society 1909, p. 85–90. [1910.1]

Meissner, V. I. 1907a. Materialien zur vergleichenden Anatomie der Knorpelganoiden: I. Der Schultergürtel der Acipenseriden [Text in Russian]. Travaux de la Société des Naturalistes de l'Université Impériale de Kazan 40, 39 p. 2 pls. & 15 figs. [1907.1]

Meissner, V. I. 1907b. Neue Beiträge zur vergleichenden Anatomie des Schultergürtels der Acipenseriden. Zoologischer Anzeiger 32: 465–468. 2. figs. [1907.2]

Meissner, V. I. 1908. Bericht über die Arbeiten der biologischen Wolgas-Station im Frühling 1907 über die künstliche Befruchtung von *Acipenser ruthenus* [Text in Russian]. Trudy Saratovkogo Obchestva Jestestvoispytatelei I Luibitelei Prirody, 5, pt. 3: 85–104. [1908.1]

Mitchill, S. L. 1814. The fishes of New-York, described and arranged. Transactions of the Literary and Philosophical Society of New-York, 1814, 1: 355-492. 6 pls. [1814.2][22] In the introductory remarks, 147 species (and in addition, 19 varieties) are summed up. These are arranged according to Shaw's modification of the Linnaean system. 60 of the species are illustrated in 6 steel-plates. The preceding work appears to have been translated into French by F.J. Meisser, a physician of Brussels, it being apparently the world referred to under the title: "Mémoire sur l'ichthyologie de; l'Amérique Septentrionale, par Mitchill, traduction de l'anglais," in Vandermaelen's Dictionnaire des hommes des lettres, des savans et des artistes de la Belgique [1837], p. 29.

Mitchill, S. W. 1858. Observations on the blood crystals of the sturgeon. Proceedings of the Academy of Natural Sciences of Philadelphia, p. 2–4. [1858.1]

Mitchill, S. W. 1859. Notes upon the effect of alcohol, glycerine, water, gum, ammomia and the vacuum upon the exposed hearts of frogs, snapping-turtle and sturgeons. The American Journal of Medical Science 37: 343–348. [1895.1]

Mojsisovics von Mojsvar, A. 1892. Ueber eine auffällige (neue) Varietät des *Acipenser ruthenus* L. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 101: 328–330. [1892.1]

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[21] This reference and the two others by the same author mention sturgeons.

[22] This article, published in 1915 contains the original description of *Acipenser oxyrinchus* Mitchill, 1815.

Molin, R. 1851a. *Acipenser vallisnierii*, n. sp. Reivista Periodica di Lavori della I.R. Accademia di Scienze, Lettere ed Arti di Padova, 1851–53, 1: 366–371. [1851.1]

Molin, R. 1851b. Sullo scheletro dell'*Acipenser ruthenus*. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 7: 357–378. pl. — Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti di Venezia 2, p. 196–198. [1851.2]

Molin, R. 1851c. Osservazioni sull'*Acipenser ruthenus* e sulla glandola delle appendici maschili dei Plagiostomi. Atti del Reale Istituto Veneto di Scienze, Lettere, ed Arti di Venezia, Ser. 2, vo. 4. [1853.1]

Murray, A. 1871. Note regarding the young stage of the sterlet [*Acipenser ruthenus*]. Proceedings of the Zoological Society of London 2: 138. [1871.1]

Nardo, G. D. 1852. Osservazioni sopra il lavoro del Professore Molin intitolato: "Monografia [sullo scheletro][23] dell'*Acipenser ruthenus*." Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti di Venezia, Ser. 2, vol. 2. Also separate: Venezia, 1853. [1852.1]

Nardo, G. D. 1873. Sulla etimologia de' nomi volgari che si danno alle varie specie de storioni [*Acipenser*] viventi nelle Venete acque, e particolarmente sull' Attilus di Plinio, detta comunemente ladano, che pescasi nel fiume Po. Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti di Venezia, Serie 4, 3: 1766–1772. [1873.2]

Nazarov, J. 1901. Ueber den Zug der Acipenseriden vom Meer in den Uralfluss und zurück ins Meer. [Text in Russian] Vestnik Rybopromyshlennosti St. Petersburg, 16: 672–674. [1901]

Nemeczek, A. 1911. Beiträge zur Kenntnis der Myxo- und Microsporidien der Fische. Archiv für Protistenkunde 22: 143–169. [1911.1] Material observed consisted of *Silurus, Tinca, Barbus, Esox, Luciperca, Aspro, Abramis, Leucisus, Aspius, Acipenser, Oncorhynchus* and *Gadus*.

Nemiloff, A. 1906. Zur Frage über den Bau der Fettzellen bei *Acipencer ruthenus*. Anatomische Anzeiger 28: 513–522. 6 figs. [1906.1]

Nicolas, A. 1904. Recherches sur le développement du pancréas du foie et de la rate chez le sterlet (*Acipenser ruthenus)*. Archives de Biologie. 20: 425–460. 3 pls. — Comptes rendus de l'Association des Anatomistes de Nancy 1902, p. 14–16. [1904.1] L'évolution des deux ébauches ventrales du pancréas chez le sterlet coïncide avec ce que l'on sait de leur développement chez certains ganoïdes et chez les téléostéens.

Nicolas, J. and C. Lesieur, 1899. Effets de l'ingestion de crachats tuberculeux humains chez les poissons. Comptes Rendus des Séances de la Société de Biologie, Paris, p. 774. [1899.1]

Nikolskiĭ, A. M. 1896. *Acipenser stenorhychus*, sp. nov [Text in Russian]. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse 1: 400–405. [1896.1]

Nikolskiĭ, A. M. 1900. *Pseudoscaphirhychus rossikowi*, n. gen. et n. sp. [Text in Russian] Annuaire du Musée zoologique de l'Académie impériale des sciences de St. Pétersbourg 5. [1900.2]

Noll, F. C. 1871. Der Stör im Rhein und Main, der Zoologische Garten, 12. Jahrgang, p. 180– 183. [1871.1]

Nordqvidst, O. F. 1899a. Afbildning af den amerikanska insjostoren. Fiskeritidskrift för Finland, 8: 199. pl. [1899.1]

Nordqvidst, O. F. 1899b. Den amerikanska insjostoren [*Acipenser rubicundus*]. Tidskrift för Jägare och Fiskare, Helsingfors, 7: 125–127; 180–186. pl. [1899.3]

O., D. C. 1703. Acipenseris sive sturionis anatome. Nouv. Lit. Germ. Hamburg, 325. [Pre-Linn 1703.1]

Olearius, A. 1647. Moscovitische und Persianische Reisebeschreibung. Slesvic, 1647. fol. [Pre-Linn. 1647.1] Other issues: Schleswig, 1656, 1663, 1671; Hamburg, 1669; Paris (French), 1656, 1659, 1679; Amsterdam, 1666, 1627, 1651 (Dutch); Utrecht, 1651 (Dutch). An English version is:

Olearius, A. 1662. The voyages & travels of the ambassadors sent by Frederick, Duke of Holstein to the Great Duke of Muscovy, and the King of Persia. Begun in . . . 1633 and finish'd in 1639. Whereto are added the travels of J. A. de Mandelslo . . . from Persia, into the East-Indies. Containing a. . . . description of Indosthan, the Mogul's Empire, the oriental islands, Japan, China, &c . . . In III books . . . London, 1662. xxiv, 424, iv, 287 p. 4 pis. 7 maps. 4°. [Pre-Linn. 1662.1] Fishes and fishing in Volga river and Caspian Sea. 2nd ed. (*Olearus* only), London, 1669. Copy, N.Y.P.

Osborn, H. F. 1902. Distinctive characters of the mid-Cretaceous fauna. Contributions to Canadian Paleontology 3: 1–81. [1902.1]

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[23] '[of the skeleton]' was omitted for the title; see www.biodiversitylibrary.org/page/7783249

Ostroumov, A. A. 1906. Zur Entwicklungsgechiche des Sterlets (*Acipenser ruthenus*). Zoologischer Anzeiger 1908–08. [1906.1] i. Embryonalcloake und Bildung des Sinus. Zoologischer Anzeiger 29: 515–517. 2 figs.

Ostroumov, A. A. Ueber das Wachstum der Jungen des Sterlets [Text in Russian]. Travaux de la Société des Naturalistes de l'Université Impériale de Kazan 42 livr. 3, 43 p. pl. [1910.1]

Ostroumov, A. A. 1911. Sur les périodes de croissance chez les sterlets [Text in Russian]. Travaux de la Société des Naturalistes de l'Université Impériale de Kazan 43 livr. 6, 48 p. pl. [1911.1]

Ostroumov, A. A. 1912. Das zweite Jahr des Wachstums des Sterlets [Text in Russian]. Trudy Kazanskogo Obchestva Jestestvoispytatelei, 45, pt. 1, p. 1–24. [1912.1]

Ostroumov, A. A. 1913. Das dritte Jahr des Wachstums von *Acipenser ruthenus* [Text in Russian]. Kazan, 24 p. pl. 8˚. [1913.1]

Ovsyannikov, F.V. 1870. Zur Entwickelungsgeschichte des *Petromyzon fluviatilis* und *Acipenser ruthenus*. St. Petersburg. Fig. 8˚. [1970.1]

Ovsyannikov, F.V. 1872a. The sturgeon's development. Abstract in Popular Science Review 1:42–427. — The American Naturalist 6: 175. [1872.1]

Ovsyannikov, F. V. 1872b. Ueber einen neuen Parasiten in den Eiern des Sterlet. Bulletin of the Academy of Science of St. Petersburg 17: 104-108. — Zeitschrift für wissenschaftliche Zoologie 22: 292. [1872.2]

Ovsyannikov, F. V. 1872c. Ueber neue Tastorgane beim Sterlet. Zeitschrift für wissenschaftliche Zoologie 22: 292. [1872.3]

Pallas, P. S. 1771-78. Reise durch verschiedene Provinzen des russischen Reiches. 3 vols. St. Petersburg, 1771-76. Illust. 4º. [1771.1].

Pallas, P. S. 1776. Auszug aus einem Briefe … die Naturgeschichte und Verpflanzung des Sterlets [*Acipenser ruthenus* L.] betreffend. Beschäftigungen der Berlinischen Gesellschaft Naturforschender Freunde 2: 532–534. [1776.1][24]

Pappenheim, P. 1905. Ueber die Acipenseriden-Gattung *Scaphirhynchus*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, p. 5–7. [1905.4]

Parchappe, M. 1848. Notes anatomico-physiologiques sur la structure du cœur de l'esturgeon et de la raie. Comptes rendus de l'Académie des Sciences Paris 27: 24–27. — Notizen (Frorien) 8: 65–68. — Abstract in l'Institut 16: 198. [1848.1]

Parker, W. K. 1873. On the development of the face in the sturgeon [*Acipenser sturio*]. Monthly Microscopical Journal 9: 254–257. [1873.1]

Parker, W. K. 1881. On the structure and development of the skull in sturgeons [*Acipenser ruthenus* and *A. sturio*]. Proceedings of the Royal Society of London 32: 142–145. [1881.1]

Pavesi, P. 1907. Gli Acipenseri nostrali. Rendiconti Reale Istituto Lombardo di Scienze e Lettere, Milano. Ser. 2. 40: 332–345. [1907.1]

Pavlov. H. 1879. A study of the teeth in the sterlet. Arbeiten der St. Petersburger Gesellschaft der Naturforscher, 9: 494–508. [1879.1]

Pavlovskiĭ, E. 1895. Sur la structure de la moelle épinière de l'esturgeon sterlet. Comptes Rendus des Séances de la Société de Biologie de Paris, 10. sér. 2, p. 487–488. [1895.1]

Peltzam, E. D. 1870. Die Zähne von Jungen des Sterlets (*Acipenser ruthenus* L.) Kazan. [1870.1]

Peltzam, E. D. 1883. Biologische Untersuchungen über störartige Fische [Text in Russian] Procès-Verbaux des Séances de la Société des Naturalistes de l'Université de Kazan, Beilage no. 65, 17 p. [1883.1]

Peltzam, E. D. 1887. Beobachtungen über die Segmentation des Sterleteies [Text in Russian]. Mitteilungen der Gesellschaft die Freunde der Naturkunde, Moscow 50, pt. 1,206. [1887.1]

Pliny (Secundus), Caius. 1601. Plinies natural historie of the world, translated into English by Philemon Holland, Doctor of Physick. 2 vols. London[25]. [Pre-Linn. 1601.1]

Post, H. The sturgeon: some experiments in hatching. Transactions of the American Fisheries Society 1890, p. 36–40. [1981.1]

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[24] Original description of *Acipenser stellatus* Pallas, 1771.

[25] There are multiple translations of Pliny's work. A detailed analysis of his writing on fish is Cotte, M.J. (1944) *Poissons et animaux aquatiques au temps de Pline.* Paul Lechevalier, Paris, 265 p. Pages 171-175 give a comprehensive discussion of sturgeon, with numerous citations to classical Greek and Roman authors, along with Medieval authors. Cotte's account also presents etymologies of *Acipenser* and other names of surgeon in various European languages.

Priem, F. 1904. Sur les poissons fossiles du Bartonien et les siluridés et acipenséridés de l'Eocène du bassin de Paris. Bulletin de la Société géologique de France, 4 sér. 4,42–47. [1904.3]

Prince. E. E. 1899. The food of the sturgeon. 31st Annual Report of the Department of Marine and Fisheries, Ottawa 1898, lv–lx. [1899.1]

Prince, E. E. 1905. The Canadian sturgeon and caviar industries. 37th Annual Report of the Department of Marine and Fisheries, Ottawa, 1904, liii-lxx. [Add. 1905.1]

Quantz, H. 1903. Störfischerei und Störzucht im Gebiete der deutschen Nordseeküste. Mitteilungdes deutschen Seefischerei-Vereins 19: 176–204. 2 figs. [1871.1]

Rafinesque-Schmaltz, C. S. 1820. Ichthyologia Ohiensis, or natural history of the fishesinhabiting the river Ohio and its tributary streams, preceded by a physical description of the Ohio and its branches. Lexington, Kentucky, 90 p. 8°. [1820.2][26] Originally printed in the Western Review and Miscellaneous Magazine, Lexington, Kentucky, 1819-20. A verbatim et literatim reprint of the original, with a sketch of the life, the ichthyologic work, and the ichthyologic bibliography of Rafinesque was published by Richard Ellsworth Call at Cleveland, 1899. It contains redescriptions of all the species previously indicated by the author, thirteen in number. The name *Silurus argentinus* is changed to *Pimelodus argyprus*, and the genus *Pimelodus* is divided into a number of subgenera and sections.

Richardson, J. 1836. Fauna Boreali-Americana; or the zoology of the northern parts of British America, containing descriptions of the objects of natural history collected on the late northern land expeditions, under the commend of Sir John Franklin, R.N. 4 vols, London & Norwich, 1831-37, pls. 4°. [1831.1] Part iii, the fish, with 24 pls., 14 of which are colored. 1836[27]

Roule, L. 1905. Le régime biologique et la pêche de l'esturgeon (*Acipenser sturio* L.) dans le Midi de la France. Bulletin de la Station de pisciculture, Toulouse-Paris 2: 59–62. [1905.3]

Rozwadowski, J. 1905. Nos poissons ; *Anguilla vulgaris*; Minożek, *Petromyzon planeri*; Ryby jesiotrowate, Acipenseridae. Okóln. Krajow. Towarz. Ryback. Kraków p. 20–23; 121–126; 218–226. 8 pls. [1905.1]

Rozwadowski, J. 1906a. Nasze ryby. Sterlet czyli czeczuga (*Acipenser ruthenus* – der Sterlet) [Nos poissons ; le sterlet]. Okóln. Krajow. Towarz. Ryback. Kraków p. 155–159; 185–187. [1906.1]

Rozwadowski, J. 1906b. Nasze ryby. Szyp (*Acipenser schypa* – der Dick) [Nos poissons:[*Acipenser schypa*] Okóln. Krajow. Towarz. Ryback. Kraków, p. 26–29. [1906.2]

Russell, A. J. 1879. Sturgeon in the Thames and Medway. The Zoologist: A Monthly Journal of Natural History 3. Ser. 3, p. 383. [1879.1]

Ryder, J. A. 1888. On the development of the common Sturgeon (*Acipencer sturio*). TheAmerican Naturalist 22: 659–660. [1888.2]

Ryder, J. A. 1890. The sturgeons and sturgeon industries of the eastern coast of the United States, with an account of experiments bearing upon sturgeon culture. Bulletin of the United States Fish Commission 8: 231–328. 19 pls. [1890.4]

Sandman, J. A. 1906. Störar fångad i Finska viken [*Acipenser sturio* L. im Finnischen Meerbusen gefangen]. Fiskeritidskrift för Finland, 15: 234–235. [1906.7]

Saville, S. P. 1860. Capture of sturgeon in fresh water. The Zoologist: A Monthly Journal of Natural History 18: 7202. [1860.1]

Sawadsky, A. M. 1911a. Die Entwicklung des rudimentalen larvalen Haftapparates beim Sterlet (*Acipenser ruthenus*). Anatomische Anzeiger 40: 356–378. pl. & 18 figs. [1911.1]

Sawadsky, A. M. 1911b. Die Entwicklung des rudimentalen larvalen Haftapparates beim Sterle (*Acipenser ruthenus*). Travaux de la Société des Naturalistes de l'Université Impériale de Kazan 44 pt. 1. 27 p. 7 figs. [1911.2]

Saxby, T. E. 1905. Sturgeon in the Shetland seas. The Annals of Scottish Natural History, 184. [1905.1]

Schalin, Z. 1883. *Pelecanus onocrotalus*, *Acipenser sturio* och *Haliaetus albicilla*. Meddelanden af Societas pro Fauna et Flora Fennica 9: 146. [1883.1]

Scherer, J. 1857. Untersuchung der Galle eines Störes. Verhandlungen der Physikalisch-medizinische Gesellschaft zu Würzburg 7: 269–270. [1857.1]

Schroeder A. E. von. 1895. The encysted stage of a *Distomum* in the muscles of a sturgeon. [Text in Russian] Vrach, St. Petersburg 16: 1200–1201. Abstract in Centralblatt für Bakteriologie, Jena, 1896, 19 (Abtheilung 1), 462. [Add. 1985.1] 487–493. 4 figs.

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[26] Contains the original description of *Scaphirhynchus platorynchus* (Rafinesque, 1820).

[27] Part iii contains the original description of *Acipenser transmontanus* Richardson, 1836.

Severtzov, A. N. 1911. Die Keimenbogennerven der Fische. Anatomische Anzeiger 38: 487–493. 4 figs. [1911.1]

Sizov, A. 1881. The auditory labyrinth of cartilaginous fish (sturgeon, sterlet, and schiffa;*Acipenser ruthenus, A. sturio*, and *A. schiffa*). [Text in Russian] Procès-Verbaux des Séances de la Société des Naturalistes de l'Université de Kazan 9, 3. [Add. 1881.1]

Skorikov, A. S. 1902. Ueber *Cystoopsis acipenseris* Wagn., den Parasit des *Acipenser ruthenus*. [Text in Russian] Vestnik Rybopromyshlennosti St. Petersburg, 17: 459–460. [1902.1]

Skorikov, A. S. 1903. Sur[28] Parasitologie der Störe. [Text in Russian] Vestnik Rybopromyshlennosti St. Petersburg, pt. 18, p. 63–82. pl. [1903.1]

Sodoffsky, W. 1849. Ueber die Störgattungen des Caspischen und Schwarzen Meeres. Korrespondezblatt des Naturforscher - Vereins Riga 3: 41–47 and 69–81. [1849.1]

Solotnizky, N. F. von. 1902. Der Sterlet in Freiheit und im Aquarium. Natur und Haus 9: 405–408. [1902.1]

Stannius, F. H. 1843. Ueber den Bau des Gehirnes des Störs. Archiv für Anatomie und Physiologie (Müller), 36–44. fig. [1843.1]

Stemann, H.G. — von. 1894. Ein Wort über Salmoniden-Störgewinnung in Schleswig-Holstein. Allgemeine Fischerei Zeitung 19(6): 91–93. [1894.1]

Stone, L. 1901. The spawning habits of the lake sturgeon. Transactions of the American Fisheries Society 1900, p. 118–123. [1901.1]

Stone L. 1902. Sturgeon hatching in the Lake Champlain basin. Transactions of the American Fisheries Society 1901, p. 137–143. [1902.1]

Storer, D. H. 1844. Descriptions of *Acipenser rubicundus*, *A. platyrhyncus* and *Rutilus storerianus*, accompanied with figures. Proceedings of the Boston Society of Natural History 1: 71. [1844.4]

Sundevall, C. J. 1854. *Acipenser huso* i Sverige. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 10: 228. [1854.1]

Sweetapple, E. 1867. Large sturgeon in the Severn. Zoologist: A Monthly Journal of Natural History. Ser. 2, 2: 836. *Ibid*., 1868, 3:1295. [1867.2]

Sweetapple, E. 1869. Sturgeons in the Severn. The Zoologist: A Monthly Journal of Natural History. Ser. 2, 4: 1836. [1869.2]

Tanaka, S. 1914. Notes on an *Acipenser* from Hakodate. [Text in Japanese] Gyogaku Zasshi [Journal of Ichthyology] 1, no. 1, p. 17–18. [1914.1]

Tavernier, J-B. 1676. [On the glue made by the Turks from body membranes of the sturgeon. Philosophical Transactions of the Royal Society 11: 714. [Pre-Linn. 1676.1] An extract from a running review in the Phil. Trans. of Tavernier's voyages. Théry, A. 1901. Note sur un esturgeon capturé dans la baie d'Alger. Bulletin de la Société d'histoire naturelle de l'Afrique du nord, 1. année, 14. [1909.1]

Theunissen, F. 1914. Over de rangschikking der motorische cellen in de hersenen van *Acipenser ruthenus* en *Lepidosteus osseus* Verslagen van de Zittingen der Wis- en Natuurkundige Afdeeling van de Koninklijke Akademie van Wetenschappen, Amsterdam 22:963–971. 2 figs. — Proceedings of the Section of Sciences, Koninklijke Akademie van Wettenschappen, Amsterdam.16:1032–1041. 2 figs. [1914.1] Close resemblance with each other and with *Amia,* with selachian and teleostean conditions.

Tichenko, S. 1906. Sur l'origine du mésenchyme[29] chez le sterlet (*Acipenser ruthenus*). Zoologische Anzeiger 30: 728–730. 2 figs. [1906.1]

Tichenko, S. 1907. Bericht über eine Fahrt nach Simbirsk im Frühjahr 1905 zwecks Befruchtung von Sterleteirn. [Text in Russian] Procès-Verbaux des Séances de la Société des Naturalistes de l'Université de Kazan 36: 1–4. [1907.1]

Tower, W. S. 1908. The passing of the sturgeon; a case of the unparalleled extermination of a species. Popular Science Monthly 73: 361–371. [1908.1]

Trois, E. F. 1896. Sopra un esemplare di *Acipenser stellatus* proveniente dall' Adriatico. Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti di Venezia. Serie 7, 7: 1175–1177. Bollettino Naturalisti Sienna 17: 25–26. [1896.1]

Tulloch, J. S. 1905. Sturgeon in the Shetland seas. Annals of Scottish Natural History, 120 [1905.1]

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[28] Here, 'Sur' should be replaced by 'Ueber die...'

[29] Misspelled 'mesenchime' in Dean's bibliography.

Vutskits, G. 1910. Unsere vaterländischen Acipenseriden. Halászat, 1910–11, 13: 4–169. [Add. 1910.3]

W. 1896. Ueber den Sterlet [*Acipenser ruthenus*]. Allgemeine Fischerei Zeitung 21. Jahrgang, 4: 58–61. fig. [1896.1]

Westberg, P. 1899. Ueber die Fischgattung *Scaphirhynchus* (Spatenschnabel). Korrespondenzblatt des Naturforscher-Vereins Riga 43: 159–160. [1899.1]

White, J. H. 1873. Large sturgeon in the Ouse. Zoologist: A Monthly Journal of Natural History. Ser. 2, 8: 3803–3804. [1873.1]

Wight, J. 1901. Sturgeon fishing in the Ural river. Strand Magazine, p. 404–409. illust. [1901.1]

Wilder, B. G. 1876. Notes on the North American ganoids, *Amia, Lepidosteus, Acipenser* and*Polyodon*. Proceeding of the American Association for the Advancement of Science 24th meeting 1875, pt. 2, p. 151–196. 3 pls. [1876.2]

Woodward, A. S. 1889. On the paleontology of sturgeons. Proceedings of the Geological Society of London 11: 24–44. pls. & 13 figs. [1889.10]

Woodward, A. S. 1890. The fossil sturgeon of the Whitby Lias. Naturalist, p. 101–108. [1890.3]

Zalenskiĭ, V. V. 1876. History of the development of the sterlet, *Acipenser ruthenus*, preliminary communication [Text in Russian] 3 parts. Protokolyu Zasedanii Kazanskogo Obchestva Estestvoispytatelei Prirody, 1876–77 (1877–78), prilozheniya, no, 23 & 27; 1877–78, no. 37. [1876.1]

Zalenskiĭ, V. V. 1878a. Embryologie der Ganoiden. I. Impregnation and cleavage of the egg of the sterlet. II. Development of the skeleton in the sterlet. Zoologischer Anzeiger 1. Jahrgang 11: 243–245; 12: 266–269; 13: 288–291. [1878.1]

Zalenskiĭ, V. V. 1878b. On the development of the sterlet, *Acipenser ruthenus* [Text in Russian] 2 parts. Trudy Kazanskogo Obchestva Estestvoispytatelei Prirody, 1878–80, 7, no. 3. iii, 545 p. 19 pls. [1878.2] The second part was originally numerated as vol. x, no. 2, and subsequently corrected

Zalenskiĭ, V. V. 1878c. Entwicklungsgeschichte des Sterlets (*Acipenser ruthenus*) Vorläufige Mittheilung [Text in Russian]. Sitzungsberichte der Gesellschaft Naturforschender der Universität Kasan 1877 (1878). 24 p. [1878.3]

Zalenskiĭ, V. V. 1879. The developmental history of *Acipenser ruthenus*. I. The embryonal stage. II. Post-embryonic development of the organs [Text in Russian] Transactions de la Société des Naturalistes de Kazan, 1879, 7, pt. 3, 226p. 9 pls. — Mémoires de la Société impériale des Naturalistes de l'Université de Kazan 1880, 10, pt 2, p. 227–545. [1879.1]

Zalenskiĭ, V. V. 1881. Recherches sur le développement du sterlet (*Acipenser ruthenus*). Archives des sciences biologiques 2: 233–3441. 4 pls. Also separate; Ghent, 1881. 4 pls. 8°. [1881.1]

Zalenskiĭ, V. V. 1899. Développement des nageoires impaires des acipenséridés. Annales des Sciences Naturelles - Zoologie 4: 299–324. Also separate; St. Petersburg, 1899. 3 pls. [1899.1]

Zavadskiĭ, A. M. 1911. Die Entwickelung des rudimentalen larvalen Haftapparates beim Sterlet (*Acipenser ruthenus*). [Text in Russian] Trd. Obšč. Jest., Kazan 44, pt. 1:1–27. [1911.1]

Zavadskiĭ, A. M. 1912. Die Morphogenese des Mundes und des Schlundes des Sterlets. [Text in Russian] Prot. Obšč. Jest. 43: 34–36. [1912.1]

Zittel, K. A. 1886. Ueber vermeintliche Hautschilder fossiler Störe. Sitzungsberichte der Bayerische Akademie der Wissenschaft 16: 261–264. [1886.2]

Zofraf, N. Y. 1887a. Beitrag zur Kenntnis der Organisation des Sterlets (*Acipenser ruthenus*) [Text in Russian] Moskau. 2 pls. & figs. 4°. [1887.1]

Zofraf, N. Y. 1887b. Les données pour l'étude de l'organisation de l'esturgeon. [Text in Russian] Moscou. 2 pls & figs. 4°. [1887.2]

Zofraf, N. Y. 1887c. Die embryonale Rückenflosse des Sterlets (*Acipenser ruthensus*). Biologisches Centralblatt 7 (17): 517–521. [1887.3]

Zograth, H. 1887. [External characters and anatomy of *Acipenser ruthenus* L.] [Text in Russian] Mémoires de la Société impériale des naturalistes de Moscou 53, pt. 3. 72 p. 2 pls. & figs. [1887.1]

Zolotniskiĭ, N. F. 1902. Le sterlet en liberté et en aquarium [Extrait du journal Natur und Haus, Berlin, traduction de M. Delaval]. Bulletin de la Société Nationale d'Acclimatation de France 49: 387–392. [1902.3]

The global catch of commercial sponges (1950 to 2019)[1]

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Abstract

The fishing for commercial sponges (genera *Spongia* and *Hippospongia* of the family Spongiidae) is reviewed, with emphasis on the second half of the 20th century, when catches declined from a level in 1950 that was already much lower than near the end of the 19th century. The review covers the local and distant-water catch of Greek sponge fishers, the sponge catches of other Mediterranean countries (mainly Croatia, Libya, Tunisia, and other countries), the partly Greek- and Cuban-driven sponge fisheries in The Bahamas and Florida (U.S.), and the Cuban and Columbian sponge fisheries, and concludes with very limited data for some small Pacific sponge fisheries (especially in the Philippines). Overall, the dry weight of sponges produced in the 1950s was 300-400 tonnes (t) per year mainly from the Mediterranean vs. 200 t per year in the 2010s mainly from the Central Western Atlantic. From 1950 to 2019, the sum of sponge catches reported to the Food and Agriculture Organization (FAO) by its member countries was 11 % of the sum of the catches reported here.

Introduction

Sponges have been fished for thousands of years for ornamental, hygienic, protective or pharmaceutical purposes (Corfield 1938; Stuart 1948; Storr 1964). The origin of this practice is located in the Mediterranean Sea and especially in Greece, where the first written description of sponges and their fisheries can be found (Voultsiadou 2007). The first description of sponges comes from Aristotle (350 BC), in his *Historia Animalium*, where sponges are reported as primitive animals living attached on the substrate and being black when alive before coloured and washed (Pronzato and Manconi 2008; Voultsiadou and Vafidis 2007). In his *Halieutica*, Oppian (200 BC) was the first to describe the sponge harvesting procedure by sponge fishers including the thick rope around their waist, the heavy weight for remaining underwater, the sickle for cutting the black sponges growing on the rocks, as well as their prayers to *Apollo* before they dive (Voultsiadou *et al.* 2011).

Sponges, belonging to the Phylum Porifera, are organisms that feed by filtering plankton and dissolved organic matter from the water surrounding them through a complex system of pores (hence the name

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[1] Cite as: Martinangeli, L., M. Fourt, M. Butler, A.C. Tsikliras, N. Smith, M.L.D. Palomares, B. Derrick, E. Chu and D. Pauly. 2022. The global catch of commercial sponges (1950 to 2019), p. 85-106. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

Porifera) and channels (Figure 1; Storr 1964; Leys *et al*. 2011; Pauly *et al*. 2022). They are sensitive to water quality conditions (Butler *et al*. 2018) so the dynamics of their populations can help us to understand the health of the ocean and the change of conditions in coastal ecosystems.

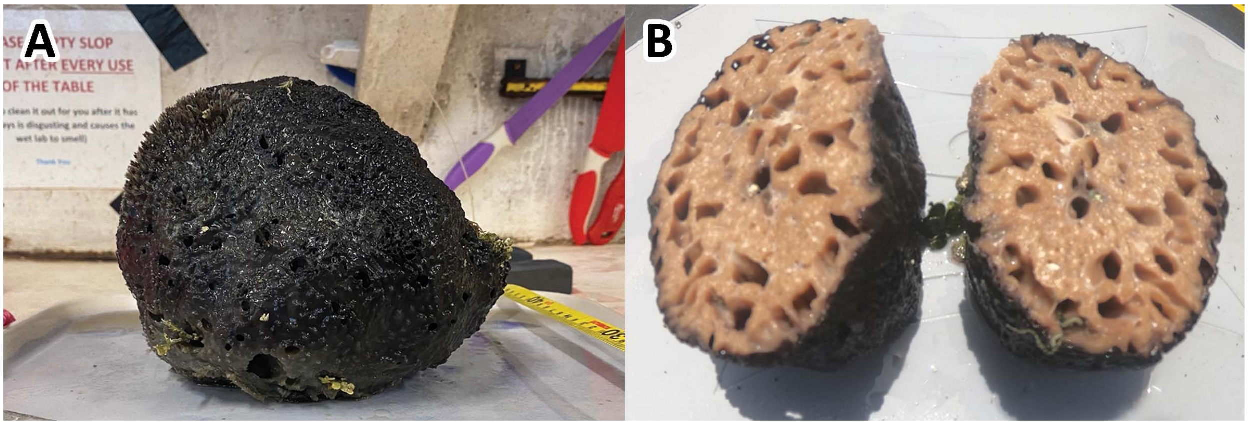

Figure 1. The wool sponge *Hippospongia lachne*. **A**: side view. **B**: horizontal cross section showing the interior canals that are usually inhabited by a wide variety of commensal invertebrates. Based on a specimen collected and photographed in Florida by M. Butler on 18 September 2021.

Commercial sponges used by humans belong to the aptly named Demospongia family (i.e., common people's sponges) and were valuable because of their capacity to absorb a large quantity of water, durability, and softness. Two genera meet these criteria, *Spongia* and *Hippospongia* (Table 1).

Only their absorbent skeleton made of spongin and which constitutes only a fraction of their wet weight (e.g., 4% of the wet weight of *H. lachne* and 11 % of *S. graminea*; Pauly *et al*. 2022) is used.

Table 1. Commercial sponge species of the genera *Spongia* and *Hippospongia* considered in this study

Scientific name	**English common name (distribution range)**
H. communis (Lamarck, 1814)	Honey comb (Mediterranean)
H. gossypina Hyatt, 1877	Velvet sponge (Central West Atlantic; Caribbean)
H. lachne (de Laubenfels, 1936)	Wool sponge (Central West Atlantic; Caribbean)
S. barbara Duchassaing & Michelotti, 1864	Yellow sponge (Central West Atlantic; Caribbean)
S. cheiris[a] De Laubenfels and Storr, 1958	---- (Central West Atlantic; Caribbean)
S. graminea Hyatt, 1877	Glove sponge (Central West Atlantic; Caribbean)
S. lamella (Schulze, 1879)	Elephant ear (Mediterranean)
S. mollissima [b] Schmidt, 1862	---- (Mediterranean)
S. obscura Hyatt, 1877	Grass sponge[b] (Central West Atlantic; Caribbean)
S. officinalis Linnaeus, 1759	Greek bathing sponge (Mediterranean)
S. pertusa Hyatt, 1877	Hardhead sponge (Central West Atlantic; Caribbean)
S. tubulifera Lamarck, 1814	Reef sponge (Central West Atlantic; Caribbean)
S. zimocca Schmidt 1862	Leather sponge (Mediterranean)

a) The status of the species is contested; see WorRMS (www.worms.org), which considers its name a junior synonym of *S. graminea*;
b) *S. mollissima* may a subspecies of *S. officinalis* (Pérez and Vacelet 2014).

Free diving and the use of a long-handled boat hook are the most common techniques used for harvesting sponges around the world, methods exported from Greece and Tunisia. From the 16th to the end of the 19th century, Mediterranean sponges dominated landings and were exported throughout Europe and, since the beginning of the 19th century, also to the United States (Voultsiadou *et al*. 2011). The Western Atlantic became a major exporter of commercial sponges at the beginning of the 19th century, especially The Bahamas and Florida in the US (Pauly *et al*. 2022), due to sponge die-offs in the Mediterranean and the subsequent emigration of Greek fishers who built on pre-existing, but small-scale sponge fisheries (Perez and Vacelet 2014). "Scaphander" (a helmet and a diving suit made of canvas, with boots and lead weights) or hard-hat diving became a common technique in Mediterranean sponge fisheries, but it was extremely dangerous (Flegel 1908). Commercial sponges in the Western Atlantic often occur in shallow water (< 4 m) where fishers rarely dive for sponges and instead tear sponges from the seafloor using a long-handle sponge hook while standing on small dinghy boats.

In the Mediterranean in the 19th century, the fishery was largely artisanal operating from small boats along coastlines. However, distant-water expeditions were also undertaken, mainly with crews from the Dodecanese Islands of Kalymnos and Symi (Aegean Sea, Greece). These expeditions would visit the waters of several Mediterranean countries in succession over several months. The fleets were composed of dozens of small catcher boats and a larger one with quarters for the crews of the smaller boats and for the storage of the sponges (Fourt 2019), a technique still used in many sponge fisheries. In the 1850s, approximately 4,500 sponge fishers were active only in the Dodecanese Islands with the number of sponge boats exceeding 600 harvesting around 120 t dry weight annually (Voultsiadou *et al.* 2011). The use of scaphander increased the annual harvest of sponges attributed to the Dodecanese fleet and fishers to 250-300 t by the end of the 19th century (Voultsiadou *et al.* 2011).

Data for this period are more abundant than since the beginning of the 20th century when a Greek fleet of ca. 300 vessels, employing around 2,400 fishers harvested around 150 t per year with similar quantities reported for Turkey, Tunisia, and other countries (Figure 4 in Voultsiadou *et al.* 2011). The number of vessels and fishers in Greece increased between 1920 and 1940 but the harvested quantities dropped to 130 t per year (Voultsiadou *et al.* 2011).

Later, commercial sponge fishing declined because of two World Wars, regional conflicts, a sponge pandemic disease, and overfishing that reduced sponge availability and the total quantities harvested (Figure 4 in Voultsiadou *et al.* 2011). Notably, a disease outbreak which started in late 1938 in The Bahamas devasted the Gulf of Mexico and Caribbean sponge fisheries (Galtsoff 1939), and another in 1986-1987 devasted the fisheries in the Mediterranean Sea (Milanese *et al.*, 2008). More recent sponge die-offs have occurred periodically in the Florida Keys since 1991 (Butler *et al.* 1995, 2022). Also, as several countries failed to report their sponge catches because of civil wars or political instability, all previous reports on catches are a compilation of various data sources (Voultsiadou *et al.* 2011). Another complicating factor obscuring accurate reporting is that once sponges are processed into their dry (skeletal) form, they can be stocked for years. Thus, it is not rare for countries to export sponges in years when sponge fishing is banned.

Although we mention some of their antecedents, the catch time series presented here start in 1950, the year when all the catch statistics of the *Sea Around Us* begin. We are aware that in 1950 the world's catch of sponges was well past its peak but this timing permits comparisons of modern fishery catch using a standard dataset that can be analysed jointly with 70 years of spatially disaggregated catch data for fish and invertebrates, including sponges (see contributions in Pauly and Zeller 2016; Zeller *et al.* 2016).

Reconstructions of sponge catches were done for the Mediterranean based predominantly on data gathered by the SACOLEVE Program (sacoleve.imbe.fr; data available from doi.org/10.1594/PANGAEA.926825), partly for the Mediterranean focusing on the Aegean Sea (Voultsiadou *et al.* 2011), and by a co-author and her associates (Fourt 2019; Fourt *et al.* 2020, 2021), and for Cuba by Lopeztegui-Castillo (2020). This contribution, however, is the first sponge catch reconstruction with a global scope. The sponge catch statistics reported here as dry (product) weight are also presented as wet weight as part of the catch statistics of the *Sea Around Us* (see www.seaaroundus.org), so sponge catch data can be compared with fish and other invertebrate catches that are expressed in wet (live) weight. Attempts at *in situ* farming or aquaculture of sponges have been investigated in some regions (Oronto *et al*. 2012), but to our knowledge none of those is commercially viable so those figures are not included in our summary.

Materials and Methods

Since 1950, the Food and Agriculture Organisation of the United Nations (FAO) has published annual global fisheries statistics, assembled and harmonized from annual submissions by their member countries (Garibaldi 2012; www.fao.org). These statistics include sponge catch statistics, but as also noted for other marine fisheries (Pauly and Zeller 2016), the annual submissions to FAO tend to strongly underestimate catches of fish and invertebrates (see, e.g., Brotz 2016). Thus, there was reason to 'reconstruct' the global catch of commercial sponges on a per-country basis using the same approach as developed for marine fisheries (see contributions in Pauly and Zeller 2016 and per-country accounts at www.seaaroundus.org) and, in the process, improve the taxonomic resolution of sponge catches to the extent possible.
Missing years of data in otherwise credible catch time series were linearly interpolated, or forward or backward projected when required to complete time series covering the 70 years from 1950 to 2019. The 'golden age' of sponge fisheries was well over in 1950; however, 1950 is the year when FAO began to publish annual global fisheries statistics that the *Sea Around Us* use as a starting point for all its reconstructions, and we made no exception for sponges. For some countries, even tentative time series of reconstructed sponge catches could not be generated, so we included them in Table 2. Note, however, the data in Table 2 were neither included in the global totals presented in figures below, nor in the *Sea Around Us* database, because we could not find publications that documented a sponge fishery in the countries in question and/or because some countries (e.g., France) only re-exports sponges imported from Greece

Sponge catches and landings are not speciose. For example, in Florida sponge landings are comprised of *H. lachne, S. graminea* and *S. barbara*, with *H. lachne* dominating by far. However, commercial sponges represent less than 5% of all sponge taxa in fished areas (Stevely *et al*. 2010, Butler *et al*. 2017b). If the catch was not reported by species, it was assumed that the most abundant commercial species of the region was the main species caught. The Pareto ratio (80/20; see en.wikipedia.org/wiki/Pareto_principle) was applied if two species were mentioned and one identified as more abundant, and a ratio of 50/50 when the two species are listed as equally abundant. When ratios were available only for certain years, they were used for all the years without information.

Table 2. Countries other than the 12 countries in Figures 2 to 5 that reported at least 1 tonne of commercial sponge catches (in t dry weight) to FAO from 1950 to 2019. These data are highly suspect and may pertain to re-export of imported sponges or mariculture. With the exception of the data for Syria, they are not included in the *Sea Around Us* database.

Countries	Years with reported catches	Sum of 'catch' reports (all years)
Australia	1998, 2003, 2005, 2007-2011, 2019	1.3
Colombia	1958-1963, 1967-1968, 1985-2016	191.0
France	1981-2018	30.6
Italy	1981-2018	7.2
Japan	1981-2000, 2013	11.9
Montenegro	1983-1991	2.0
New Zealand	1998-2001, 2008-2019	71.9
Spain	1963-1964, 1966, 1983-2018	6.9
Syria	1950-1969, 1983-1987	151.0
Taiwan	1968, 1972, 1974, 1976, 1978, 1986-1978	4.3

Results and Discussion

The results of this study consist of catch statistics of sponges by country from 1950 to 2019 in tonnes (t, i.e., metric tons) dry weight, but which are presented in t wet weight on the website of the *Sea Around Us* (www.seaaroundus.org) to enable comparison with the biomass of other organisms removed from the marine ecosystem by fisheries[2]. The presentation of these results starts with Greece, then covers other Mediterranean countries, then the Mediterranean as a whole. Then, the results for the Western Central Atlantic are presented for The Bahamas, the US (Florida), and the Caribbean. Finally, we cover a few Pacific countries and end up with a global estimate.

The Greek sponge industry

Greece has a long and complex history of sponge fishing; notably, the island of Kalymnos is well known for its fishers and knowledge about sponges (Fourt 2019). Since Antiquity, Greek fishers have caught sponges, and gradually exported their fishing techniques to neighbouring countries, then around the world. Entire Greek communities left Greece to develop sponge fisheries, especially in Tunisia, and later in Florida and The Bahamas (Fourt 2019; Pauly *et al.* 2022).

Anon. (1949c) writes that "*Sponge fishing represents approximately 20 percent of the fishing industry in Greece (the total industry producing around $ 15 million a year, of which sponge fishing brings in about $ 3 million), and is important to the Greek Government mainly because all sponges are exported, thus providing a source of badly needed foreign exchange.*" Thus, after World War II, the Greek agricultural bank issued low-interest loans for national sponge fleets and in the 1970s, the state supported the Greek sponge fishing industry with subsidies to renew and modernize its equipment (Fourt *et al.*, 2020).

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[2] For wool sponge *Hippospongia lachne*, the dry weight is set at 4% of wet weight, and at 11% for grass sponges *Spongia graminea* (from Pauly et al. 2022) which leads to an average of 7.5%, suggesting that dry weights should be multiplied by 13.3 to obtain wet weights. However, we will assume here a percentage of dry to wet weight of 10%, implying that dry weights should be multiplied only by 10 to obtain wet weights, in line with the conservative assumptions of earlier catch reconstructions as performed by the *Sea Around Us*.

Until the 1970s, in addition to the Aegean Sea (mainly Dodecanese and Cyclades Islands), Greek fleets fished in the waters of Tunisia, Libya, Italy, Egypt or Cyprus, which makes the reconstruction of Greek sponge catches taken from Greek waters particularly difficult. Their distant-water fleets allowed Greek businesses to export all four species of commercial sponges occurring in the Mediterranean Sea: *Hippospongia communis* and *Spongia zimocca, S. lamella* and *S. officinalis*.

Important events that have impacted the Greek sponge fisheries outside of Greece's Exclusive Economic Zone (EEZ) are:

- In 1952 and 1953, bans of foreign sponge fishing were proclaimed in Egypt and Libya;
- In 1953, Tunisia signed a decree defining its national waters and an overhaul of its legislation regarding costal fisheries, which involved the suppression of illegal sponge fisheries;
- From 1954 to 1959, on the basis of a new agreement, Greece was allowed to fish in Libya's waters; Greek sponge fishers operated until 1972 in Libya, probably on the basis of formal agreements between the two countries (Anon. 1965), or their fishing was both illegal and tolerated;
- In 1954, 1955, and 1956, Greek sponge fishers operated around Lampedusa Island (Italy), in addition to going there from 1956 to 2004 every 5 years or so because the trip, requiring complex logistics, was costly (and thus may have required some stock rebuilding during the years of 'fallowing');
- Greece had been fishing in Libya, Tunisia and Egypt for several years before 1950, with similar catches in each of these countries. Thus, this approximate distribution of the Greek catch in the countries was maintained until the end of the sponge fisheries in these countries by Greece;
- Egypt closed its coastal waters to Greek and other foreign fishing in 1963;
- In 1986, Greeks fished along the south coast of Sicily, because a sponge disease ravaged the Greek sponge beds;
- In 1987, an agreement was signed with Egypt to allowed 10 Greek ships to fish sponges in their waters, with Egypt keeping 30% of the catch;
- In 2008, fishers from Kalymnos Island operated in Libya on board of a Libyan boat. Only *Hippospongia communis* was fished and the catch was divided 50-50 between Greeks and Libyans;

Here, in line with the general procedures of the *Sea Around Us*, we assigned to Greece only the catch made in what is currently in Greek waters, while the 'Tunisian' catch consists of the catch by any country in what is currently the Tunisian EEZ (see Halouani *et al.* 2016), and similarly for other countries.

Figure 2A shows the catch of sponges in Greek waters, of which 90% originates from the Dodecanese Islands. It will be noted that this catch declined year after year, from 170 t in 1950 to nearly zero in 1991, especially since the epizootic disease of 1986/1987 (Voultsiadou *et al.* 2011). Annual catch dropped to less than 5 t in the late 1980s (immediately after the disease outbreak) and never recovered (Voultsiadou *et al.* 2011), with only 2 t harvested today. A similar decline also occurred in the number of sponge fishing boats from around 60 (150 crew) in the 1980s to 17 (100 crew) in the 2010s (Voultsiadou *et al.* 2011) and 10 boats (80 crew) today. Since the 2000s, the use of 'gangaves' (or '*gagava'* in Greek, i.e., small beam trawls) have been banned because of impact on the sea floor, and only scuba diving is practiced in the Greek sponge fisheries.

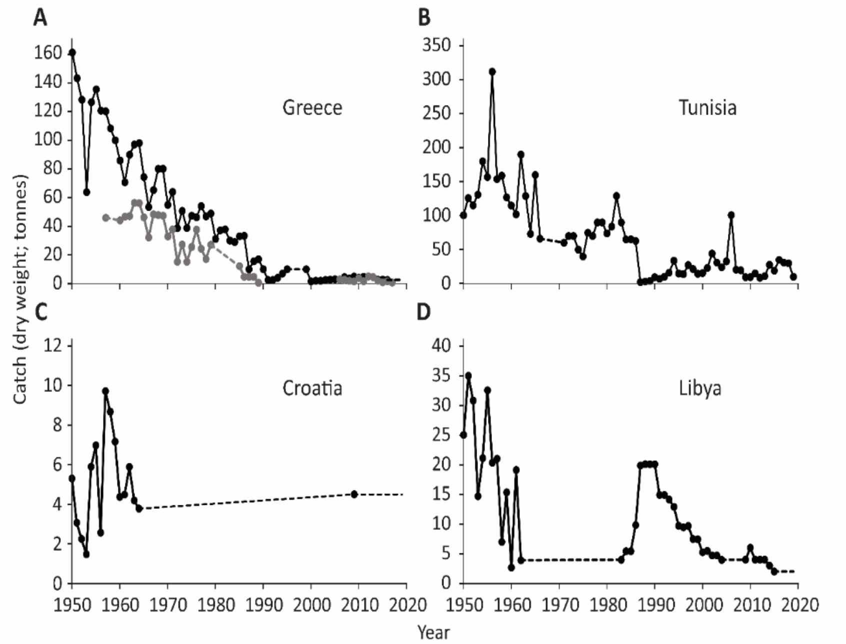

Figure 2. Catch of commercial sponges (in t dry weight) in the coastal waters of four Mediterranean countries with more or less continuous data from 1950 to 2019. **A**: Greece; note here the importance of the catch (grey dots) from the Dodecanese Islands (based mainly on Fourt 2019); **B**: Tunisia; **C**: Approximate trajectory of the catches of commercial sponges in the regions of Istria and Dalmatia (actual Croatia), consisting of annual Yugoslav catch report from 1950 to 1964 and a linear interpolation to the estimate reported by Rančić (2010) for 2009, projected forward to 2019; **D**: Libya; the data for 1983 to 2004 were read off Figure 3 in Milanese *et al.* (2008).

The Tunisian sponge fisheries

Tunisia is currently the most productive Mediterranean country with 8% of global sponge catch over the 10 last years, and one of the last areas in the region where sponge fisheries still occur. The main commercial species occurring along the Tunisian coasts are *H. communis* and *S. lamella* which, at the beginning of the 20th century, were still abundant in the north of the country, toward the Cap Bon (de Fages and Pronzevera 1908; Gaudillère 1954a, 1954b; Postel 1956). The bulk of sponge catches consist of *H. communis*, which is true to its species name in the South of Sfax, in the Gulf of Gabes, where the waters are relatively shallow (Rützler 1976; Camps-Fabrer 1996).

The second half of the 19th century saw a increase of sponge catches from Tunisian waters, when the Greek fleet introduced fishing techniques such as trawling with a '*gangave*' and diving with scaphanders whereas the main techniques used by Tunisian fishers were the use of trident from a boat and shore fishing.

Tunisia has specific terms to differentiate two types of sponge fisheries: the term "black fishery" applies to fisheries where the sponges are landed raw, while the term "white fishery" applied to fisheries which land (partly) processed (i.e., de-fleshed and dried) sponges (Anon. 1951), the only case of this distinction in a Mediterranean country. The three main Tunisian ports where sponges are landed are Sfax, Zarzis and Djerba, which are all in the Gulf of Gabes. Also, Tunisian fishers often go to Lampedusa and Pantelleria in Italy to fish sponges, but these catches are difficult to distinguish from the catch taken from Tunisian waters.

The Tunisian fishery has been severely impacted by the epizootic disease of 1986/1987 and its catches dropped from about 150 t per year 1950s to about 75 t per year in the 1970s, down to a few tonnes per year in the second part of the 1980s before stabilizing at around 20 t per year since 1995 (Figure 2B). This also had the effect of changing the habits of fishers. Sponges in waters less than 40 m were strongly impacted by the epizootic disease, which drastically reduced trident and shore-based fishing. However, the development of hookah diving makes it possible to access sponges in deeper waters. Currently, Tunisia has the greatest variety of fishing techniques in the Mediterranean Sea (Fourt 2019).

Anon. (1953) reported that "*Tunisian sponge production in 1953 amounted to 130.8 metric tons or 13 percent more than the 115.2 metric tons produced the previous year. It is possible that the increased production was due to the currently growing efforts by the Tunisian Government to find and exploit export markets for all domestically-produced commodities including sponges. During 1953 the United States imported only 2 metric tons of Tunisian sponges as compared to 3 metric tons.*"

A large fraction of Tunisian sponges is exported to western Europe (i.e., to France or Germany), but also to the United States, where sponges are less valuable. Since 1950, the Tunisian catch, which had represented 45% of Mediterranean catch, dropped by 90% in less than 40 years, simultaneously following and shaping the Mediterranean trend (Figure 2B).

The sponge fishery of Croatia

Croatia is currently one of the three major sponge exporters in the Mediterranean Sea. Part of the ex-Yugoslavia until 1991, Croatia has a coast that is very much longer than those of Bosnia & Herzegovina and Montenegro, the other two countries with access to the Adriatic Sea spawned by the breakup of Yugoslavia. The data up to 1964 from Basioli (1965) concern the region of Istria and Dalmatia, i.e., regions of the actual Croatia.

Contrary to the other Mediterranean countries, since 1950 Croatian sponge catches have been small, but relatively stable, with *S. officinalis* representing 90% of the catch and *S. lamella* the rest (Fourt 2019). The reason for the relative stability of Croatian sponge catches may be the fact that the epizootic disease of 1986/1987 did not occur in the Adriatic Sea. Precise catch data are missing since 1965, but an estimate of 4.9 tonnes in 2009 is available (Rančić 2010) which allowed for inter- and extrapolation (see Figure 2C). FAO has data for the periods with missing catches, but these data refer to the catch of hard-hat divers which, besides sponges, include corals and various molluscs (Fourt *et al.* 2019).

The Libyan sponge fishery

Anon (1949a) described the Libyan sponge fishery as follows: *"The sponge beds of Libya extend almost the entire distance from the Tunisian border to the Egyptian border. However, the most important beds are located near Zuara and Homs in Tripolitania, and near Benghasi and Derna in Cyrenaica. The beds vary in distance from the coast from two or three miles to more than fifty miles. The most popular and productive method of harvesting sponges in Libya is through the use of* <u>*machine diving boats*</u> *employing fully outfitted divers. The best growths usually found in water from 75 feet to 100 feet deep, are taken by this method. The second most generally used method in Tripolitania is* dredging *with a weighted net behind a slow-moving ship, but the sea bottom is too rough in Cyrenaica to permit this type of fishing.* Fernezen *(helmet only) diving is practiced in relatively shallow water beds in both territories with fair results.* <u>*Harpooning*</u> *is at present used somewhat more in Cyrenaica than in Tripolitania.* <u>*Nude diving*</u> *is the least productive method, although used fairly extensively in Cyrenaica.*"

Data are scarce for this country mostly because of political instability since WWII and the end of the Italian colonial administration. In fact, we were unable to find quantitative information for 1963 to 1983; thus, catch data were interpolated for this period. For the period from 1984 to 2004, the catch data were read off Figure 3 in Milanese *et al.* (2008). Note that the data in the figure, which reflect the strong catch declines in Greece and Tunisia that were due to the 1986/1987 epizootic disease, suggest that the Libyan sponge fishery was not similarly affected and indeed, may have increased the output due to the the unmet demand. However, these catches dropped from about 20 t in the 1990s to 4 t in the 2010s (Figure 2D).

In 1965, the U.S. 'Commercial Fisheries Review' informed its readers that "*The Government of Libya allowed Greek trawlers and sponge vessels to operate in certain Libyan territorial waters in 1964 after paying the following license fee: trawler […] U.S.$ 1400; sponge vessel […] $ 700 and simple fishing vessel […] $ 280* (Anon. 1965). Note that this illustrative statement does not imply that licences fees were not required from Greek fishers operating in Libya before 1964, or in other countries.

The two main commercial sponges fished in Libya are *H. communis* and *S. zimocca,* with a great dominance of the former since the 1950s; it is the only species fished today (see also Rawag *et al.* 2004). Nowadays the production of sponges is low. In 1980, only two boats were still fishing sponges (Anderson and Blake 1982). Currently, "*fishing for sponges in Libyan waters is being forbidden from 1 November to 30 May of each year*" (Anon. 2016, p. 207), and incidentally in Greece as well (M. Fourt, pers. obs.).

The sponge fishery of Turkey

Turkey was once one of the three most productive countries in terms of commercial sponge landings (Figure 3A), from 1950 to 1970 (Voultsiadou *et al.* 2011; Şahin 2013), which were nearly all exported (Arısoy 1971; Topaloğlu 2015). The Turkish government promoted this fishery in 1970 through bank loans to fishers, which may explain the massive increase of catches that followed. Turkey has access to and fisheries for sponges in three seas: the Marmara, Black Sea and Mediterranean Sea; however, catches were minimal in the Black Sea (Sariköse and Arslan 2018). Turkish archives mentioned a species called *Spongia mollissima* that was also present in Greece, Egypt, and the east coast of Libya (Fourt, 2020), and which may be a morphotype of *S. officinalis*, but described as two different species in the World Register of Marine Species (WoRMS; www.marinespecies.org/). Two other species were reported in Turkey (*H. communis* and *S. zimocca),* but they now both seem to be extirpated from Turkish waters.

The Turkish government banned sponge fishing right after the epizootic disease of 1986/1987. However, sponge exports from Turkey seem to have occurred after 1987, probably from warehouse stocks of imported sponges (Topaloğlu, 2015), or illegal fisheries.

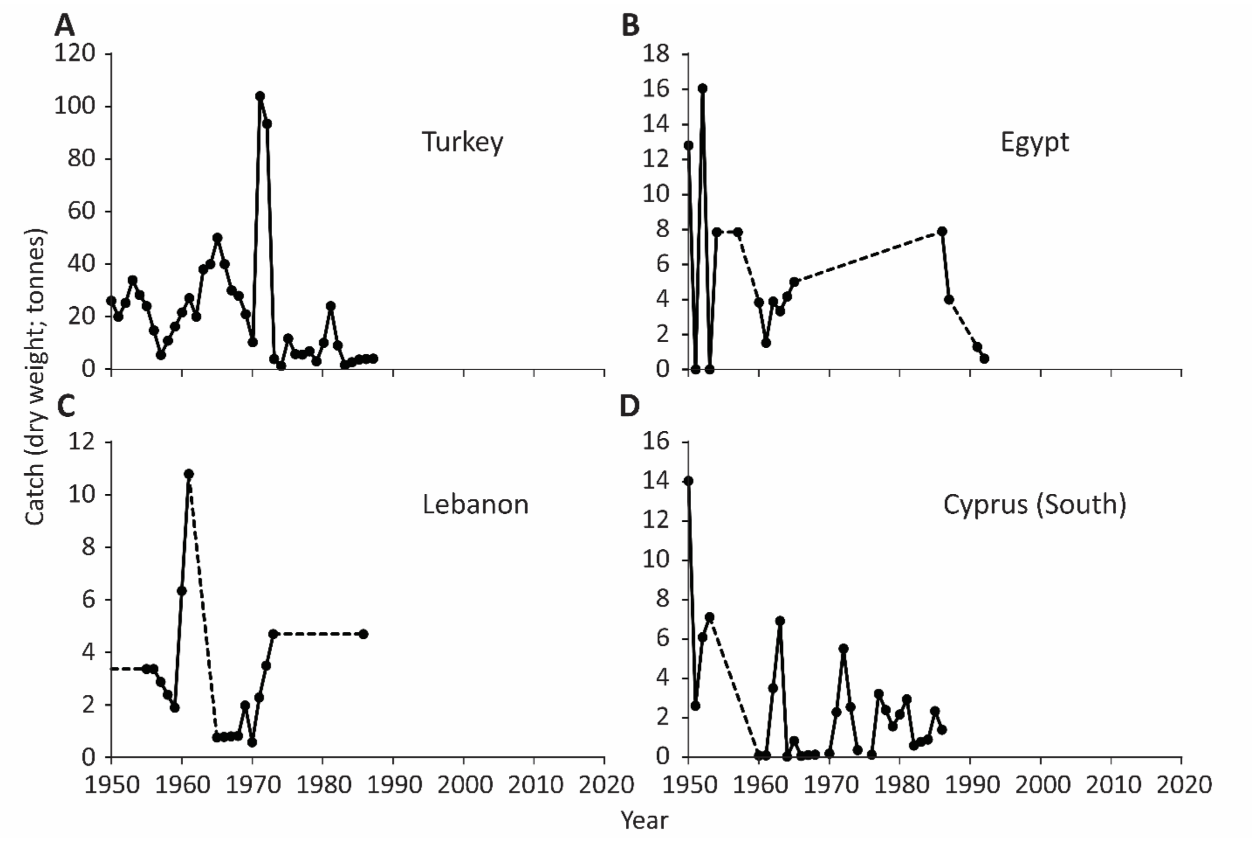

Figure 3. Catch of commercial sponges (in t dry weight) reported taken since 1950 in waters of four Mediterranean countries whose sponge fishery did not continue in the 21st century. **A**: Sponges reported as legally caught from Turkish waters from 1950 to 1987. Catches are here assumed be nil after 1987; **B**: Sponge catches from the Mediterranean coast of Egypt, 1950 to the early 1990s (note interpolations); **C**: Lebanon, as inferred from the figure of 10.8 t in 1961 of Kassis (1967), the ratio of Lebanese to Greek catches in Lebanon, and including a flat backward projection from 1955 to 1950, and a forward projection from 1973 to 1986, after which the catch is assumed to have become nil; **D**: **S**outhern Cyprus, with dotted lines represented interpolation; after 1986, the catch is assumed to have been nil.

The Egyptian sponge fishery

From 1950 to 1965, Egypt's Mediterranean waters were exploited by Greek fishers in addition to an Egyptian sponge company which, until 1949, had exclusive exploitation rights, with Egypt keeping 20% of the catch while the rest went to Greece (Anon 1949b; Anon. 1966). The species *H. communis* always was the main fished species even at the beginning of the 20th century (Fourt, 2019), but in 1949, *S. zimocca* and *S. officinalis* were also fished. This remained the case until 1987 when *S. officinalis* disappeared off the Egyptian coasts during the epizootic disease (Castritsi-Catharios 2005). The sponge fishery in Egypt ceased around 1995 (Figure 3B) and no data can be found after 1990 (Fourt, 2019).

The Lebanese sponge fishery

Possibly due to the destruction of the archives of the Departments of Fisheries Wildlife in Beirut during the Lebanese Civil War (1975-1990; Nader *et al.* 2016), time-series data on the Lebanon's sponge fishery do not appear to exist for the period considered here. Only one report was found with a production figure of 10.8 t of dry sponges in 1961 by Kassis (1967). Thus, we computed the ratio between 10.9 t and the tonnage of Lebanese sponges imported by Greece as reported (SACOLEVE; sacoleve.imbe.fr/). Assuming this ratio to be constant allowed tentative sponge catches to be estimated for Lebanon for a number of years. However, the epizootic disease of 1986/1987 seems to have also impacted sponge beds in Lebanon, and we assume that catches dropped to near zero in 1987 and remained there (Figure 3C), as confirmed by Lelli (2017).

According to Kassis (1967), the sponge fisheries of Lebanon were regulated through bans of local and foreign fishing. On the other hand, according to Fourt (2019), interviewed Lebanese sponge fishers mentioned that they were also fishing incidents, which raised the issue of whether sponges fished in Cyprus were declared in Lebanon. According to data collected during the SACOLEVE programme (Fourt *et al.* 2021), two Lebanese boats were fishing in Cyprus in 1965, suggesting that during the Lebanese ban of sponge fishing, Lebanese fishers began to operate along the coast of Cyprus to compensate their loss. In any case, the catches involved here are very small.

The sponge fishery of Cyprus

The Island of Cyprus is divided between the North and the South (see Ulman *et al.* 2016a, 2016b), but reported catch were only found for the southern part. As in Turkey, *S. mollissima* was present but *H. communis* represented the major part of the catch. Some countries, such as Libya or Greece used to fish in this area before the epizootic disease of 1986-1987 (Fourt 2019), which strongly impacted the fishery for sponges along the Cypriot coast where sponge populations seem not to have recovered (Costa *et al.* 2018). The available time series (see Economou and Konteatis 1990) had gaps from 1954 to 1959, in 1962 and 1978 and they were filled by interpolated values (Figure 3D).

Summary: the sponge fisheries in the Mediterranean, 1959 to 2019

Until 1989 and the outbreak of the epizootic disease of 1986-1987, Mediterranean countries were the major producers of commercial sponges and represented more than 90% of the global production (Figure 4A). Currently, the 3 Mediterranean countries that produce sponges are Greece, Tunisia, and Croatia; Table 2 lists a few other Mediterranean countries with scattered sponge 'catches' that appear in FAO statistics. The most important sponge species caught in the Mediterranean is *Hippospongia communis*, distantly followed by *Spongia* species (Figure 4B).

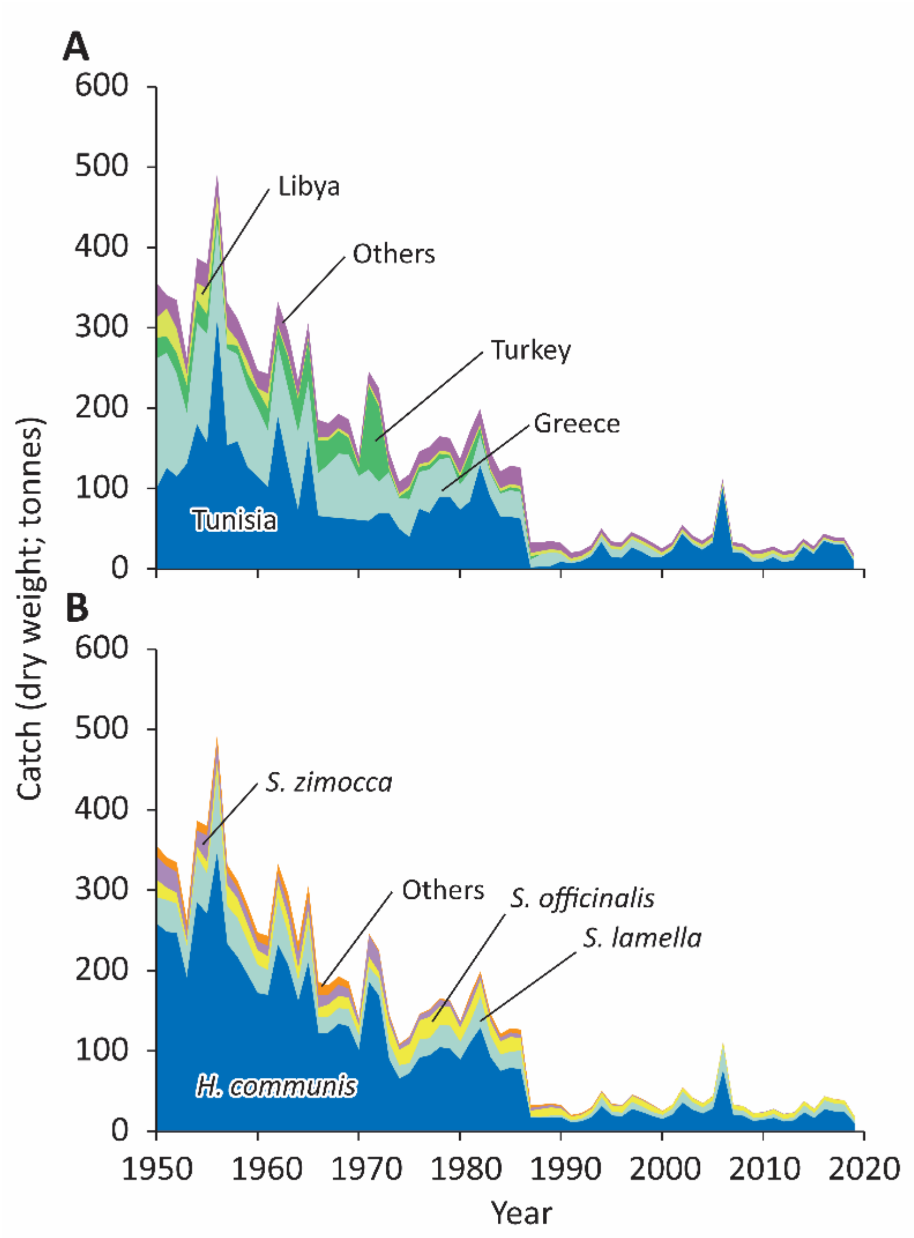

Figure 4. Sponge catches from the Mediterranean, 1950-2019. A: by major country; note the important contributions of Tunisia and Greece; **B**: by species, with *Hippospongia communis* dominating, and *Spongia lamella, S. zimocca* and *S. officinalis* also contributing.

Our coverage of the Mediterranean Sea is incomplete. Notably, we were unable to find information (beyond a few tonnes reported by FAO; see Table 2) on the catch of sponges for the period 1950 – 2019 from the coast of Syria, which was "*the main producer of Levantine sponge, or 'fine Syrie' in the nineteenth century. Its production is now completely stopped"* (Pérez and Vacelet 2014). This last point, about "production now [being] completely stopped" is made relative to the definition of 'now', because in 1964, the Syrian Government (i.e., during the period covered here) still required sponge divers to keep logbooks and "*land their catch in the locality mentioned on the permit*" (Cacaud 2005).

Sponges in the Western North Atlantic

With regard to sponges, the Western Atlantic zone covers The Bahamas, Florida in the USA, and Cuba; Table 2 also provides estimates of from the Caribbean Coast of Colombia, but they are very likely too high, and not considered further. Western Atlantic sponge catches were very high at the beginning of the 20th century, but diseases and overfishing depleted a good part of their sponge populations and led to limits or bans on sponging. Thus, catches were low in the 1950s, but increased markedly thereafter. Indeed, since 1988, Western Atlantic countries produce between 70 to 90% of the commercial sponges, a great majority coming from the USA.

Sponging in The Bahamas

In 1841, The Bahamas became the first country in the Americas to commercially export sponges when a shipment of between 500 to 600 specimens was sold in Paris by a French merchant who had previously been shipwrecked in the small archipelago (Corfield 1938; Stuart 1948). From that point onwards, the industry quickly gained momentum. Close to its peak in 1917, the industry included the harvesting, processing, and trading of sponges and employed one-third of the Bahamian workforce (Oronti *et al.* 2012; Bethell 2017). By 1935, The Bahamas was ranked the third largest exporter of sponges globally (Bethell 2017). However, the fishery collapsed in 1938 due to a fungal disease that killed between 70% and 95% of sponges (Galstoff *et al.* 1939). Currently, there is a resurgence of the sponge fishery in The Bahamas, as global demand for natural sponges rises (Figure 5A).

At the end of the 1980s, sponge catches and exports from The Bahamas increased, most probably in response to the collapse of Mediterranean sponge population in 1986/87. In the last decades, sponge exports from The Bahamas decreased again; however, it maintained its position as the world's second most important sponging country (Moultrie *et al.* 2016).

The sponge species that currently contributes most to the catch is the grass sponge (*Spongia obscura*), distantly followed by reef (*S. tubulifera),* yellow (*S. barbara*), hardhead (*Spongia pertusa*), glove (*S. graminea*) and wool sponge (*Hippospongia lachne*).

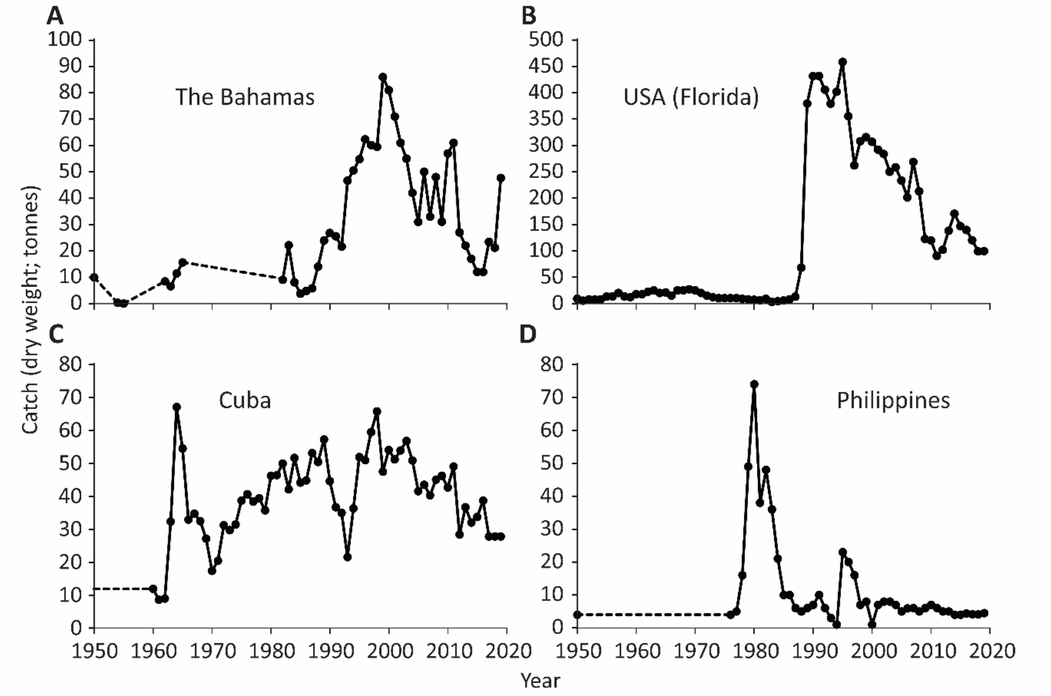

Figure 5. Catch of sponges (t dry weight in three countries of the Central Western Atlantic and one in Pacific. **A**: Reported sponge exports from The Bahamas, assembled from various sources (see Pauly *et al.* 2022). The data shown therein, referring to exports rather than catches render invisible short periods where catching sponges was banned, but warehoused stocks were available. Export figures were not available from 1966 to 1980, and the exports for these years were interpolated. **B:** Catch of sponges in Florida (USA), based for 1950 to 1962 on U.S. reports, from 1963 to 1987 on FAO data, and Florida Fish and Wildlife Reports for subsequent years. **C**: Sponge catch data from Cuba, 1950 to 2019 (based on Lopeztegui-Castillo 2020), with the 1960 catch extrapolated back to 1950. **D**: Catch of sponge in the Philippines; based on Philippine National Reports.

The sponge fishery of Florida, USA

In the USA, sponge fisheries only occur in Florida. Sponges are fished mainly from St. Marks on the northwest coast of Florida to Miami on the southeast coast (Witzell 1998). The main commercial species harvested in Florida are wool sponge (*Hippospongia lachne*; Figure 1), yellow sponge (*Spongia barbara*; Figure 6) and grass sponge (*Spongia graminea*), although the glove sponge (*S. graminea*) is also harvested. In total, the commercial sponges only represent between 2% and 5% of Florida's abundant shallow water marine sponge population (Torres *et al.* 2006; Stevely *et al.* 2010). Commercially valuable sponges do not occur on Florida's coral reefs where non-commercial sponges are especially abundant and diverse.

The first landings of sponges began in 1822 in Key West, Florida by Greek fishers who emigrated to the US; that fishery quickly became the dominant fishery in the Western Atlantic region and the most valuable one (Petrof 1967). The use of "scaphanders" or hard-hat diving suits was quickly adopted and problems of regulation raised soon after (Flegel 1908). Average production at the beginning of the 20th century was more than 200 t per year. However, overfishing, several disease outbreaks in 1937 and 1947, competition from synthetic sponges, pollution and change in temperature drastically reduced catches in mid-century (Witzell 1998; Suver 2012). The population eventually recovered, and catches increased rapidly in the mid-1980s, peaked at 450 t per year in the early 1990s, and then gradually declined to current values of 100 t per year (Figure 5B). Today, diving for sponges is permitted off the Gulf coast but forbidden in the Florida Keys, where fishers use traditional techniques developed in Cuba whereby fishers stand on dinghys and use a *kamaki* (a gear combining the properties of a harpoon and trident; Stevely *et al.* 2010) to pluck sponges from the shallow (< 4 m) seafloor. Figure 8 shows a typical commercial sponge boat.

Recent declines in landings in south Florida are due to a series of sponge die-offs caused by blooms of sponge-killing cyanobacteria (Butler *et al.* 1995) and changes in water quality in part associated with Everglades restoration (Butler *et al.* 2017a, 2018). Overfishing may also have contributed to the gradual decline in sponge harvest (Cropper and DiResta 1999), although an assessment of commercial sponge fishing impacts in the Florida Keys fishery conducted in 2003-2005 judged the fishery at that time to be sustainable but under-regulated (Butler *et al.* 2017b). The large-scale sponge die-offs in the Florida Keys also sparked research on and the development of sponge community restoration (Butler *et al.* 2021) as a means of restoring the ecosystem functions supplied by sponges, particularly: sponge filtration of bacterioplankton, biogeochemical cycling of nitrogen in the water column, and provisioning of shelter for benthic fauna and fishes (Herrnking *et al.* 1997, Peterson *et al.* 2006, Bell 2008, Valentine and Butler 2019).

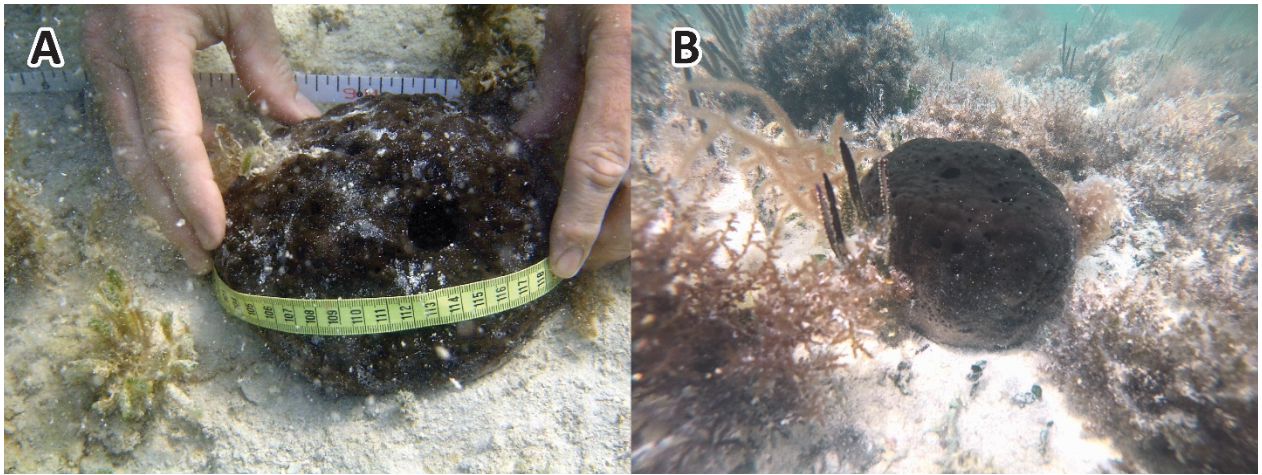

Figure 6. The yellow sponge *Spongia barbara*. **A**: measuring the diameter of a specimen; **B:** an undisturbed specimen. Photos by M. Butler.

Figure 7. A sponge "mother" boat in the Florida Keys; fishers work from smaller dinghys that supply the mother boat. Photo by M. Butler.

The sponge fishery of Cuba

Cuba was and is still an important producer of sponges, and since the beginning of the 20th century the use of the *kamaki* is the major harvesting technique (García Ramón 1970; Baisre and Páez. 1981; Abel *et al.* 2019). Currently the third biggest producer of sponges, Cuba's landings peaked at over 500 t per year in the 1920s. After a disease in the 1940s, Cuban sponge fisheries were reorganized and divided into two zones: the Gulf of Batabanó where the fishery is primarily for *Hippospongia lachne*, and the more productive Sabana-Camagüey Archipelago (Alcolado 2004), where several *Spongia* species are fished such as *S. barbara*, *S. graminea* and/or *S. obscura*, all reported as '*Spongia* spp.' (Blanco Rodríguez and Formoso Garcia 2009; Lopeztegui-Castillo 2020). Overall, since the early 1960s Cuban sponge catches increased until the end of the 20th century, then declined steadily; tentative Cuban catches in the 1950s were obtained by backward extrapolation of the catch in 1960 (Figure 5C).

Commercial sponge catches in the Pacific and the World

Sponge catches in countries bordering the Pacific Ocean

Of the countries with Pacific coastlines, only the Philippines appears to have regular, if small sponge fisheries (Figure 5D). The FAO reports occasional catches from Japan, China, New Zealand, and Australia, but no published reports on sponging in Japan or China could be found. The experimental farming of sponges for possible commercial purposes is reported from the Torres Strait, Australia and Kennedy Bay, New-Zealand (Duckworth 2007; Kelly 2004).

Sponge catches for the Philippines

The Philippines has never been a major sponging country. Approximately 3 tons were landed in 1940, and most of the catch was for local use because none of the production is exported (Anon. 1948). National reports from 1889 to 2001 are available, and were used to generate Figure 5D. The species that are exploited appear to include a "yellow sponge" similar to *Spongia zimocca* (Longakit *et al*. 2005), but is probably another species, as *S. zimocca* doesn't appear to occur outside of the Mediterranean. Figure 5D suggests that Philippine yields of commercial sponges increased rapidly at the end of the 1970s and hit 74 t in 1980 before decreasing until today to around 4 t per year; we have no explanation for the catch peak.

The global catch of sponges

Figure 9A suggests that the global catch of sponge fisheries is shaped entirely by the catch of Mediterranean and countries in the Central West Atlantic, and can be divided into two periods: 1950 to 1988 and 1989 to 2019, both with strongly decreasing trends. The first period is dominated by the catch in the Mediterranean, which dwarfed those from the Western Atlantic, whereas in the second period, the reverse was true following a massive increase in sponge landings in the Western Atlantic from 1988 to 1989. Figure 9B shows the approximate composition of the world catch, composed mainly of Mediterranean species (especially *Hippospongia communis*) from 1950 to 1987, and of Western Atlantic species from 1988 onwards (especially *Hippospongia lachne*).

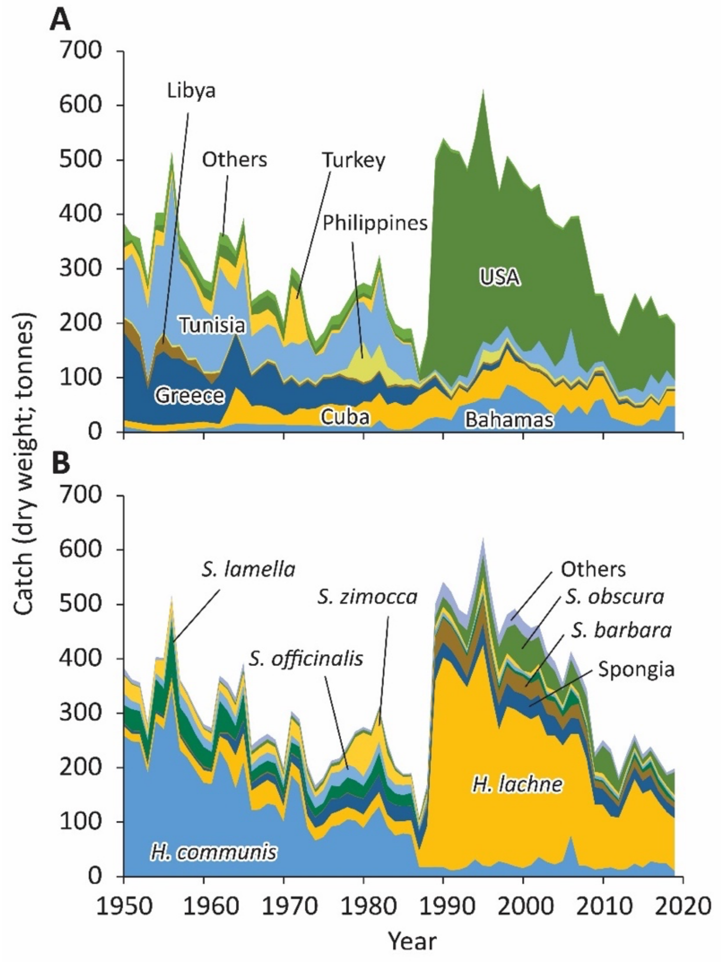

Figure 9. Global catch of sponges (t dry weight). **A:** by countries; **B**: by species. Note in A the initial dominance of Mediterranean catches, followed by that of catches from the Western Atlantic, mirrored in B by the dominance of Mediterranean species (especially *Hippospongia communis*), succeeded by Western Atlantic species from 1988 on (especially *Hippospongia lachne*).

Finally, Figure 10 shows the world catch (t, dry weight) as reconstructed here compared with the catch reported annually or occasionally to FAO by its member countries. This figure suggests that the 'official' catch of commercial sponges by FAO member countries represents only about 11% of the global catch as reconstructed here for 1950 to 2019. This degree of underestimation is high, but not impossibly so, given that similar estimates were obtained for some countries and territories in the course of reconstructing marine fish catches (see contributions in Pauly and Zeller 2016). Also note that this underestimation would be far worse if the statement that FAO reports sponge catches as wet weight were correct.

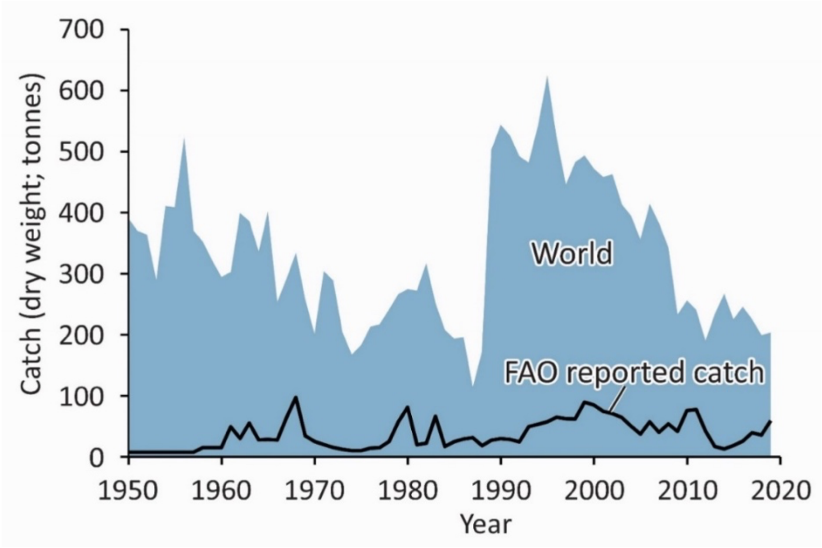

Figure 10. World catch of commercial sponges (t dry weight), contrasting the catches reconstructed here (**Figures 2-5**) complemented with the data summarized in **Table 2** (overall sum 23,220 t), to the sum of annual catches reported by FAO member countries (i.e., 2554 t).

We will abstain here from elaborating on the causes for declines of sponge fisheries. A thorough treatment of the issue would have to consider, simultaneously, market forces leading to overfishing, habitat destruction, diseases, declines in water quality and increasingly, ocean warming due to climate change, all of which are outside of the scope of this contribution (but see Webster 2007; Cebrian *et al.* 2011; Simster *et al.* 2012; Powell *et al.* 2014; Butler *et al.* 2018; Idan *et al.* 2020 and Micaroni *et al.* 2021). However, dealing with these issues will require time series of catches by eco-regions rather than countries, corresponding data on local environmental change, and experimental studies on sponge population resilience. The time-series data reported here are a step in this direction. We do not claim to have resolved all the ambiguities related to the origin of the catch of these data, or the year(s) in which some of the catches were actually made, as opposed to the year(s) when the dry sponges were exported. To the extent that such ambiguities can be resolved in the future, the sponge catches in the database of the *Sea Around Us* (see www.seaaroundus.org) will be corrected in the course of its annual updates. The documentation of these corrections and updates will, as well, correct and update the information in this contribution.

Acknowledgments

Many thanks to Nicolas Bailly for answering various questions about sponge taxonomy, to Çetin Keskin for checking the section on Turkey and its references, to Daw Haddoud for his explanation on Libyan sponge fishing and its regulation, and to the numerous other colleagues who answered our queries.

Authors' contributions

The bulk of this work was done by L.M. during a stage of 6 months in late 2021 and early 2022 with the *Sea Around Us,* where he worked under the guidance of the D.P. and with the assistance of M.L.D., B.D.

and E.C, the co-authors who are also members of the *Sea Around Us* team. Subsequently, L.M. reached out to M.F., M.B., A.C.T., N.C and D.H who helped complete the paper.

References

Abel, B.V., M.S.J. Manuel, F.G. Mario and A.Q.M. Araceli. 2019. Sponge fishery and aquaculture in Cuba: impacts and challenges, p. 102 *In*: S. Ray, G. Diarte-Plata and R. Escamilla-Montes (eds). *Invertebrates-Ecophysiology and Management*. IntechOpen, London.

Alcolado, P.M., A. Grovas-Hernández and Z. Marcos. 2004. General comments on species inventory, fisheries, culture and some community features of the Porifera in Cuba. *BMIB-Bollettino dei Musei e degli Istituti Biologici*, 68: 175–186.

Anderson, E. and G. Blake. 1982. The Libyan fishing industry, p. 85–104. *In:* J.A. Allan (ed). *Libya Since Independence*. RLE Economy of the Middle East, Routledge.

Anon. 1948. *Explore sponge resources in Philippines*. Reichek – Int. 2879. Fish and Wildlife Service, Department of the Interior of the Philippines – Information Service, Philippines. 2 p.

Anon. 1949a. The sponge fishing industry in Libya (Africa). *Commercial Fisheries Review*, 12(2): 62.

Anon. 1949b. Egypt: sponge fishery 1949. *Commercial Fisheries Review*, 12(5): 60–61.

Anon. 1949c. Greece: Sponge fishery and market, 1949. *Commercial Fisheries Review*, 12(6): 44–49.

Anon. 1951. Décret du 26 juillet 1951 (22 chaoual 1370), portant sur la refonte de la législation de la police de la pêche maritime. *Journal officiel de la République tunisienne, 31 juillet 1951*, 949–955.

Anon. 1953. Tunisia: Sponge production. *Commercial Fisheries Review*, 16(8):58.

Anon. 1957. Bahama Islands: Sponge Industry. *Commercial Fisheries Review*, 196(9): 61

Anon. 1965. Greek vessels licensed to operate in Libyan waters. *Commercial Fisheries Review*, 27(1):81–82.

Anon. 1966. United Arab Republic: Sponge Fishing [along the Mediterranean coast of Egypt]. *Commercial Fisheries Review*, 28(1): 96.

Anon. 2016. Report of the eighteenth session of the Scientific Advisory Committee on Fisheries. Nicosia, Cyprus, 21-23 March 2016. FAO Fisheries and Aquaculture Report No. 1154. FAO, Rome. 255 p.

Arısoy, S. 1971. Türkiye süngerciliği ve ihracat sorunu / Sponges in Turkey and Its Question of Export. *Et ve Balık Kurumu Genel Müdürlüğü, Balık ve Balıkçılık [Meat and Fish Institution, Fish and Fisheries]*, 19(4): 15-16 [In Turkish] www.esk.gov.tr/upload/Node/14394/files/Balik_ve_Balikcilik_Dergisi_Cilt_19_Sayi_4_EBK_Yil_1971_.pdf

Baisre, J.A. and J. Páez. 1981. *Los recursos pesqueros del archipiélago cubano*. Programa Interregional de Ordinación y Desarrollo Pesqueros. Estudios WECAF No 83. 79 p.

Basioli, J. 1965. *Naše spužvarstvo na Jadranu*. Društvo za proučavanje i unapređenje pomorstva Jugoslavije. 32 p.

Bell, J.J. 2008. The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science*, 79(3): 341-353

Bethell, K. 2017. Revival of the sponging industry. *The Tribune*, 1 March 2017. Available at: www.tribune242.com/news/2017/mar/02/revival-sponging-industry

Blanco Rodríguez, J.C. and M.F. Formoso García. 2011. Estimado de la abundancia de esponjas comerciales en áreas correspondientes a las plataformas suroccidental (Golfo de Batabanó) y norcentral (Archipiélago Sabana-Camagüey) de Cuba/Estimation of the abundance for commercial sponges in southwest Bataban. *Revista de Investigaciones Marinas*, 30: 99–106.

Brotz, L. 2016. Jellyfish fisheries: a global assessment, p. 110–124 *In:* D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A critical appraisal of catches and ecosystem impacts*. Island Press, Washington D.C.

Butler, M.J. IV, J.H. Hunt, W.F. Herrnkind, T. Matthews, M. Childress, R. Bertelsen, W. Sharp, J.M. Field, and H. Marshall. 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster Panulirus argus. *Marine Ecology Progress Series,* 129: 119-125

Butler, M.J. IV and T.W. Dolan III. 2017a. Potential impacts of Everglades restoration on lobster and hard-bottom communities in the Florida Keys, FL (USA). *Estuaries and Coasts*: 40(6): 1523-1539. doi.org/10.1007/s12237-017-0256-8

Butler, M.J., D.C. Behringer and M.M. Valentine. 2017b. Commercial sponge fishery impacts on the population dynamics of sponges in the Florida Keys, FL (USA). *Fisheries Research,* 190: 113-121.

Butler, M.J. IV, J.B. Weisz, and J. Butler. 2018. The effects of water quality on back-reef sponge survival and distribution in the Florida Keys, Florida (USA). *Journal of Experimental Marine Biology and Ecology,* 503:92–99.

Butler, J., W.C. Sharp, J.H. Hunt and M.J. Butler IV. 2021. Setting the foundations for renewal: restoration of sponge communities to aid the ecological recovery of Florida Bay, FL (USA). *Ecosphere,* 12(12): e03876. doi.org/10.1002/ecs2.3876

Butler, J., E.R. Anderson and M.J. Butler IV. 2022. Habitat Restoration Restores Underwater Soundscapes and Larval Recruitment. *Frontiers in Ecology and Evolution*. 10: 785986. doi.org/10.3389/fevo.2022.785986

Cacaud, P. 2005. *Fisheries laws and regulations in the Mediterranean: a comparative study*. General Fisheries Commision for the Mediterranean, Study and Reviews 75. 64 p

Camps-Fabrer, H. 1996. Éponge. *Encyclopédie berbère*, 17: 2658–2664. doi.org/10.4000/encyclopedieberbere.2163

Castritsi-Catharios, J., H. Miliou, K. Kapiris and E. Kefalas. 2011. Recovery of the commercial sponges in the central and southeastern Aegean Sea (NE Mediterranean) after an outbreak of sponge disease. *Mediterranean Marine Science*, 12(1): 5–20.

Cebrian E., M.J. Uriz, J. Garrabou and E. Ballesteros. 2011. Sponge Mass Mortalities in a Warming Mediterranean Sea: Are Cyanobacteria-Harboring Species Worse Off? *PLoS ONE,* 6(6): e20211 doi.org/10.1371/journal.pone.0020211

Corfield, G.S. 1938. Sponge industry of the Caribbean Area. *Economic Geography,* 14: 201–206.

Costa, G., V. Guissani, D. Kletou, P. Kleitou, M. Pansini, A. Setti, R. Pronzato and M. Bertolino. 2018. A first preliminary study of the shallow water sponge fauna from Cyprus Island (Eastern Mediterranean). *Zootaxa*, 4450(5): 594–596.

Cropper, W.P. and D. DiResta. 1999. Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. *Ecological Modelling,* 118: 1–15.

de Fages, E. and C. Ponzevera. 1908. *Les pêches maritimes de la Tunisie*. Imprimerie J. Picard.

Laubenfels, M.W. de and J.F. Storr. 1958. The taxonomy of American commercial sponges. *Bulletin of Marine Science of the Gulf and Caribbean,* 8(2): 99–117.

Duchassaing de Fonbressin, P. and G. Michelotti. 1864. Spongiaires de la mer Caraibe. *Natuurkundige verhandelingen van de Hollandsche maatschappij der wetenschappen te Haarlem,* 21(2): 1–124

Duckworth, A.R. and C. Wolff. 2007. Bath sponge aquaculture in Torres Strait, Australia: Effect of explant size, farming method and the environment on culture success. *Aquaculture*, 271(1–4): 188–195.

Economou, E. and D. Konteatis. 1990. *Sponge fishery in Cyprus 1900-1989*. Ministry of agriculture and natural resources department of fisheries, Nicosia Cyprus.

Flégel, C.H. 1908. *The abuse of the scaphander in the sponge fisheries. United States Bulletin of the Bureau of Fisheries*, 28: 513–543.

Fourt, M. 2019. *Histoire de la pêche des éponges en Méditerranée et son adaptation récente au changement régional*. Doctoral thesis, Université Aix-Marseille, France. 324 p.

Fourt, M., D. Faget, T. Dailianis, D. Koutsoubas and T. Pérez. 2020. Past and present of a Mediterranean small-scale fishery: the Greek sponge fishery—its resilience and sustainability. *Regional Environmental Change,* 20 (1). doi.org/10.1007/s10113-020-01581-1

Fourt, M., D. Faget and T. Pérez. 2021. Compilation of multi-source historical data on Mediterranean sponge fisheries. *Aix-Marseille University, CNRS, IRD and Avignon University, PANGAEA*. doi.org/10.1594/PANGAEA.926825

Galtsoff, P.S., H.H. Brown, C.L. Smith and F.W. Smith. 1939. Sponge mortality in the Bahamas. *Nature*, 143(3628): 807–808.

García Ramón, M.D. 1970. Las pesquerias cubanas: el golfo de Batabano y el puerto de Surgidero como caso-modelo. *Revista de Geografia*, January 1: 43–68.

Garibaldi, L. 2012. The FAO global capture production database: a six-decade effort to catch the trend. *Marine Policy*, 36: 760–768.

Gaudillière, J. 1954a. La pêche sur le littoral oriental de la Tunisie. *Bulletin Economique et Social de la Tunisie*, 86: 45–72.

Gaudillière, J., 1954b. *La pêche des éponges en Tunisie. Presented at the Conseil général des pêches pour la Méditerranée*. Débats et documents techniques, FAO, Rome.

Halouani, C., F. Ben Rais Lasram, M. Khalfallah, D. Zeller and D. Pauly. 2016. Tunisia, p. 415 *In:* D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A criticalappraisal of catches and ecosystem impacts*. Island Press, Washington D.C.

Herrnkind, W.H., M.J. Butler IV, J.H. Hunt, and M. Childress. 1997. The role of physical refugia: implications from a mass sponge die-off in a lobster nursery. *Marine and Freshwater Research,* 48: 759–770

Hyatt, A. 1877. Revision of the North American Poriferae; with Remarks upon Foreign Species. Part II. *Memoirs of the Boston Society of Natural History,* 2: 481–554.

Idan, T., L. Goren, S. Shefer and M. Ilan. 2020. Sponges in a Changing Climate: Survival of *Agelas oroides* in a Warming Mediterranean Sea. *Frontiers in Marine Science,* 7: 603593. doi.org/10.3389/fmars.2020.603593

Kassis, G. 1967. *Marine sponges of Lebanon*. Master thesis, American University of Beirut, Lebanon. 93 p.

Kelly, M., S. Handley, M. Page, P. Butterfield, B. Hartill and S. Kelly. 2004. Aquaculture trials of the New Zealand bath-sponge *Spongia* (*Heterofibria*) *manipulatus* using lanterns. *New Zealand Journal of Marine and Freshwater Research*, 38(2): 231–241.

Lamarck, J.-B. de. 1814 [1813]. Sur les polypiers empâtés. *Annales du Museum national d'Histoire naturelle.* 20: 294–312; 370–386; 432-458.

Laubenfels, M.W. de. 1936. *A Discussion of the Sponge Fauna of the Dry Tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera. Carnegie Institute of Washington Publication no.* 467. *Carnegie Institute of Washington, Washington.* 225p.

Lelli, S. 2017. *Contribution to a better knowledge of biology, distribution and diversity of demersal species along the Lebanese coast, eastern Mediterranean: a focus on Lessepsian fish species.* Doctoral dissertation, Université de Perpignan, France. 278 p.

Leys, S.P., G. Yahel, M.A. Reidenbach, V. Tunnicliffe, U. Shavit and H.M. Reiswig. 2011. The sponge pump: the role of current induced flow in the design of the sponge body plan. *PLoS ONE,* 6(12): e27787.

Linnaeus, C. 1759. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus II. Editio decima, reformata. - pp. [1-4], 825–1384. Holmiæ.

Longakit, M.B., F. Sotto and M. Kelly. 2005. The shallow water marine sponges (Porifera) of Cebu, Philippines. *Science Diliman*, 17(2): 52–74.

Lopeztegui-Castillo, A., A. Betanzos-Vega and M. Formoso-García. 2020. Abundancia y talla de esponjas comerciales (Spongiidae) en el Golfo de Batabanó, Cuba: Actualización y recomendaciones de manejo. *Revista de Investigaciones Marinas*, 40:72–85.

Micaroni, V., F. Strano, R. McAllen, L. Woods, J. Turner, L. Harman and J.J. Bell. 2021. Adaptive strategies of sponges to deoxygenated oceans. *Global Change Biology*, 28(6): 1972–1989. doi.org/10.1111/gcb.16013

Milanese, M., A. Sarà, R. Manconi, A.B. Abdalla and R. Pronzato. 2008. Commercial sponge fishing in Libya: Historical records, present status and perspectives. *Fisheries Research*, 89(1): 90–96.

Moultrie, S., E. Deleveaux, G. Bethel, Y. Laurent, V.D.S. Maycock, S. Moss-Hackett and R. van Anrooy. 2016. *Fisheries and aquaculture in The Bahamas: a review.* Food and Agriculture Organisation of the United Nations/Department of Marine Resources, Nassau, The Bahamas. 79 p.

Nader, M.N., S. Indary, N.R. Moniri and K. Zylich. 2016. Lebanon, p. 318 *In:* D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A critical appraisal of catches and ecosystem impacts.* Island Press, Washington D.C.

Oronti, A., A.J. Danylchuk, C.E. Elmore, R. Auriemma and G. Pesle. 2012. Assessing the feasibility of sponge aquaculture as a sustainable industry in The Bahamas. *Aquaculture International,* 20: 295–303. doi.org/10.1007/s10499-011-9457-5

Pauly, D. and D. Zeller (eds). 2016. *Global Atlas of Marine Fisheries: A critical appraisal of catches and ecosystem impacts*. Island Press, Washington D.C. xii +497 p.

Pauly, D., N. Smith and M. Butler. 2022. Growth and related traits of the wool sponge *Hippospongia lachne*: practical and theoretical considerations. *Fisheries Bulletin,* 120(2): 99–112. doi.org/10.7755/FB.120.2.1

Pérez, T. and J. Vacelet. 2014. Effect of Climatic and Anthropogenic Disturbances on Sponge Fisheries, p. 577–587 *In:* S. Goffredo and Z. Dubinsky (eds). *The Mediterranean Sea: its history and present challenges*. Springer, Dordrecht.

Peterson, B.J, C.M. Chester, F.J. Jochem and J.W. Fourqurean. 2006. Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series,* 328: 93–103.

Petrof, J.V. 1967. A study of the Florida natural sponge industry with special emphasis on its market problems. PhD Thesis, University of Florida, United States. 227 p. ufdc.ufl.edu/UF00097837/00001

Postel, E. 1956. *La Pêche en Tunisie viii: Pêche aux Eponges*. Cotte De Classement No 3134, La Pêche Maritime. 9 p.

Powell, A., D.J. Smith, L.J. Hepburn, T. Jones, J. Berman, J. Jompa and J.J. Bell. 2014. Reduced Diversity and High Sponge Abundance on a Sedimented Indo-Pacific Reef System: Implications for Future Changes in Environmental Quality. *PLoS ONE,* 9(1): e85253. doi.org/10.1371/journal.pone.0085253

Pronzato, R. and R. Manconi. 2008. Mediterranean commercial sponges: over 5000 years of natural history and cultural heritage. *Marine Ecology*, 29(2): 146–166.

Rančić, I.P. 2010. *Quantitative and qualitative annual catch analysis of the commercial sponges in the Croatian part of the Adriatic Sea with the special emphasis on the sustainable exploitation*. Master's thesis, University of Zagreb, Croatia. [In Croatian]

Rawag, A.A., D.A. Haddoud and S.W. Zgozi. 2004. Commercial demersal marine species of Libya. *MedSudMed Technical Documents,* 2: 75–81.

Rützler, K. 1976. Ecology of Tunisian commercial sponges. *Tethys,* 7(2/3): 249–264.

Şahin, G. 2013. Türkiye'de yitirilen bir iktisadi faaliyet: Süngercilik / A lost economic activity in Turkey is sponge fishing. *Akademik Bakış Uluslararası Hakemli Sosyal Bilimler Dergisi,* 39: 1–22. [In Turkish]

Sariköse, B. and R. Arslan. 2018. Cumhuriyet Dönemi Türk Süngerciligi (1923–1990) / Sponge Fishing in Turkey during the Republican Period (1923–1990). *Turkish Studies History,* 13(24): 185–213. doi.org/10.7827/TurkishStudies.14204 [In Turkish]

Schmidt, O. 1862. *Die Spongien des adriatischen Meeres*. Wilhelm Engelmann, Leipzig. viii+ 88 p.

Schulze, F.E. 1879. Untersuchungen über den Bau und die Entwicklung der Spongien. Siebente Mittheilung. Die Familie der Spongidae. *Zeitschrift für wissenschaftliche Zoologie,* 32: 593–660.

Simister, R., M.W. Taylor, P. Tsai and N. Webster. 2012. Sponge-Microbe Associations Survive High Nutrients and Temperatures. *PLoS ONE,* 7(12): e52220. doi.org/10.1371/journal.pone.0052220

Stevely, J.M., D.E. Sweat, T.M. Bert, C. Sim-Smith and M. Kelly. 2010. Commercial bath sponge (Spongia and Hippospongia) and total sponge community abundance and biomass estimates in the Florida middle and upper Keys, USA. *Proceedings of the Gulf and Caribbean Fisheries Institute,* 62: 394–403. aquadocs.org/handle/1834/31305

Storr, J.F. 1964. *Ecology of the Gulf of Mexico commercial sponges and its relation to the fishery*. U.S. Fish and Wildlife Service Special Scientific Report – Fisheries No. 466. 73 p.

Stuart, A.H. 1948. *World Trade in Sponges*. U.S. Department of Commerce, Industrial Series No. 82. 95 p.

Suver, M. 2012. *Environmental Change and Place-Based Identities: Sponge Fishing in Tarpon Springs, Florida*. Master's thesis, University of South Florida. 79p.

Topaloğlu B. 2015. Sponges of the Aegean Sea, p.188-199. *In:* T. Katağan, A. Tokaç, Ş. Beşiktepe and B. Öztürk. (eds). *The Aegean Sea Marine Biodiversity, Fisheries, Conservation and Governance*. Turkish Marine Research Foundation (TUDAV), Publication No. 41, Istanbul.

Torres, R.C., M.J. Butler and B. Shellito. 2006. A GIS-based characterization of commercial sponge populations in the Florida Keys, FL (USA). *Proceedings of the Gulf and Caribbean Fisheries Institute,* 57: 1043–1044.

Ulman, A., B.A. Çiçek and I. Salihoglu. 2016a. Cyprus (North), p. 234. *In:* D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A criticalappraisal of catches and ecosystem impacts*. Island Press, Washington D.C.

Ulman, A., A. Petrou and M. Patsalidou. 2016b. Cyprus (South), p. 235. *In:* D. Pauly and D. Zeller (eds). *Global Atlas of Marine Fisheries: A criticalappraisal of catches and ecosystem impacts*. Island Press, Washington D.C.

Valentine, M.V. and M.J. Butler IV. 2019. Sponges structure water column characteristics in a shallow, tropical coastal ecosystem. *Marine Ecology Progress Series,* 608: 133–147.

Voultsiadou, E. 2007 Sponges: an historical survey of their knowledge in Greek antiquity. *Journal of the Marine Biological Association of the United Kingdom*, 87: 1757–1763.

Voultsiadou E. and D. Vafidis. 2007. Marine invertebrate diversity in Aristotle's zoology. *Contributions to Zoology*, 76: 103–120

Voultsiadou E., T. Dailianis, C. Antoniadou, D. Vafidis, C. Dounas and C.C. Chintiroglou. 2011. Aegean bath sponges: historical data and current status. *Reviews in Fisheries Science*, 19: 34-51

Webster, N.S. 2007. Sponge disease: a global threat? *Environmental Microbiology,* 9: 1363–1375.

Witzell, W.N. 1998. The origin of the Florida sponge fishery. *Marine Fisheries Review*, 60(1): 27–32.

Zeller, D., M.L.D. Palomares, A. Tavakolie, M. Ang, D. Belhabib, W.W.L. Cheung, V.W.Y. Lam, E. Sy, G. Tsui, K. Zylich and D. Pauly. 2016. Still catching attention: *Sea Around Us* reconstructed catch data, their spatial expression and public accessibility. *Marine Policy,* 70: 145–152.

On meeting the Dalai Lama[1]

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Abstract

A brief account is given of the participation by the author at a Buddhist conference held in Nalanda in March 2017, and of various personal experiences during and after this event. Jointly, they strengthen the view that India consists of two overlapping countries, one held backward by religion and elite corruption, the other a source of brilliant people and ideas that have conquered the world.

Introduction

On March 17, 2017, I met the Dalai Lama for a brief moment, following a long keynote speech he gave at a conference on 'Buddhism in the 21st Century', held in Nalanda, in the Indian State of Bihar. But I have no cellphone, so no photo to prove it.

It was not that I had suddenly given up on my freedom from religion. Rather, when I was invited to participate at this conference – along with a few 'Western' scientists involved in environmental conservation and animal welfare – I did not find any good reason why I should not accept, given that Buddhism appears to be the rare faith that does not require you to check your knowledge of physics, biology and history (as well common sense) at the door.

The Dalai Lama's and the other speeches

And indeed, the Dalai Lama's speech, sometimes interrupted by giggles (he giggles a lot), was about the need for Buddhists to love each other, across their own divisions, to love people of other faiths, or none (a nice touch), and especially to embrace secularism and modern science, and give less attention to holy books – the Buddhist ones included. The secularism bit was presented as a good thing in the article in *The Times of India* reproduced here, but in 2022, this probably would not have happened….

I cannot tell what the audience made of this. About one third consisted of Buddhist monks from Asia – including quite a few females – and other continents, most of the rest being, I guess, lay Buddhists.
The conference also featured various speakers claiming, as seems to be the fashion in India these days, that the Ancient Indian had discovered quantum dynamics and space travel, and that the elephant-headed god Ganesha was evidence of Ancient Indian surgical skills…

As if such mendacious nonsense was required to demonstrate the scientific prowess to a people that invented a superior way of doing arithmetic (try to do it without the concept of zero…which came from India) and produced geniuses such as the physicists Satyendra Nath Bose or Subrahmanyan Chandrasekhar, or the mathematician Srinivasa Ramanujan!

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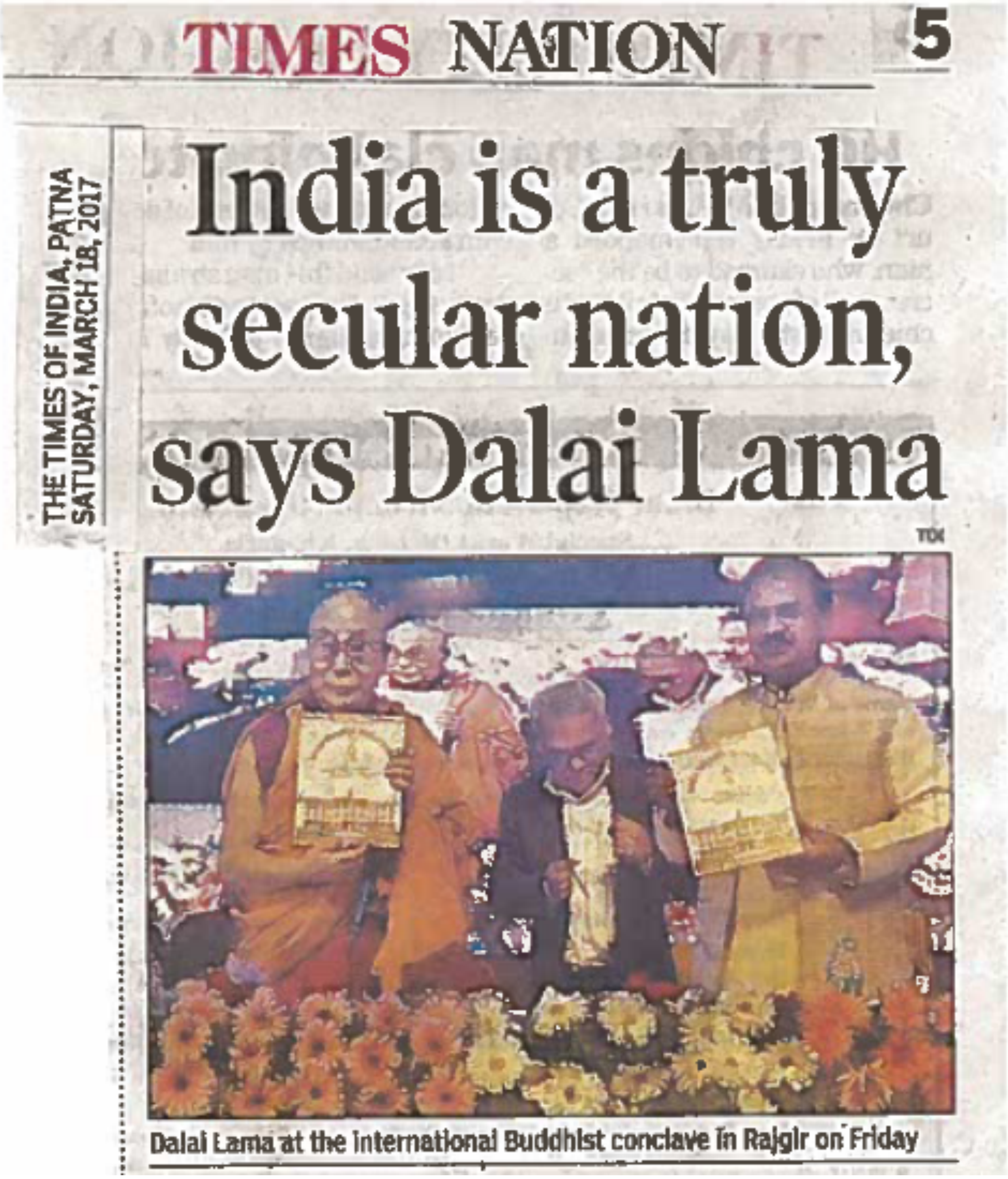
[1] Cite as: Pauly, D. 2022. On meeting the Dalai Lama, p. 107-110. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

And yes, I presented what we do to the biodiversity of the oceans[2] in a breakout session that also included Buddhist monks, of which one dragged the audience through an interminable account of how the holy scripture shows that Gautama Buddha loved trees and other plants, in flat contradiction to the admonition of the Dalai Lama.



TIMES NATION 5

THE TIMES OF INDIA, PATNA
SATURDAY, MARCH 18, 2017

India is a truly secular nation, says Dalai Lama

TNN

Dalai Lama at the international Buddhist conclave in Rajgir on Friday

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[2] Pauly, D. 2017. *World Fisheries: why there are no longer enough fish in the sea*. Session on Environment, Nature Conservation & Animal Welfare, Conference Buddhism in the 21st Century: Perspective to Global Challenge and Crises, Nalanda, Bihar, India.

Farrukh Nadim

Rajgir: Buddhist spiritual leader the Dalai Lama called India a truly secular country where every religious group lives in peace without fear. He said India should take the lead for global peace and harmony. While inaugurating the three-day International Buddhist Conclave (IBC) with Union minister of state for tourism and culture Dr Mahesh Sharma at Rajgir's international convention centre on Friday, the Dalai Lama called himself the 'son of India'.

"India preached non-violence for over 2,000 years and it is the only country where people of all faiths live in harmony and without fear," he said and added, "I have been living in this country for the past 58 years and call myself the son of India". On his association with Nalanda, he said, "All my knowledge comes from the Nalanda thoughts, The Tripitaka-Pali Canon, physically and mentally."

On intercaste or interfaith conflicts, he said, "Despite philosophical differences, all religions preach peace and harmony, but the modern day education, which is based on consumerism, has made people devoid of love, affection, friendship and trust. The solution lies in controlling surge of emotion taught in great Indian traditional system of education which teaches tolerance, forgiveness and contentment."

The exiled Tibetan spiritual leader said when he was in Tibet, his thoughts were confined to Tibet only. But, during his stay in India, his thoughts got broadened or globalized.

"Buddha cannot remove sufferings or the cause of sufferings. He only shows the path to control destructive emotions through meditation — Vipassana," he said and added, "Buddha Dharma is relevant in the field of science. So, we say, Buddhism is relevant in the 21st century."

The Union minister, who is also chancellor of Nav Nalanda Mahavihara (NNM), the co-sponsor of the event, praised the Dalai Lama not only for promoting Buddhist values but also for his contribution to world peace. He also assured the NNM to extend every possible cooperation it required for its growth and development.

NNM vice-chancellor M.L Srivastava said, "Buddhism mitigated the cause of conflicts and promote interfaith harmony, globally." He said the NNM was founded for the promotion of Pali which contributed a lot in understanding Buddhism since its inception in 1951.

Union secretary of culture department, N K Sinha, welcomed the guests and scholars from 30 countries.

The Dalai Lama also unveiled the new version of Tripitaka or Pali Canon and declared open the Buddhist Science department at NNM.

A nightly visit and a harrowing trip

While the trip to the conference site had been uneventful direct 14+ hour flight from Vancouver to Delhi, then a short flight to Patna, Bihar's capital, followed by a 3 hours bus ride to Nalanda, a city near an ancient site of Buddhist learning, I made two noteworthy experiences the night before, and during my return trip to Patna.

The first experience was that, as I was trying to fall asleep, a half dozen Indian soldiers armed with submachine guns broke into my room with their commanding officer telling me that I should not move. I did not move. They went through my suitcase, my backpack and the pockets of my pant but clearly, didn't find what they were after. So, they abruptly left, disappointed I presume. I concluded that my lifelong policy of not doing drugs (if this is what they were after) has been a wise choice. The other experience was the return trip, which I had to take before the conference organizers could hand me the long-promised cash refund of my travel cost (somebody else got that…). This road trip confronted me with the reality that escapes one when hopping from one conference to the next (this was pre-Covid).

Some trucks had caused an accident-induced traffic jam (Bihar's roads appear to have far more old, dilapidated trucks than anything else, bicycles included), and the quick-witted driver of our jeep-like vehicle left the highway via a back road just in time, before our car became immobilized within an immobile mass of trucks. The harrowing back roads we then took went through numerous squalid villages of the State of Bihar, one of the poorest in India, where big landowners rule over millions of poor farmers, who have only religion (Hinduism, with its ubiquitous cows and castes) to transcend their misery – which it doesn't.

Also prominent along the roads were monumental ruins of abandoned infrastructure development projects (half-constructed bridges, segments of incomplete pipelines, un-erected electric pylons, etc.) which I recognized from the Philippines, where I lived for a long time, as the concrete achievements of corrupt politicians.

The two Indias

I was shaken when we finally made it to the airport in Patna, even more than when I visited India for the first time in the 1980s. Then, in Delhi, before returning to Vancouver (via London this time) I met in a swanky neighborhood an old colleague and friend, Michael Vakily, whom I had previously visited in the Philippine countryside, in Sierra Leone and in Thailand, where he ran various field projects for the research center we both worked for. The 4-year, German-funded project in India that he was assigned to was meant to create biodiversity reserves, including marine protected areas. However, it took 3 years to get the clearances required for the project to officially start….

On the other hand, he had a brilliant Indian PhD as a counterpart, who was enthusiastic, and who seemed to know precisely what ought to be done to protect India's biodiversity. He is India as well. I wonder which India will prevail.

Accepting a BBVA Frontiers of Knowledge Award [1]

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Abstract

This is the slightly edited speech given by the author upon accepting the 2019 Edition of the BBVA Frontiers of Knowledge Award in Ecology and Conservation Biology in Bilbao, Spain in September 2021. Relevant references were added to better define the topics successively covered in that speech, i.e., the tropicalization of fisheries science, the creation of FishBase, the study of fisheries as a global system, the products of Sea Around Us research initiative, and the development of the Gill-Oxygen Limitation Theory (GOLT).

Introduction

Ladies and Gentlemen,
It is a privilege to be able to stand here and to thank you as a co-winner of the 2019 BBVA Frontiers of Knowledge Award in Ecology and Conservation Biology because it means that one's work has been recognized by the jury of what is now one of the most prestigious awards in these fields.

But what is my field? I normally describe myself as a fisheries biologist, or when I feel very bold, as a 'fisheries scientist.' However, let's face it, fisheries science is not very prestigious, and it usually provokes a flight reaction when, in the rare instances when I attend parties, I respond to innocent questions about what I do.

The point is that most people perceive fisheries as the art of catching one kind of fish, using one kind of gear, in a lake or marine embayment… - what is the science in that? The point is that fish are the big group of wild animals that we hunt. And because we live in an industrial age, we hunt fish industrially.

People think that fishes know no borders, no limits. This is wrong: fishes have borders that they don't cross, of temperature and of depth. Also, they have limits to the extent that they can maintain their abundance when under human exploitation. It is our industrial fishing which knows no borders and no limits, because we can fish inshore and in the high seas, in polar and tropical waters, at the surface and at depths of thousands of meters. Moreover, the global market for fish is tightly integrated, and the demand it generates is essentially insatiable.

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[1] Cite as: Pauly, D. 2022. Accepting a BBVA Frontiers of Knowledge Award, p. 111-113. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

Fisheries as a Global System

All of this suggests that fisheries must be understood as a global system, similar to the global weather systems[2] or the global financial system, whose calms and storms at any place can be understood only by considering what occurs at other places on Earth.

I did the field work for my first graduate degree studying the ecology of a coastal lagoon in Ghana[3], and the two years spent on surveying fish abundance in Indonesia in the mid-seventies[4] inspired my doctoral thesis. The job I then got in an international research center in the Philippines included developing and teaching throughout the Tropics, in Africa, Asia, Oceania and South America, 'tropicalized' methods for what fisheries scientists call 'stock assessments,' i.e., assessing have much fish are (still) is the waters, and how much could be taken sustainably[5]. This is when I noted that fisheries issues are similar between countries, despite the different traditions that maritime anthropologists so painstakingly describe[6]. Also, I noted that the response of exploited ecosystems exhibited common patterns, irrespective of location or the identity of the species that were targeted.

However, there was another worrying pattern: the results of multiple fisheries and ichthyological studies conducted in the tropics, by both local scientists and by short-term 'experts' from the Global North, were not widely available, and remained largely unused by the fisheries and aquatic science community. The creation of FishBase[7], a free online database with scientific information of all (35,000 +) species of fish in the world was my answer to this challenge, obviously with hundreds of colleagues helping to make it the success that it is.

Having key biological data on all exploited fishes of the world made it t easy to demonstrate global patterns of fisheries activities and catches. This is how much-cited papers emerged, on "the primary production required by global fisheries", on "fishing down marine food webs," or on the geographic, bathymetric and taxonomic expansions of fisheries, the latter group referring to fishing vessels going further, and fishing deeper for previously spurned species. Doing this work required getting familiar with the database of fisheries catches that is assembled by the Food and Agriculture Organization of the United Nations, which assembles annual catch reports from its member countries and releases them as "the" world's fisheries catch data. This very useful database has flaws, however, such as ignoring the fish discarded by industrial fisheries, or that caught by small-scale fishers. This is important, because catching fish is one of the major ways we interact with the ocean, the other being for transportation and for dumping refuse.

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[2] See Edwards, P.N. 2010. *A Vast Machine: Computer Models, Climate Data, and the Politics of Global Warming*. MIT Press, Cambridge, MA. 552 p.

[3] Pauly, D. 1975. On the ecology of a small West African lagoon. *Berichte des Deutschen wissenschaftlichen Kommission für Meeresforschung,* 24(1): 46–62.

[4] See Pauly, D., P. Martosubroto and J. Saeger 1996. The Mutiara 4 surveys in the Java and southern South China Sea, November 1974 to July 1976, p. 47–54. *In:* D. Pauly and P. Martosubroto. (eds.) *Baseline studies in biodiversity: the fish resources of western Indonesia*. ICLARM Studies and Reviews 23, Manila.

[5] Pauly. D. 1998. Beyond our original horizons: the tropicalization of Beverton and Holt. *Reviews in Fish Biology and Fisheries,* 8(3): 307–334.

[6] Pauly, D. 2006. Major trends in small-scale marine fisheries, with emphasis on developing countries and some implications for the social sciences. *Maritime Studies (MAST)*, 4(2): 7–22.

[7] See www.fishbase.org

The Emergence of the *Sea Around Us*

Thus, with the support of various philanthropic foundations, the *Sea Around Us*, an initiative I founded in 1999 at the University of British Columbia, in Vancouver, Canada, undertook the huge task of correcting the world's catch, as reported by coastal countries since 1950. The correction process, which we call 'catch reconstruction' took about 15 years and involved over 400 persons from all over the world.

Its first results were that the world's marine catch was not about 90 million tonnes per year, but over 130 million tonnes, and that since 1996, this catch declines by 1-2%, which was unreported by the FAO[8]. Another result is that in the process of catch reconstruction generated a huge database of spatialized catch data and derived statistics which we also made freely available through the *Sea Around Us* website[9]. This website is now used – as is FishBase – by thousands of university-based and other researchers, NGO staff and government over the entire world.

And the Gill-Oxygen Limitation Theory (GOLT) at the End

Besides helping with dealing with fisheries management issues, this database of reconstructed and spatialized catches from 1950 help us assess the impact of climate change, specifically ocean warming on fish. We were able to model rather well the poleward movement of fish that started in the 1970s and 1980s, due to fishes being exquisitely sensitive to temperature changes[10].

The reason for this sensitivity is that fish breathe water, which contains little oxygen, and use gills, i.e., a 2-dimensional surface, to meet the oxygen demand of a 3-dimensional body. This means that the gill area per volume must decline as fish grow, causing oxygen stress. This intensifies until a size is reached at which they don't get enough oxygen to grow further. I wrote my doctoral dissertation about this idea, which, although simple, was idea[11], but later, I could work only occasionally on this topic, which at first interested no one. Now, these long-neglected considerations are becoming a major explanation for what fish are forced to do in the face of global warming[12]. It is a sad way to be right.

I thank the BBVA Foundation and the Jury of its Frontiers of Knowledge Award in Ecology and Conservation Biology for having realized that developing concepts, software tools and freely accessible database on the biology of fishes and their catches are contributions to Ecology and Conservation Biology.

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[8] Pauly, D. and D. Zeller. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications*, 7:10244. doi.org/10.1038/ncomms10244\

[9] See www.seaaroundus.org.

[10] Cheung, W.W.L., R. Watson and D. Pauly. 2013. Signature of ocean warming in global fisheries catch. *Nature*, 497: 365–368.

[11] Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Doctoral thesis, Berichte aus dem Institut für Meereskunde an der Universität Kiel. No. 63. xv + 156 p. oceanrep.geomar.de/41323/

[12] See Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7(2). doi.org/10.1126/sciadv.abc6050

On receiving the Beverton Medal of the Fisheries Society of the British Isles[1, 2]

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Abstract

The presents a slightly edited version of the acceptance speech given upon the acceptance, on July 7, 2021, by the author, of Beverton Medal of the Fisheries Society of the British Isles. The speech, after recalling a Roman anecdote about Ray Beverton, lauds the broad, encompassing nature of his work, much of which done jointly with Sidney Holt, which contrasts which the scattered nature of current work, where only occasional meta-analyses providing oases of understanding within arid expanses of scattered, disconnected irrelevancies. Seeking consilience between studies and disciplines appears one effective way to counter this trend which incidentally, mimics a societal trend toward people becoming separated from each other by ethnic, gender or other divisions.

Introduction

Dear Professor Carvalho, President of the Fisheries Society of the British Isles, members of the Society, conference participants….

First of all, I thank you from the bottom of my heart for awarding me the Beverton Medal for 2021. Anything named after Ray Beverton is serious, and your Society's award of the Beverton Medal requires one to think seriously thought what it means.

Yes, I am truly humbled. I knew Ray Beverton, and thus I know what it means to have one's name associated with his. Before elaboration on this theme, I will, however, mention one anecdote. Ray and I attended in the mid-1980s a workshop in Rome at FAO, and we were housed in the same hotel. At the end of the workshop, on the way back to the hotel, Ray asked me very hesitantly - and in the extremely polite way that was his style - if I would mind accompanying him to a jeweler, where he intended to purchase a gift for his wife, Kathy. The point was that he had considered the possibility of being robbed – Rome had a bad reputation then – and having a 6'1" Black man as a bodyguard would be an excellent deterrent to any bag snatcher, and so it was. I am proud to be the only fisheries scientist to have served as a bodyguard to Ray Beverton.

What I am not proud of is to having misunderstood the instructions of the organizers of this conference. I proposed as the title for tomorrow's keynote "The need for synthetic studies in Ichthyology, or putting Humpty Dumpty together again," which it won't be, because tomorrow I will try to answer the question "Why do fish reach first maturity when they do?[3]"

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[1] Cite as: Pauly, D. 2022. On receiving the Beverton Medal of the Fisheries Society of the British Isles, p. 114-118. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea IV*. Fisheries Centre Research Reports 30(4). Institute for the Oceans and Fisheries, University of British Columbia, Vancouver.

[2] Given via Zoom on July 7, 2021, to the participants of the Online Symposium of the Fisheries Society of the British Isles "Fish, Fisheries and Ecosystems in the Anthropocene," Leuwen, Belgium.

[3] Now published as: Pauly, D. 2021. Why do fish reach first maturity when they do? *Journal of Fish Biology*, 101(2): 333-341. doi.org/10.1111/jfb.14902

I will now speak about Humpty Dumpty, who does indeed need to be put together again, a task that Ray would have agreed with and, in fact, contributed to.

A fragmented discipline

Our disciplines - Ichthyology and its applied, sister discipline, Fisheries Science – are old. Some 2350 years ago, Aristotle wrote up reasonable observations on fish and fisheries and may be considered to be the Father of it all. But let's face it: there is not much about fish in the pre-Linnaean literature, as can be ascertained by consulting the three volumes of *Dean's Bibliography of Fishes*, published from 1916 to 1923. The literature has exploded since, with hundreds of journals devoted to fish and fisheries.

To this 75-year-old man[4], who has been in fish and fisheries for 50 years - since beginning fieldwork for my Master's thesis in a coastal lagoon in Ghana - it looks as if we are drowning in facts and factoids. However, these data are not used to perform the syntheses that we need to answer questions that society expects us to have answers for.

For example, in the 1960s to 1980s, FAO and NOAA published species synopses, each of which brought together 'everything' known about a given fish species. These were extremely useful not only for managing their fisheries or their aquaculture, but also because they re-assembled these species into a coherent whole, just as they are in the water.

FishBase, which most of you will know, attempts to do the same, but encoding the required information, which involves about 50 person-years per year worldwide, is constantly faced with a flood of data that threatens to drown this effort.

We need more meta-analyses to make sense of the multitude of studies reporting a few measurements made on single species somewhere.

Ray Beverton, sometimes with Sidney Holt[5], sometimes by himself[6], performed the kind of meta-analyses that I have in mind. Notably, these meta-analyses showed that the von Bertalanffy growth equation parameters co-vary in a reproducible fashion and are also related to natural mortality.

Theses meta-analyses were not as sophisticated as those we can read now, often with a farrago of alternative models and no firm conclusion. However, they inspired and guided subsequent research and still provide criteria for assessing the questionable validity of claims based on smaller data sets and outlandish hypotheses. We don't do enough of such metanalyses, and this is one of the reasons why, in the onset of an age that will be dominated by nefarious effects of global warming, we are still debating, for example, how temperature affects fish.

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[4] This speech was held 1 year ago. The issue has become direr since…

[5] See, e.g., Beverton R.J.H. and S.J. Holt. 1959. A Review of the Lifespans and Mortality Rates of Fish in Nature, and Their Relation to Growth and Other Physiological Characteristics, p. 142-180 *In:* G.E.W. Wolstenhome and B.A. Maeve O'Conner (eds). *Ciba Foundation Symposium - The Lifespan of Animals (Colloquia on Ageing).* John Wiley & Sons.

[6] Beverton, R.J.H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *ICES Journal of Marine Science,* 154: 44-67.

Indeed, one recently published paper – which I will not cite here[7] – proposed that temperature has the effect of reducing the maximum size that some fish species can reach while increasing the size that other species can reach. In chemistry, the equivalent statement would be that some burning is due to part of combusting substances becoming associated with oxygen, while the other part releases phlogiston. Or put differently: How can something be the cause for A and simultaneously for the opposite of A? Why such rot?

Accuracy vs Precision

I believe that much of what I criticize here is because we have lost track of the need for accuracy, and instead concentrate on precision (note that I couldn't make the point in French, which doesn't distinguish between the two terms). Indeed, I think we allow in what a friend of mine called 'precisionism.'

Let me illustrate this point by recalling a figure I saw in *Scientific American* many decades ago, and in which the various historic methods to estimate the speed of light were compared.

What was fascinating to me is that the results of these different methods not only differed, but that their confidence intervals did not overlap. That's when I finally, really, understood the difference between accuracy and precision. Precision, I realized, had little to do with the process one studies, i.e., the actual speed of light in this case, but only with the fiddly part of the method that was supposed to measure it.

The reason why we can now assume that we know the speed of light accurately is because different methods give the same result, not because they have narrow confidence intervals.

Consilience between the results of different methods, and even between those of different disciplines is what we need to obtain reliable results, not '*p*-hacking'! Incidentally, as very well-known German physicist described some of his contemporaries as 'Dünnbrettbohrer', i.e., driller of thin boards;' we don't want to do that.

The word 'consilience', referring to the 'jumping together' of ideas, was coined by William Whewell in the early 19th century, but it is E.O. Wilson, who, in a widely misunderstood book[8], revived and relaunched the concept.

Essentially, the notion of consilience, in the sciences, implies that every statement of a given discipline should be downward compatible with more fundamental disciplines and upward compatible with more derived disciplines.

Thus, physics must be compatible not only with its own experiments, but also needs to be downward compatible with mathematics (though sometimes, new mathematics must be invented to accommodate new physics…) and must be able to link upward with chemistry. And any new discovery in chemistry must fit connect with physics and be able to link upward with geology and biochemistry, etc.

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[7] Because I still hope that its authors may recant.

[8] See Pauly, D. 2002. Consilience in oceanographic and fishery research: a concept and some digressions. p. 41-46. *In:* J. McGlade, P. Cury, K.A. Koranteng and N.J. Hardman-Mountford (eds). *The Gulf of Guinea Large Marine Ecosystem: environmental forcing and sustainable development of marine resources*. Elsevier Science, Amsterdam.

For ichthyology, this obviously implies that all our biological considerations must be not only be currently compatible with evolutionary biology, but refer to entities or processes that can have evolved – which is the reason why we don't have fish with propellers driven by electric motors, though they would be quite efficient, especially since they have already evolved stunningly good batteries.

However, it also means that it is not sufficient, when describing something that fish do, to demonstrate, even with beautiful math and neat graphs, that what they do leads to an evolutionary stable strategy. Rather, we must also be able to demonstrate how an individual fish decide to do that thing so it - or its genes - benefit from what that decision. My presentation at this conference dealt with a problem of this sort[9].

Doing science is working on 'why' – for the 'what,' we have artists and entertainers. When we know why something is, we have made it a particular case of something more general. In that sense, we have simplified the world. Look at the Ancient Greeks: they needed a huge array of hyperactive Gods, assisted by armies of Nymphs and Fauns constantly intervening in our lives to 'explain' natural phenomena. Now, we simply have the Earth turning around the Sun, geology, evolution… et voilà, all the previously supernatural phenomena are explained.

Fungi and viruses

For my part, I have always been better at joining ideas – making them jump together – than at digging deep into any one topic. This has to do with the fact that I not particularly good at math in a field that is strongly quantitative. Another constraint is that I am quite impatient, and I never saw myself generating the primary data that I needed to test the ideas I had.

Thus, following 2 years of inspiring boat-based surveys of the marine biodiversity of Indonesia, I wrote a doctoral thesis on fish growth without having read a single otolith[10]. Indeed, I never returned to field sampling of primary data. In effect, I became a big fungus, turning the primary production that other generates into a wide-ranging network of mycelia. You need decomposers in a healthy ecosystem…

The present times, finally, call for some reflecting on one's position vis-à-vis current societal challenges of our time, which perhaps unexpectedly, given our advances in science and technology, is shaped by a resurgence of nationalism and virulent racism, two viruses far worse than that which has ruined our lives since early 2020.

I have tried to avoid dealing with these viruses throughout much of my life and career, because thinking about things that make people go insane is not really good for one's scientific productivity. However, I am a Black, or as they say in Canada, a 'visible minority', and the massive protests in the US and in Europe as well, asserting that Black Lives Matter, have made me think, as it has many others.

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[9] This presentation led to an article are of same title: Pauly, D. 2021. Why do fish reach first maturity when they do? *Journal of Fish Biology*, 101(2): 333–341. doi.org/10.1111/jfb.14902

[10] Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Doctoral thesis. Berichte aus dem Institut für Meereskunde an der Universität Kiel No. 63. xv + 156 p. oceanrep.geomar.de/41323/

I was reminded that, as Frantz Fanon noted, as a biracial person – yet another term – I am often forced to understand two positions, or to navigate between two sides. Throughout my life and career, this has been a tremendous advantage, and not the burden that many ‘mono-chromatics’ think it is.

However, since people cannot choose their parents, and thus their ethnicity, I would say that they should be open to ‘others’, whatever they are. And in science, this is a must: we need the ferment that a diversity of points of views, generated by people of different ethnicities, cultures, backgrounds, and yes, races and genders will generate. Because if our ideas can ‘jump together’, then they will also elevate us, and our science, and put back together the pieces of our shared humanity.

Thank you.