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DIRECTOR'S FOREWORD

I called Marine and Freshwater Miscellanea I (FCRR 26(2)), a “vinegret* of contributions covering a variety of fish and fishery related topics” from Dr. Daniel Pauly. In this, the second collection of articles by Pauly and colleagues that were deemed not suitable for peer-reviewed scientific journals, but which readers may find of interest, it is less of a salad course and more of a meal. There is very little that Daniel Pauly writes that is not of interest to fisheries researchers, whether peer-reviewed or not. Such are the trials of a man whose lifetime of work has been so foundational in the fields of fisheries science and biodiversity research. We should all aspire to such tribulations.

Here, Dr. Pauly pays homage to two of his mentors, as well as with his colleagues sharing articles that range from marine biodiversity in the Indo-Pacific to fisheries management in the Small-Island States, from marine mammals in the Sea of Okhotsk to the Gill-Oxygen Limitation Theory (GOLT). The topics are widespread, but all are interesting, and I invite you to enjoy.

Regards,

Prof. Evgeny Pakhomov
Director, Institute for the Oceans and Fisheries
The University of British Columbia

PREFACE

Like its immediate predecessor*, this Fisheries Centre Research Report (FCRR) is a collection of articles not suitable for peer-reviewed scientific journals, but which may still find interested readers. As in the case of its predecessor, in this FCRR, “the majority of chapter are authored or co-authored by one of us (DP.). The only excuse he think he has for this is that he is [73] years old and the he would not like to find, when he retires, too many manuscripts that he would have liked to share earlier”.

Still, as was the case for its predecessor, this FCRR covers a wide range of topics, ranging from the marine biodiversity of Palau and New Caledonia in the tropical Indo-Pacific to the marine mammals of frigid Sea of Okhotsk, from the high of humanism to the low of post modernism, and from fisheries management in the Small-Island States to Apartheid in South Africa.

Also, we present in this FCRR three more chapters recounting the details of the peer-review of scientific papers, mainly for the purpose of throwing more light on the rewards and perils of the peer-review process. Two of these accounts deal with contributions on aspects of the Gill-Oxygen Limitation Theory (GOLT), which continues to be dear to one of us.

We hope that this collection, eclectic as it is, will indeed find interested readers.

We take this opportunity, finally, to thanks Ms Elaine Chu for formatting this report and its many tables, and Dr Evgeny Pakhomov for his preface.

Daniel Pauly
Valentina Ruiz
February 2020

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

THE OCEANS, THEIR ISLANDS AND THEIR STUDY

INDO-PACIFIC FISHERIES*

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Abstract

This contribution briefly reviews the main biological, historic, and fleet-operational features of the fisheries in the Indian and Pacific Oceans, with some emphasis on the South China Sea, whose fisheries, largely dominated by China, exemplify the many biological, economic, and political challenges that beset the sector throughout much in the Indo-Pacific.

Introduction

The Indo-Pacific, here defined as an ensemble encompassing the Indian Ocean and the Pacific Ocean, but excluding waters south of the Antarctic convergence, covers 233 million km², i.e., 64% of the world's oceans.

In spite of the immense area it covers, the Indo-Pacific is rather homogeneous in terms of its fish fauna, which, while remarkably diverse, does not change much from South Africa in the west to Central America in the east. Both the high diversity of these fishes and the wide distribution ranges that some species result from the Indo-Pacific fauna being derived from the ancient Tethys Ocean, hundreds of millions of years ago. While the fish fauna along the tropical east-west axis is remarkably similar, there are obviously major latitudinal differences, which become particularly important in the North Pacific, where a cold-water fish fauna occurs that is similar to that of the North Atlantic.

In contrast to the relative uniformity of its fish fauna, Indo-Pacific regions are home to vastly different people and cultures. Thus, we have, from West to East, East Africa, the Arabian Peninsula, India and its South Asian neighbors, Southeast Asia, China, Japan and the Russian Far East, and further south, Australia, the island states of Oceania, and finally the coast of America from Alaska in the north to Chile in the south. This enormous range encompasses people with long fishing history, such as the Polynesians, and people relying mostly on nearshore subsistence fishing such as in the Solomon Islands and Vanuatu, and others with a tradition of industrial distant-water fishing such as Japan which operated before WWII throughout the Pacific, including Alaska (Finlay 2011), as well as relative newcomers in long-range fishing, such as Thailand (Panayotou and Jetanavanich 1987) and China (Colin 2016).

Indo-Pacific Fisheries post-WWII

Prior to WWII, most fisheries in the Indo-Pacific were local. Following WWII and the opening of “Mac Arthur’s Box,” which had confined Japanese vessels to their domestic waters, they re-initiated in the 1950s their distant water fishing operations across the entire Indo-Pacific and into the Atlantic (Swartz *et al.* 2010), therein closely followed by South Korea and Taiwan. In the Eastern Pacific, tuna fishing was dominated by the U.S.A., but their reach was gradually challenged by South American countries claiming a “*Mar Patriótica*”, extending up to 400

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This is the original text of the contribution published in French as Pauly, D. 2019. La pêche en Indo-Pacifique: une ressource qui se raréfie et source de tensions. *Diplomatie - Affaires stratégiques et relations internationales*. Octobre/Novembre - Les Grand Dossiers No 53: 94-95.

miles in the open ocean, claims that were initially dismissed, but which led to the adoption in 1982 of the U.N. Convention on the Law of the Sea (UNCLOS), then strongly opposed by Japan, the then Soviet Union, and the U.S.A. UNCLOS gave each maritime country the right to claim a 200-mile Exclusive Economic Zone (EEZ). This enabled them to implement their own fishery development either by developing domestic fisheries capable of exploiting the entirety of their newly acquired EEZ, or by offering countries with distant water fleets access agreements, usually at a moderate fee, which allowed them to continue exploiting coastal resources now within EEZs.

In the 1970s, the newly emerging Thai trawl fishery, initiated by a German aid project and massive subsidies by the Asian Development Bank 'spill out' of the Gulf of Thailand, and expanded into neighboring countries, ultimately reaching all the way to Somalia in the west and Eastern Indonesia in the east. This expansion was partly reversed by a massive fuel price increase in the late 1970s and then by the newly claimed EEZs of Indo-Pacific countries, which required funds to pay for access agreements. Thus, began a period where Thai distant-water fishing consisted of a mixture of legal operations with access agreements and illegal fishing, i.e., fishing without access agreements, or deploying more vessels than initially agreed upon.

From 1985 on, China got into the picture and, like Thailand, China deployed trawlers equipped for coastal fishing in its overseas operations, in contrast to Japan, South Korea, and Taiwan, which concentrated on tuna fishing in the high seas. Thus, China, as with Thailand before, quickly became embroiled in a series of problematic ventures along the coasts of multiple countries, many resulting in conflicts with local artisanal fishers (Pauly *et al.* 2014).

China now has the largest fishery catch in the world, and thus also of all Indo-Pacific countries, followed by Peru, which exploits essentially one low-value species (an anchovy overwhelmingly reduced to fishmeal), and a number of countries such as Russia, Japan, Thailand, India and others, which jointly catch about 75 millions of tonnes annually, down from about 85 million tonnes in mid-1990. Jointly these fish and invertebrates are worth about \$130 billion annually, of which China has the lion's share, over \$20 billion annually (see www.seaaroundus.org).

The South China Sea is at the center of the Indo-Pacific region and may be seen as its microcosm, although it is also a giant water body, which, while severely overfished, generates a fishery catch of 10 million tonnes per year. Here China dominates even more, both in terms of its catches and the fleets it deploys (Pauly and Liang 2019). However, more importantly, China claims sovereignty over most of the South China Sea, while negating the EEZ claim of other countries such as Vietnam, Malaysia, and the Philippines. This last country, indeed, complained to the International Court and won (Holmes and Phillips 2016). However, this decision is not recognized by China, which has rather armed its fishers and their vessels such that they can impose their presence wherever they want to operate (Denier 2016).

This has led to an extremely dangerous situation where conflicts between fishers could quickly escalate. Moreover, China's plan for 2020 still foresees an increase - although a modest one - of its distant-water catch. At the same time, China is proposing to involve many of the countries bordering the South China Sea, as well as Indian Ocean countries in their Maritime Silk Road Initiative, which, according to its founding documents, aims at mutual benefits for all the countries involved. How these contradictory policies can be harmonized is not clear.

What is clear, however, is that the competition for dwindling fisheries resources in the Indo-Pacific will lend to their further decline. This is regrettable because fish is crucial to the food security of numerous countries around

the region (Golden *et al.* 2016). They would be better served by dedicated programs of rebuilding the depleted fish populations in their EEZs, including in China.

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ISLAND FISHERIES IN A GLOBAL CONTEXT AND THE IMPORTANCE OF TUNA*

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Abstract

Islands' waters cover the majority of global national fishing grounds and their oceanographic features differ both from the high seas and the waters adjacent to the mainland. Yet the overall characteristics of fisheries around islands in comparison to the rest of the ocean remain largely unidentified. Here we frame fisheries developments around islands between 1950 and 2014 in a global context. We find that waters around small islands (<30,000 km²) contribute little to global catch biomass, but have been gaining increasing importance in the world's tuna fisheries, which is largely operates around islands in the Western Pacific. Overall, tuna catches near islands have surpassed tuna catches taken near the mainland, and recently also of the high seas; even though this pattern may vary geographically. Waters around small islands alone provide (under a spatially heterogeneous distribution) as many tunas to world catches as all near-mainland fishing grounds combined, while the majority of tuna caught around small islands is fished by third countries. The trends we observe suggest that the waters around islands may in some places be among the remaining fishing grounds where migrating tuna are intercepted at an increasing rate.

Introduction

In the field of fisheries research, fishing and fished entities are often categorized as developed versus developing countries, small-scale versus large-scale, or Exclusive Economic Zones (EEZs) versus high seas. Here we introduce a novel approach, by dividing the global ocean into the waters around small islands, large islands, near the mainland and the high seas. By doing so, fisheries around islands are framed into a global context.

Fish resources - especially tuna - are important for many islands' economies (Mwikya 2006) and food security (Charlton et al. 2016; Bell et al. 2009). Notably around Pacific islands, which contribute large and increasing shares of global tuna catches (Parris and Grafton 2006), foreign fleets extract large quantities of tuna (Mwikya 2006). Underscoring the importance of sustainable fisheries around small islands, the aim to increase sustainability in and local economic benefits from the fisheries sector of small island developing states is explicitly mentioned in the United Nations' Sustainable Development Goal 14.7 (United Nations 2019).

The Island Mass Effect has long been known to increase primary productivity around oceanic islands (Doty and Oguri 1956; Caldeira et al. 2002), which also attracts pelagic predators (Gove et al. 2016). Tunas, highly migratory, pelagic predatory fishes, are usually exploited by the fleets of several countries, which renders these

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fish prone to overexploitation (McWhinnie 2009). Combining the above, it is obvious that islands firstly depend on sustainable tuna extraction rates outside their own waters, and secondly, in the light of global overfishing (Watson et al. 2013), that islands may - as fisheries expand (Swartz et al. 2010) - become important targets of fleets that experienced overexploited stocks elsewhere.

In the past decade, some islands in the Pacific have directly or indirectly acquired legal protection from unsustainable foreign fisheries (especially targeting tuna), particularly aiming at reducing the use of certain fishing methods, which concerns the Parties to the Nauru Agreement including some high seas areas (The Guardian 2014; Pala 2010). Some US islands' EEZs were even turned into no-take zones (Pala 2010). Also - despite being legally questionable (Government of Mauritius 2015) - the Chagos Archipelago was turned into a no-take zone by the United Kingdom, thus protecting large amounts of tuna in the Indian Ocean (Pala 2010). In this study, we separated reconstructed catch data from the *Sea Around Us* (Pauly and Zeller 2015) into our area classification, as well as into “foreign” and “domestic” and “tuna” and “non-tuna” species. In many regards, large islands, such as the UK or Indonesia, resemble the mainland as much as, or more, than they resemble small islands; thus, we distinguished between “large islands” and “small islands”, where the threshold was chosen to be 30,000 km² of land area (dividing the dataset between Taiwan and the Solomon Islands).

The aim of this research is to frame recent fisheries developments around islands into a global context. We also investigate trends concerning those developments between 1950 and 2014, across the global ocean.

Materials and Methods

An island is here defined as any land mass smaller than Australia that is surrounded by ocean, including solitary islands as well as archipelagos. Islands or countries whose EEZs are separated in fractions in the *Sea Around Us* database were left separated to maintain the given sample size and resolution, e.g., Haiti and the Dominican Republic, or Japan's outlying and main islands.

Large islands were defined as island entities of more than 30,000 km² land area. Japan's outlying islands were classified as “small islands”, while its main islands were classified as “large islands”. Data on land area to classify each island as “small” or “large” were gathered from a very diverse literature.

Data on catches, primary production, EEZ sizes and shelf sizes were downloaded for each EEZ or EEZ-equivalent in mid-January 2019 from the *Sea Around Us* website (www.seaaroundus.org), while high seas catch data were downloaded in mid-February. The fishing entity “Unknown Fishing Country” was considered foreign because we assume that unidentified vessels are more likely to be foreign than domestic. That entity, however, contributes less than 0.5% of overall catches. Fishing activities within the EEZs (or EEZ-equivalents) of islands by their respective mother country were considered domestic fishing (e.g., French mainland fleets fishing in the waters of Corsica or Mayotte would be domestic fishing). The Arctic Sea, which has no fisheries, was excluded from catch density calculations. All data compilation, plotting and analyses were performed in R (R Core Team 2018), using the external packages dplyr (Wickham et al. 2017), plyr (Wickham 2011), reshape (Wickham 2007), ggplot2 (Wickham 2009) and SDMTTools (VanderWal et al. 2019). All data underlying this research are publicly accessible as indicated.

Results

Fisheries around islands in a global context

The global catch, divided into foreign and domestic shares within the respective ocean parts demonstrates the low catch shares of small islands (Figure 1).

Catch densities in tonnes per EEZ square kilometer are highest in the EEZs of mainland countries, followed by large islands (Figure 2a). Small islands have much lower catch densities, being solely undercut by the high seas, both having relatively unproductive waters (Figure 2b; Longhurst et al. 1995).

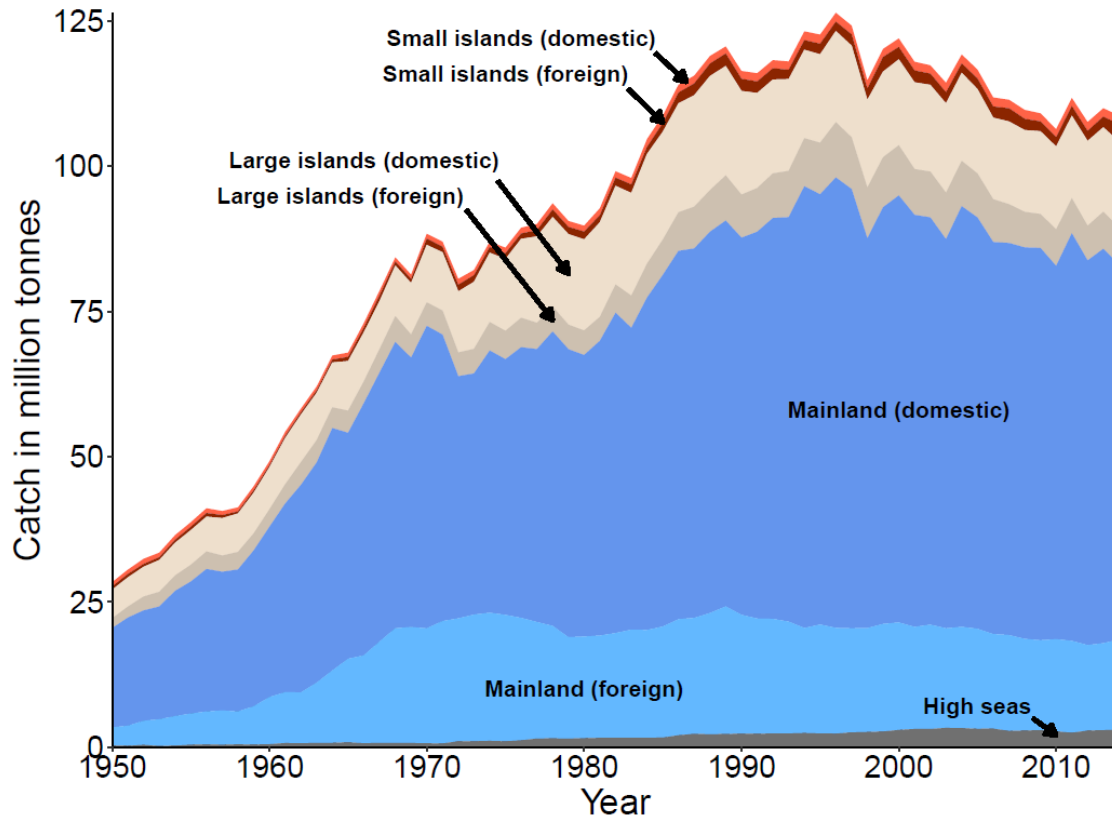


Figure 1. Global catch of marine fisheries in relation to islands. See methods for our exact definition of “foreign” and “domestic”. Adapted from the *Sea Around Us* data)

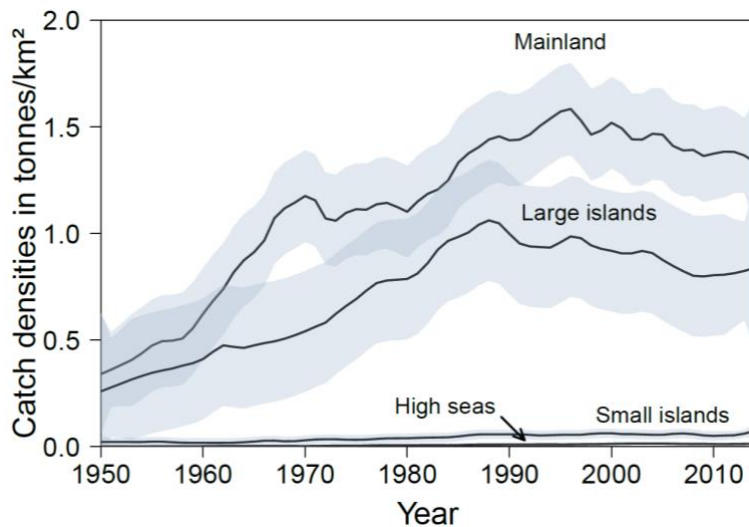
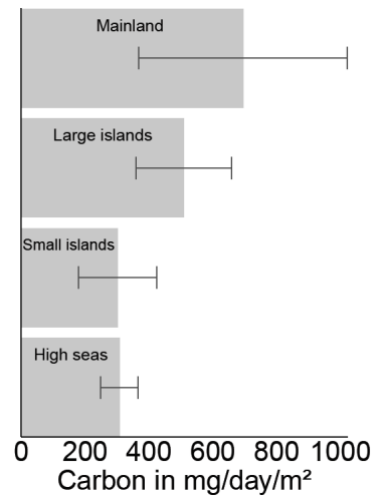
A**B**

Figure 2. Catch densities and primary production. **A:** Catch densities: catches by year and area were divided by the corresponding surface areas (Pauly and Zeller 2015, 2016). Solid lines depict fitted LOESS curves at a smoothing span of 0.1; the respective areas were included as weighting factors. Grey shadings represent 95% confidence intervals. **B:** Primary production: the primary production values of each EEZ or high seas area (Platt and Sathyendranath 1988; Longhurst et al. 1995; Bouvet et al. 2002; Hoepffner et al. 1999; Pauly and Zeller 2015) were also weighed against respective areas. Bars depict weighted means; error bars show standard deviations. The ice-covered Arctic Sea was excluded from a and b, as there are no catches.

To get an impression of the technological sophistication of domestic fishing fleets, we contrasted industrial fisheries with subsistence fisheries (not considering recreational, artisanal, or foreign catches), as depicted in Figure S1. Small islands have higher fractions of subsistence fishing relative to total catches occurring in their waters than large islands or mainland countries. Despite having undergone strong decreases in relative subsistence fishing, and increases in relative industrial fishing, absolute catch biomass in the subsistence sector of small islands did not considerably change over time, in contrast to increasing domestic industrial catches. In relation to other sectors, catches by islands' industrial fleets show almost constant increases over time, which is not the case for large islands (strong increase and then levelling off) or the mainland (rather slow increase, followed by a slightly abating trend).

Small islands show particular increases in tuna catches - in contrast to other fish groups - that now constitute a large fraction of overall catches around small islands (Figure S2). While tuna catches increase only slowly in mainland EEZs and recently even decreased in the high seas after peaking in 2003, tuna catches around islands rapidly gained importance in the world tuna fisheries (Figure 3). Reversing the stacked layers in Figure 3 reveals declines in catches around large islands after peaking in 2010. Tuna catches around small islands are still increasing with the highest catch rates in the latest year of record.

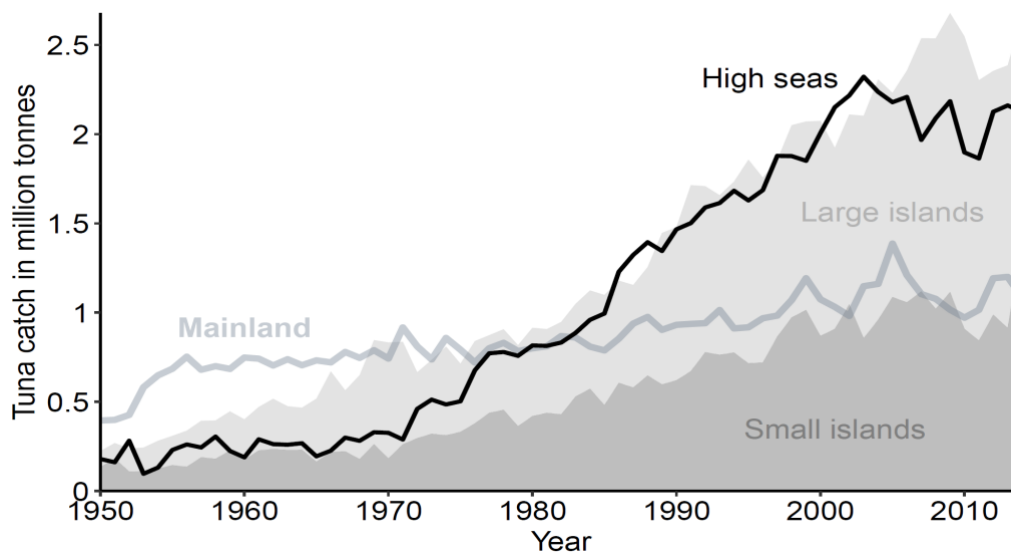


Figure 3. Tuna catches in different parts of the ocean. Large and small islands are represented as stacked layers.

The lowest portion of foreign catches was made in mainland EEZs, followed by large islands and then small islands; the high seas are common fishing grounds (UN, 1994), as depicted in Figure S3A. Overall (not shown), catches around small islands were dominated by foreign fleets, in contrast with large islands and mainland EEZs (67%, 30%, 19% respectively). The extraction of tuna around small islands is also strongly dominated by foreign fleets (Figure S3B). Overall (not shown), domestic tuna catches around small islands in 2014 accounted for less than 20%, while over 80% were caught by foreign fleets. This value decreases for large islands and mainland EEZs (48% and 32% foreign respectively). In 2014, tuna catches accounted for almost one third of the catches in small islands' EEZs (Figure S4), underlining the immense (and increasing) importance of tuna as a resource around many islands (Gillett et al. 2001). The entities in 'mainland' and 'small islands' represent by far the majority of area entries, many of which had no, or negligible, tuna catches in recent years (Figure S5). We also confirm the common notion that islands which provide tuna to the world are mainly located in the Pacific. The waters of the Parties to the Nauru Agreement in the Pacific provided 69% of the tuna catches around small islands between 2010 and 2014, and 21% globally. In fact, the top-ranking tuna suppliers in terms of small islands between 2010 and 2014 are almost exclusively Parties to the Nauru Agreement, with the exception of the Galapagos Islands (Ecuador). They are followed by the Maldives, which are located directly adjacent to the protected Chagos Archipelago.

Especially large islands show high tuna catch densities (Figure S6), in particular archipelagos in the Western Pacific, such as Indonesia (notably the eastern part), the Philippines, Papua New Guinea, and Japan. In recent years (2010-2014), skipjack tuna (*Katsuwonus pelamis*) constituted about half of the tuna catches in the high seas and around islands (for small islands it accounted for 65% of tuna catches), whereas on the mainland this species constitutes only 21% of the tuna catch biomass (Table S1). Skipjack tuna catches are followed by yellowfin tuna (*Thunnus albacares*) in the high seas and around both small and large islands (26%, 21% and 23% respectively), whereas in mainland EEZs yellowfin tuna is the most caught species, with a catch share of about 29%.

In mainland EEZs, the ratio of big (> 2 m max. length) to small (< 2 m max. length) tuna underwent wide fluctuations, but small tuna comprised most of the catches in all of our four area classes (Figure 4). Around large

islands, catches of small tunas tended to outpace big tunas in their increase rate, but was still not comparable with small islands and the high seas, where this trend is very clear and rapid (Figure 4).

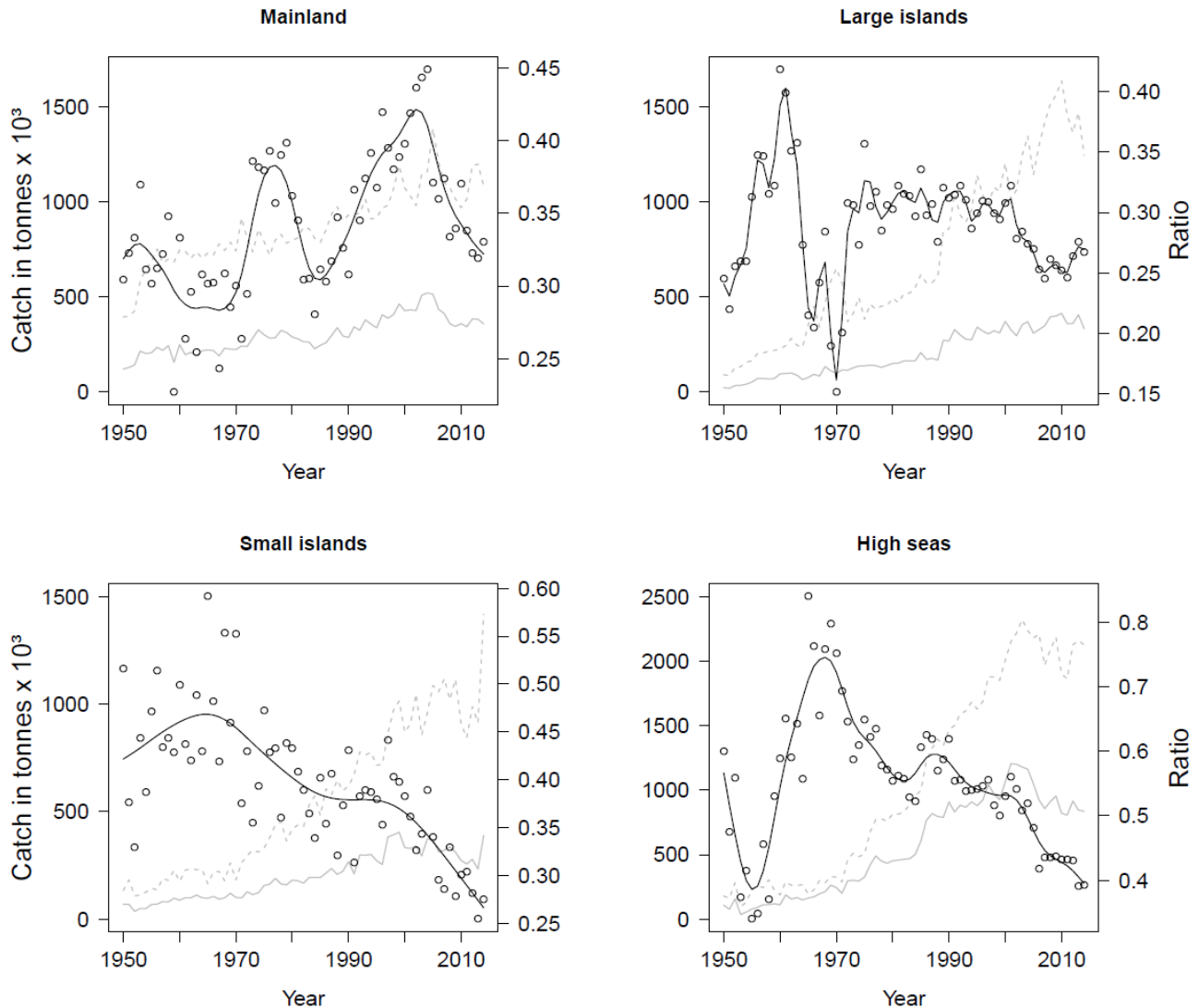


Figure 4. Catches of small and big tuna. Catches of big (maximum length as reported in www.fishbase.org above 2 m; solid grey line) and small (< 2 m maximum length; dashed grey line) and their ratio (big/small tuna; circles and smooth spline as solid black line).

Biogeographical metrics of our area categories in the context of the global ocean reveal how islands differ in their features from the mainland and the high seas (Figure 5). Islands hold large surface area shares of global EEZs (small islands alone about as much as all mainland countries together), while their shelf sizes are comparably small (Figure 5). In terms of productivity of their waters, islands do not - despite their larger surface area - reach levels comparable to the mainland (Figure 5).

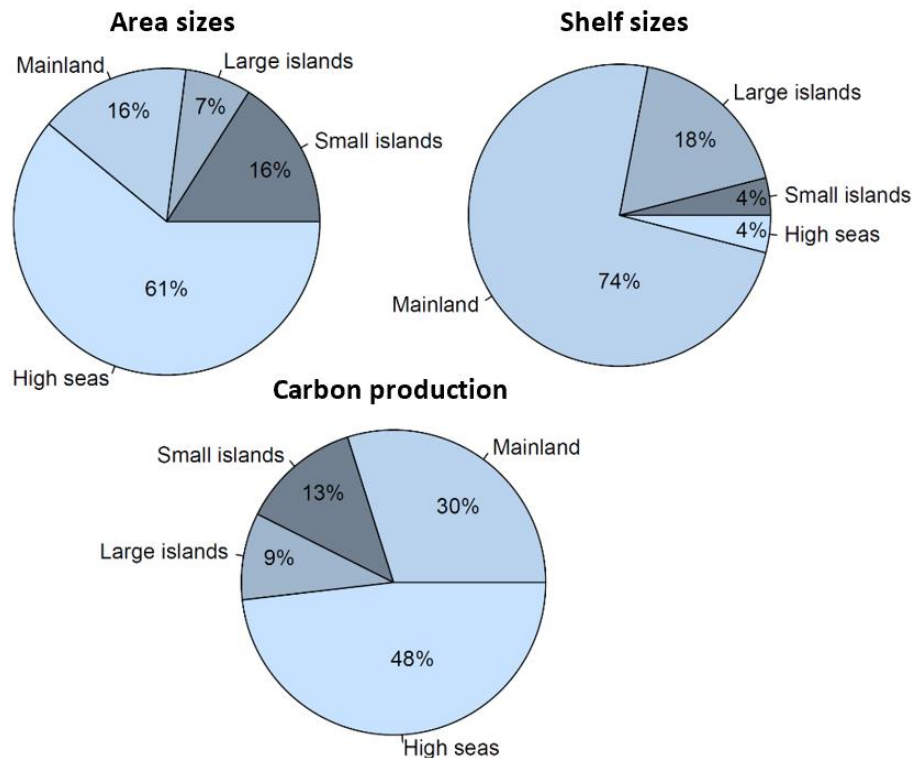


Figure 5. Relative area, shelf sizes and productivity of parts of the ocean. Area sizes of islands and the mainland refer to their EEZs (Pauly and Zeller 2015, 2016). Primary production (Platt and Sathyendranath 1988; Longhurst et al. 1995; Bouvet et al. 2002; Hoepffner et al. 1999; Pauly and Zeller 2015) is total carbon production per day.

Given the negative correlation between the proportion of tuna in the total catches and the respective shelf- to EEZ-size ratio (Spearman correlation, $\rho = -0.57$, $p\text{-value} < 0.001$, for the year 2014), it is not surprising that many islands are - due to the large fraction of deep waters in their EEZs - strongly dependent on tunas, as well as other pelagic fishes (e.g., Hermida and Delgado 2016; Parris and Grafton 2006).

Discussion

In terms of overall catch developments, large islands tend to resemble mainland countries, whereas small islands rather resemble the high seas (e.g., Figure 2).

The net declining catches within EEZs of the mainland and large islands and at the same time increasing catches around small islands (Figure 2) may be the result of the well documented fact of capacity overshoot in world fisheries (Watson et al. 2013; Pauly and Christensen 1995). Possibly, some areas enhanced their fleet capacities beyond what their waters can provide resources for, while remote, small islands with large EEZs might not have the capacity to establish fleets capable of extracting all their resources (Mwikya 2006). That also makes it unsurprising that small islands showed particularly high shares of foreign catches. Small islands, as well as the high seas have often long distances to travel, to find waters of only low productivity, compared with EEZs of the mainland or large islands. Presumably, this only makes sense to explore when alternatives diminish or cannot satisfy demand anymore. One drawback from the perspective of foreign fleets fishing around islands is access agreements that they need to negotiate and pay for, which is not the case for the high seas (UN 1994).

Given the Island Mass Effect (Doty and Oguri 1956; Gove et al. 2016), high or even increasing tuna catches around islands should be regarded with caution because they may originate from higher catchability, rather than

from higher reproduction rates compared to non-island waters. A similar phenomenon occurred during the legendary collapse of anchoveta in the early 1970s off the Peruvian coast, when an El Niño event concentrated this fish at a few remaining upwelling plumes, resulting in higher catchability (Csirke 1981). The highest catch in 1970, which contributed a large fraction of the world catch of that year, was followed by two decades of very low catches and has - despite a recovery of the fisheries - never been reached again. Those hyper-stable dynamics, where aggregation of fish keep catch per unit effort at a high level, in spite of (and masking) potential stock declines, may be aggravated further by the recent, rapid increase in use of Fish-Aggregating Devices or FADs (Maufroy et al. 2016), which are also used by tuna fisheries around islands (Maufroy et al. 2016; Itano and Holland 2000; Leroy et al. 2009).

It has furthermore been suggested that the use of FADs may alter the migrations of mainly small tuna (*Katsuwonus pelamis*, and juvenile *Thunnus albacares* and *Thunnus obesus*), causing them to move away from productive coastal feeding grounds (Marsac et al. 2001). To what extent the distribution of FADs inside versus outside waters surrounding islands influence our findings may be subject to future studies.

The large tuna catches around the islands which are Parties to the Nauru Agreement are subject to large-scale fisheries management to protect tuna resources, including effort control, temporal closures on FADs and of the high seas (Havice 2013). Fees that need to be paid for individual fishing effort on tuna were feared to deter fishermen to the high seas; which is (partly the reason) why some adjacent high seas pockets were closed to fishing, forcing fleets back into the islands' EEZs (Havice 2013). This process of regulating and motivating fishing on tuna in those Pacific islands' EEZs was gradual, from the first establishment of their EEZs in the 1970s, to the official recognition of such claims by the United Nations Convention on the Law of the Sea, ratified in 1982 and the initiation of capacity controls on purse seiners in 1990, to the transferable effort system under the Vessel Day Scheme as one of the world's largest fisheries management conventions, which came into effect in 2007, but without stabilizing neither fishing effort nor capacity (Havice 2013). Obviously, those and other market and management changes may successively drive spatial catch distributions just as actual tuna abundances do.

The *Sea Around Us* data we used are reconstructed catch data, i.e., including catches added to on officially reported statistics and accounting for unreported fishing activities (Pauly and Zeller 2015). During the reconstruction process, catch data missing in official statistics were reconstructed using various sources and sometimes underwent expansions from known anchor points, application of rising factors and interpolations. By compiling and supplementing official catches from, e.g., the Food and Agriculture Organization of the United Nations (FAO) or regional fisheries management organizations, such as the Western and Central Pacific Fisheries Commission, the *Sea Around Us* probably provides the most reliable fisheries catch data that currently exist. It should be emphasized that the tuna catches provided by the *Sea Around Us* are based on a harmonization of official databases from regional fisheries management organizations, while keeping resolutions at the highest possible levels (Coulter et al. 2020). Unfortunately, vessels running under 'flags of convenience' often impede correct assignment of the vessels' origins and may contribute to partly confound, e.g., foreign and domestic fishing (Miller and Sumaila 2014).

We conclude that small islands may easily be overlooked in global fisheries debates, as they only make up a small fraction of global catches. They do, however, play a crucial role in the world tuna fisheries, at least in the Pacific; although most of the tuna is not being caught by the islands themselves, but by foreign fleets. Reaching the UN's Sustainable Development Goal 14.7 could help to ensure that tuna stocks are fished at sustainable rates around small islands.

Acknowledgements

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Supplementary Information

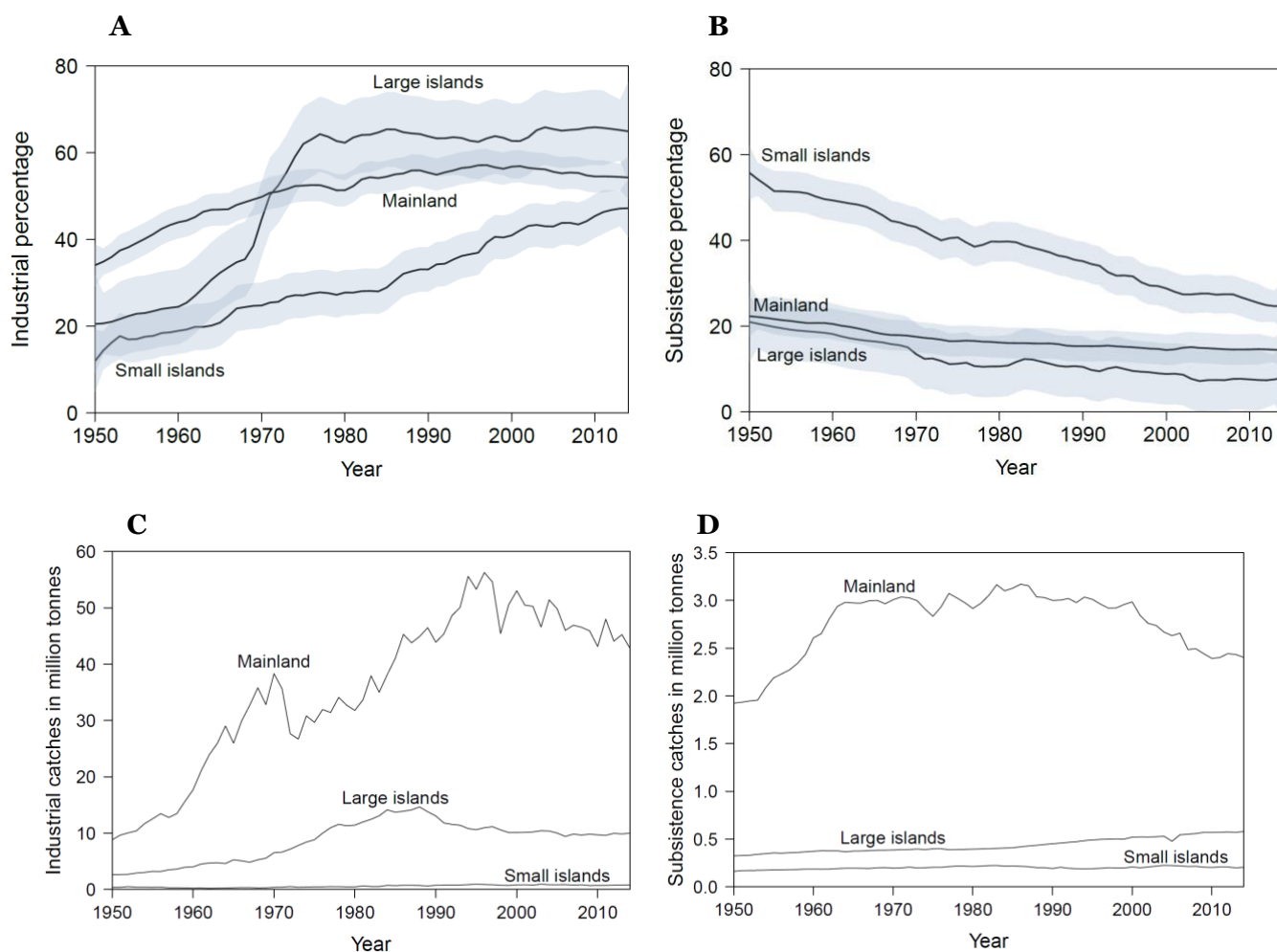


Figure S1. Subsistence versus industrial catches. LOESS-smoothed catch shares (span: 0.1) with area sizes included as weighting factors in **A** and **B**. Grey areas are within 95% confidence intervals. In **C** and **D**, absolute catches are shown. Note that all four panels refer to domestic catches.

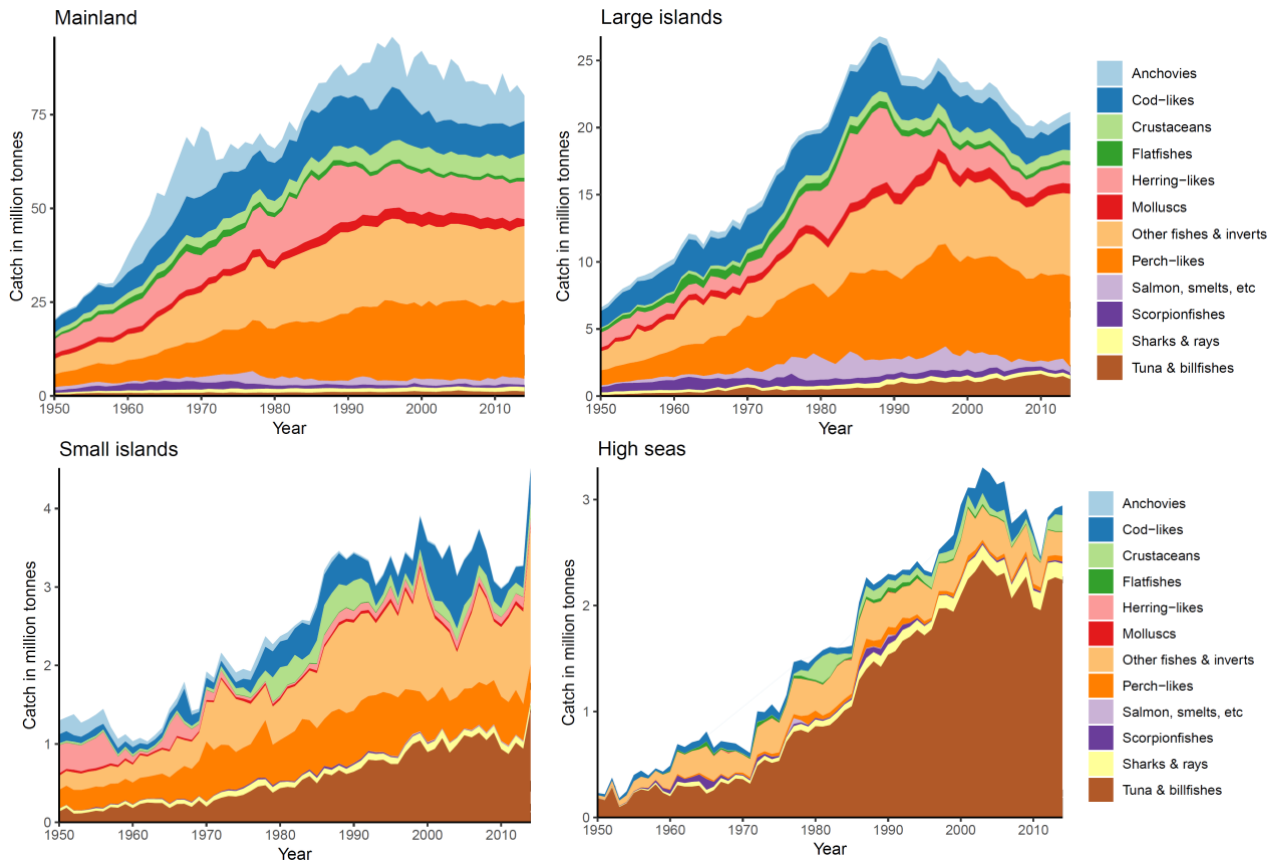


Figure S2. Commercial fish groups as categorized by the *Sea Around Us*

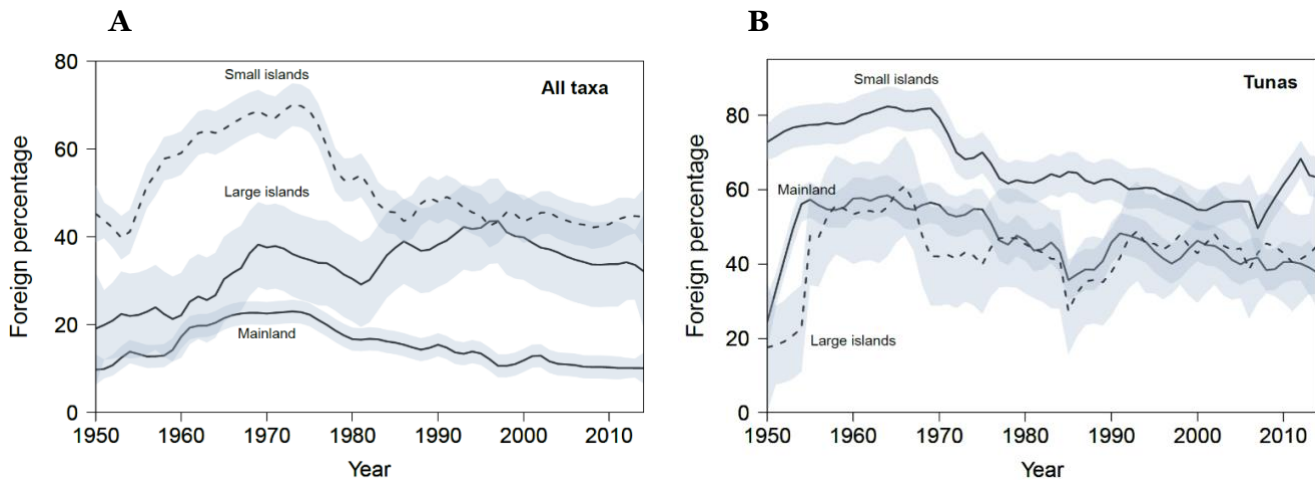


Figure S3. Foreign contribution to catches. LOESS-smoothed foreign catch shares (span: 0.1) with area sizes included as weighting factors. The line for small and large islands is dashed for better distinguishability in **A** and **B** respectively. Grey areas represent 95% confidence intervals. **A**, Foreign catch shares of catches made within the EEZs of small islands, large islands and mainland countries. **B**, Foreign catch shares as in **A**, but specifically for tuna catches.

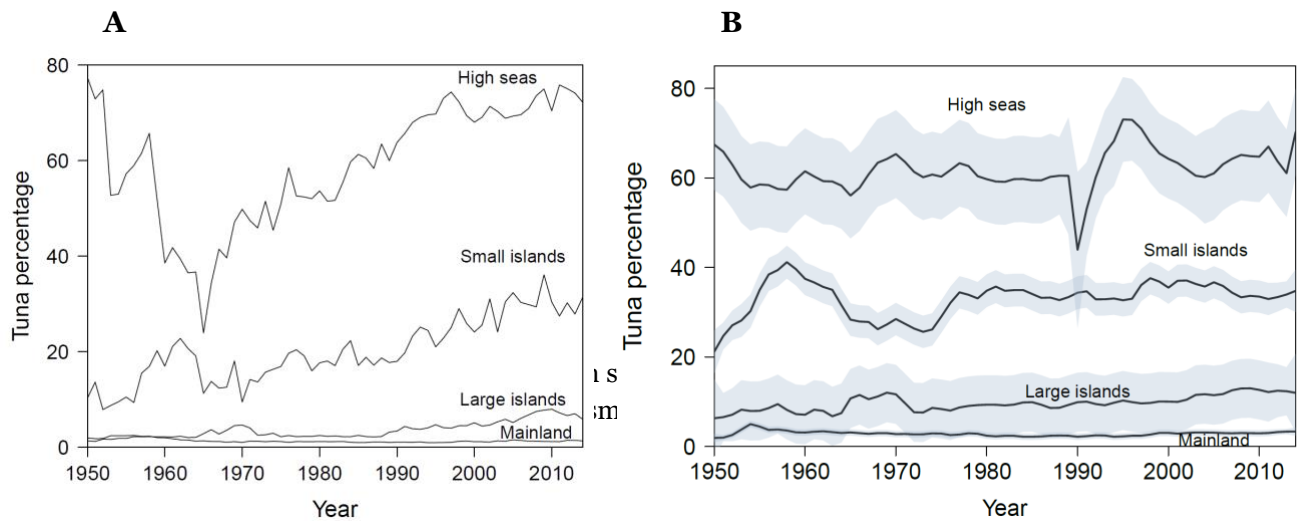


Figure S4. Tuna shares among EEZs and the high seas; **A**, Tuna shares of total catches. **B**, Tuna shares per island, mainland EEZ and high seas area; LOESS-smoothed (span: 0.1) with area sizes included as weighting factors and 95% confidence intervals shaded in grey.

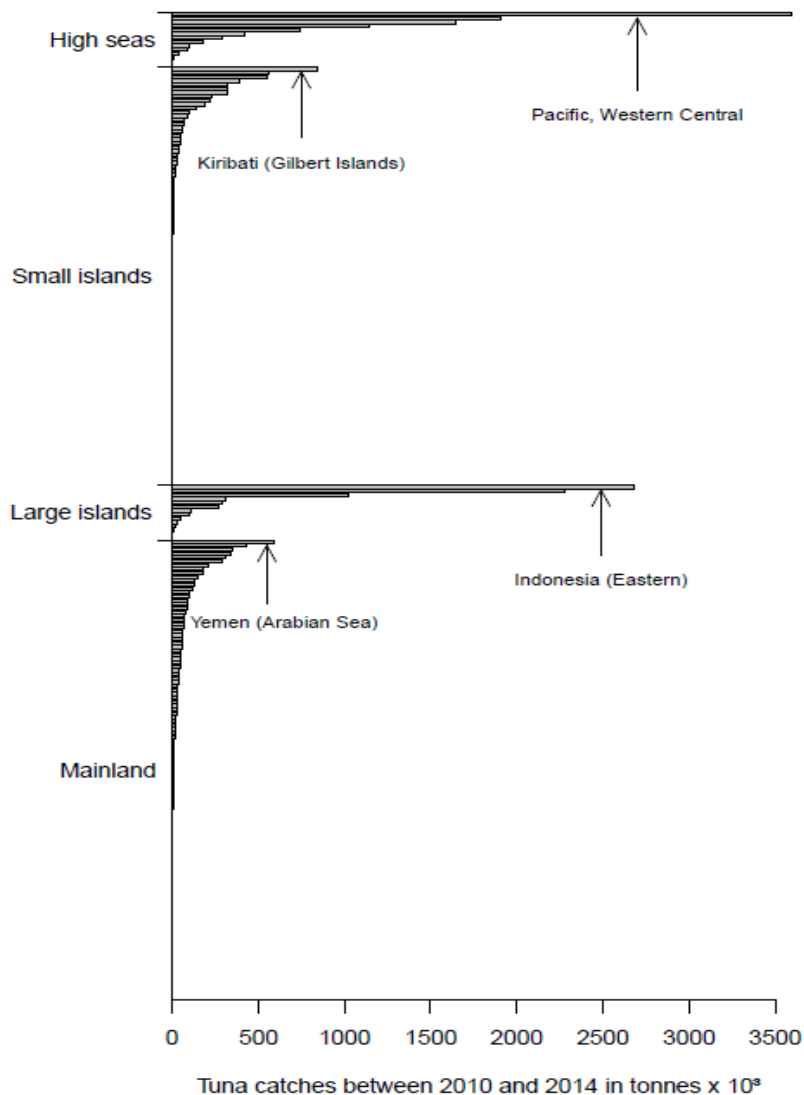


Figure S5. Tuna catch distributions of the different areas (2010-2014). Tuna catches were summed for the five-year period for each entity of the area classes: mainland (n=118), large islands (n=14), small islands (n=107) and the high seas (n=14). The area of each area class, where catches were highest are highlighted by arrows. The two high bars in "Large islands" that follow Eastern Indonesia are Papua New Guinea and the Philippines respectively. The Western Central Pacific is followed by the Eastern Central Pacific and then the Eastern Indian Ocean.

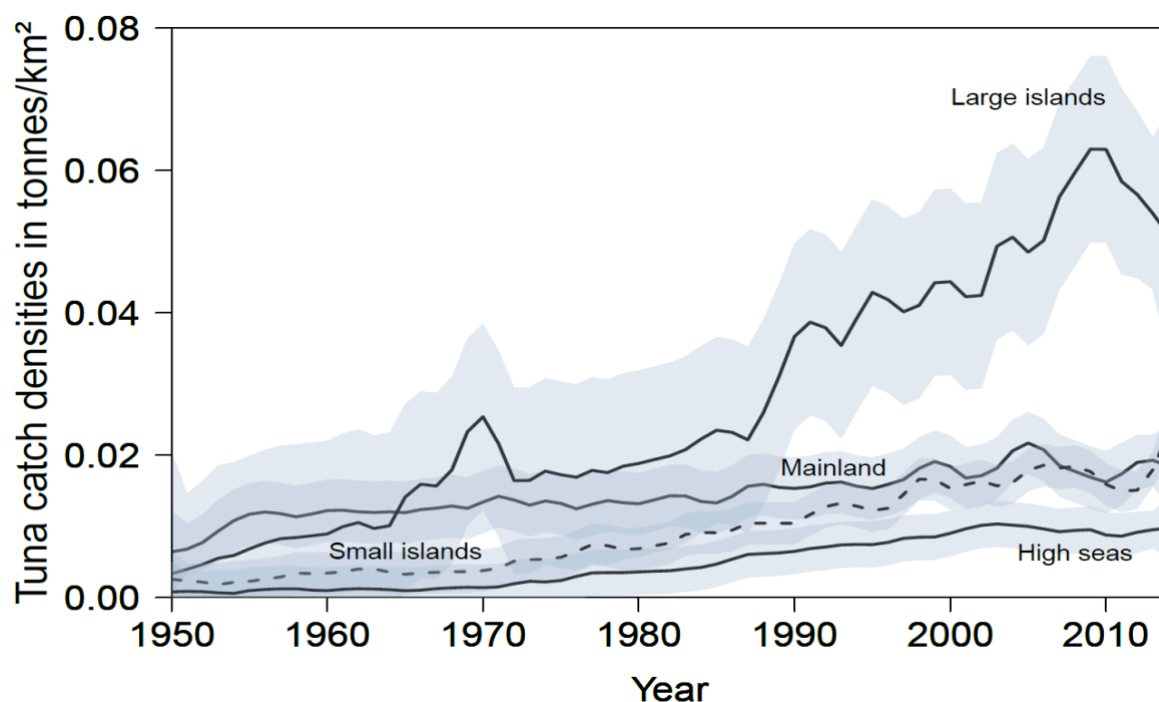


Figure S6. Tuna catch densities. LOESS-smoothed catch densities (span: 0.1) with area sizes included as weighting factors. The line for small islands is dashed for better distinguishability. Grey areas represent 95% confidence intervals.

Tab. S1. Taxonomical tuna compositions. The table shows the five most contributing species to the catches of each of the respective area classes between 2010 and 2014.

Area class	Common name	Percentage	Area class	Common name	Percentage
High seas	Skipjack tuna	51.41	Large islands	Skipjack tuna	47.66
	Yellowfin tuna	25.95		Yellowfin tuna	22.71
	Bigeye tuna	15.09		Frigate tuna	16.25
	Albacore	6.51		Bullet and frigate tunas	5.25
	Frigate tuna	0.34		Bigeye tuna	2.81
Small islands	Skipjack tuna	64.73	Mainland	Yellowfin tuna	28.66
	Yellowfin tuna	20.73		Skipjack tuna	20.54
	Bigeye tuna	6.85		Atlantic bonito	8.98
	Albacore	5.25		Kawakawa	7.23
	Tunas, bonitos, billfishes	0.48		Longtail tuna	5.50

A MODEL OF THE OKHOTSK SEA WITH A FOCUS ON MARINE MAMMALS†

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Abstract

This contribution summarizes previous research performed on the biomass, production and other parameters of different species in the Okhotsk Sea ecosystem for the 1980s period into an Ecopath model. The model was then compared to a previously published food web diagram for the same region and period based on biomass, energy flow, and numbers of trophic levels. The applications of the model in the research of the effects of fisheries on marine mammals were also investigated. It was found that the biomass distribution in the model was similar to that in the previously published food web. However, the estimated transfer efficiency and number of trophic levels in the model were greater than that of the earlier food web. The new model of the Okhotsk Sea indicated that a large amount of energy flow in the system originates from detritus. Ecosim time simulations showed that an increase in the fishing effort did not cause a uniform decrease in the biomass of marine mammals.

Introduction

The impacts of fishing activities on the ocean systems all over the world have been receiving increased attention (National Marine Fisheries Service, 1999). Pauly *et al.* (1998) suggested that overfishing tends to decrease mean trophic level of major species groups in the ecosystem, i.e. generate a gradual change in the overall catch composition, which shifts from large benthic fish with higher trophic levels to smaller pelagic fish with lower trophic levels. Research focused on fisheries impacts on the ecosystem could therefore aid in improvement of managing policies. This, in turn, could help to reduce deleterious impacts of overfishing and protect endangered species.

Unfortunately, most of the research conducted in the past focused mainly on the changes occurring to single species. This single-species approach ignores the complex web of prey-predator interactions that take place in any marine ecosystem and can have a significant effect on the population of study animals.

Recently many researchers have begun to utilize ecosystem-based approach (NMFS, 1999). This broadening concept allows researchers to assess not only direct impact of fisheries on the health of target species, but also to investigate their effects on the entire ecosystem. Fisheries can induce changes to the trophic balance and food web relationships. It is possible to estimate the full impact of human disturbance on certain species only in the context of the entire system. Study species can be directly affected by a disturbance itself as well as through the changes in the abundance of their prey, competitors and predators. For example, even though direct competition between marine mammals and fishing operations due to prey overlap is relatively small, it was suggested that the amount of primary production in the region necessary to sustain populations of marine mammals significantly declines with increases in fishing activities (Trites *et al.*, 1997).

Due to its high productivity, the Okhotsk Sea has been an area of interest to researchers. Several attempts to summarize the energy and biomass flow in the entire Okhotsk Sea have been undertaken by Russian scientists, resulting in multiple flow diagrams (Shuntov and Dulepova, 1997; Sorokin *et al.*, 1997; Sorokin and Sorokin, 1999;

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Based on Chaikina, N. 2004. A trophic mass-balance model of the Sea of Okhotsk for the 1980s period. BSc. thesis, Faculty of Science, University of British Columbia, 49 p.

Shuntov and Dulepova, 1996). This ecosystem supports almost 70% of the total Russian catch in the Far East region and is populated by more than half a million tonnes of marine mammals. The fishery industry in this region is regulated via “fishery regulations” that set limits on fishing areas and on the total catch allowed for a certain period of time (Lapko and Radchenko, 2000).

The goal of this research was to summarize various studies done in the region of the Okhotsk Sea during the 1980s in a coherent Ecopath model. This Ecopath model (further referred to as NE model) was then compared to the already existing food web created by Shuntov and Dulepova (1997) for the same region and for same period. Comparison was made based on the biomass and energy flow values, as well as the number of the trophic levels. In order to make this comparison possible, food web was transformed into a second, somewhat simplified, Ecopath model (further referred to as SD model). It was hypothesized that the main parameters of the system’s energy flow in the NE Ecopath model would be similar to the conclusions drawn by Shuntov and Dulepova (1997) based on their energy diagram.

The Ecopath modeling software was used to evaluate the impacts of fisheries on marine mammals in the ecosystem of the Okhotsk Sea (see www.ecopath.org). This approach analyzes food web interactions between the trophic levels of the entire region and is based on the works of Polovina (1984). It allows for a construction of a mass-balance model based on the prey-predator relationships between main groups of animals in the system (Christensen and Pauly, 1992a, 1992b). The model is based on information collected in the 1980s mostly by Russian scientists on all major species or groups of species found in the Okhotsk Sea. Ecosim simulation was performed to examine the impact of fisheries on the modeled system throughout a set period. It was hypothesized that increase in fishing effort would cause a reduction in the biomass of the higher-trophic level animals, such as marine mammals.

Materials and Methods

The Okhotsk Sea is located on the north-eastern the of Asian continent. It is bound by the Russian Federation and Japan. According to Shuntov (2001), the Okhotsk Sea is located in the temperate climate zone. The total area of the region is estimated to be about 1,590,000 km². The Okhotsk Sea is the coldest of all of the Russian Far East seas with more than 50% of the region covered by ice for almost one third of the year. The average depth of the sea is about 821 meters with maximum depth of 3916 meters (Dobrovolsky and Zalogin 1982).

Large phytoplankton blooms and active immigration of many species of fish and mammals occur in the region in the summer season. The Okhotsk shelf is one of the most productive regions in the Russian Far East. Because of the high productivity of the region, native people are highly dependent on the Okhotsk Sea resources (Okey 2003). Agriculture in the surrounding regions is not developed well enough to have a significant impact on the health of the ecosystem. Commercial fisheries have a considerable influence on the area. In the 1960s, total annual catch in the region was about 1 million t, increasing to 2.4-2.6 million t in 1980s. Some of the parts of the Okhotsk Sea, such as West Kamchatka suffer from especially intensive fishing effort. Catches ranged from 8 to 22 t·km⁻²·year⁻¹ in 1970s (Lapko and Radchenko 2000).

The 1980s were chosen because, due to the increased amount of funding available from the Soviet government, there was a vast amount of research carried out at that time. Also, the Okhotsk Sea did not appear to have suffered significant disturbances or changes during this period (Shuntov and Dulepova 1997).

Shuntov and Dulepova (1997) also selected the 1980s for their energy-balanced food web of the Okhotsk Sea. This diagram had to be converted into a SD Ecopath model. The original food web consisted of eleven functional groups, including detritus. The SD Ecopath model had nine functional groups, including bacterioplankton and microzooplankton. These organisms play an important role in most ecosystems, and many ecologists, including

Pomeroy (1974) argue that they form a “microbial loop” that recycles dead organic matter (DOM) and releases nutrients that can be used by primary producers. However, bacteria and protozoa operate largely outside of the food web that leads to fishes and marine mammals. Thus, they are not included in NE model of the Okhotsk Sea and many other Ecopath models (Trites et al. 1999; Pauly and Christensen 1996; Aydin et al. 2002). In order to compare the SD model to NE model, the bacteria and microzooplankton links were taken out of the food chain and represented as part of the detritus group.

NE model included twenty-nine functional groups. Species were assigned to functional groups based on the similarities in the diet, production and consumption characteristics, and importance in the ecosystem

The biomass, production, and consumption parameters of most species change with the season. Average annual parameters were calculated based on mean of summer, spring, fall, and winter parameters, weighted to the number of months that made up each season.

The Ecopath modeling is an approach to the food web analysis that was first emerged in the works of Polovina (1984). Which was further developed by Christensen and Pauly (1992a), and made available in form of software program (Christensen and Pauly 1992b). Currently, Ecopath is widely employed by more than 2700 users in 126 countries. The last up-to-date version of this program, as well user manuals and other publications can be found on the Ecopath website.

The Ecopath approach is based on the assumption that in any ecosystem the production of a functional group is equal to the sum of biomass accumulation, total catch, loss due to predation, other mortality, and loss of biomass to the other systems. Ecopath also assumes that consumption of a group A biomass by group B is equal to a sum of production, respiration and unassimilated food of group A. Thus, the Ecopath mass-balance model relies on the master equation:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum [B_j \cdot (Q/B)_j \cdot DC_{ji}] + BA_i + NM_i$$

where

- B_i is biomass of functional group i ; B_j is biomass of functional group j ;
- P/B_i is the ratio of production/biomass, which is equivalent to mortality in most cases (Allen 1971);
- EE is ecotrophic efficiency or a fraction of production utilized by other components of the system. Ecotrophic efficiency must be below 1, otherwise it would mean that certain component of the system is being consumed at a greater rate than it is produced. In this way EE serves as a primary method of Ecopath model calibration;
- Q/B_j is the ratio of consumption per unit of biomass;
- Y_i is equal to the fisheries catch per unit area;
- DC_{ij} is a proportion of i in the diet of j ;
- BA_i is the accumulation of the biomass; and
- NM_i is net migration, or emigration minus immigration.

The construction of Ecopath model of Okhotsk Sea consists of the following steps:

1. Defining the ecosystem;
2. Defining the functional groups in the system. Living organisms in one functional group must possess similar consumption, production and diet matrix values;
3. Gathering the information regarding biomass, production, consumption, and unassimilated consumption parameters for every functional group. Data was collected from various published and unpublished sources in Russian and English;
4. Gathering information about the diet matrix of functional groups;
5. Gathering information about fisheries in the region of the Okhotsk Sea;

6. Entering the information into the Ecopath program; and
7. Balancing the model, so that no EE values are greater than 1.

Balancing was done in two stages. First, gross adjustments were done manually. Auto balance routine of Ecopath (Kavanagh et al. 2004) was used to complete the balancing. No balancing was required for the SD Ecopath model since all of its ecotrophic efficiencies were less than one.

The Ecosim software allows tracking of trophic interactions for a set period time, recording changes in biomass, diet composition and other parameters of functional groups in the system. Simulation time period was set to 10 years. Effect of threefold increase in fishing effort on the biomass of baleen whales, toothed whales, sperm whales, and pinnipeds was evaluated.

Results

The input parameters and estimated trophic level of the functional groups in two balanced Ecopath models of the Okhotsk Sea are expressed in Tables 1 to 4.

Table 1. Parameters of a balanced models of the Okhotsk Sea ecosystem for the 1980s.

Group name	Trophic level	Biomass (t·km ⁻² ·year ⁻¹)	Prod./biom. (year ⁻¹)	Cons./biom. (year ⁻¹)	Ecotrophic Efficiency	Production / consumption
1. Baleen whales	3.92	0.958	0.02	8.31	0.365	0.002
2. Toothed whales	4.56	0.010	0.02	13.11	0.657	0.002
3. Sperm whales	5.10	0.011	0.02	4.55	0.000	0.004
4. Pinnipeds	4.96	0.053	0.05	17.10	0.527	0.003
5. Seabirds	4.69	0.005	0.33	91.63	0.000	0.004
6. Walleye pollock	3.74	2.475	0.55	10.00	0.997	0.055
7. Juv. pollock	3.75	2.119	0.55	12.30	1.000	0.045
8. Pacific herring	3.95	0.818	0.79	9.66	0.807	0.082
9. Salmon	3.88	0.147	7.00	10.95	0.303	0.639
10. Capelin	3.50	2.580	2.00	18.00	0.801	0.111
11. Pacific Sardine	2.16	0.667	1.20	9.31	0.812	0.129
12. Other Gadidae	3.92	0.306	0.55	10.59	0.350	0.052
13. Pleuronectidae	3.40	1.186	0.40	3.03	1.000	0.132
14. Cottidae	4.27	0.212	0.48	3.21	1.000	0.149
15. Other bottom fishes	3.86	0.515	0.50	3.21	1.000	0.155
16. Ammodytidae	3.00	0.314	2.00	18.00	0.508	0.111
17. Myctophidae	3.21	1.491	0.80	3.65	0.503	0.219
18. Bathylagidae	3.76	14.698	0.80	5.04	0.138	0.159
19. Other mesopelagic fishes	4.09	1.578	0.80	6.79	1.000	0.118
20. Crabs and shrimps	3.04	2.599	0.80	7.14	1.000	0.113
21. Squids	4.19	1.541	5.48	10.95	0.473	0.500
22. Jellyfish	3.33	0.980	1.50	3.00	0.025	0.500
23. Carnivorous invertebrates	3.00	12.948	1.06	7.14	0.811	0.148
24. 2nd level benthos	2.00	143.052	1.52	3.33	0.515	0.456
25. Predatory zooplankton	3.21	86.792	4.17	17.46	0.998	0.239
26. Herbivorous zooplankton	2.00	197.480	8.03	31.54	0.858	0.254
27. Phytobenthos	1.00	12.579	4.00		0.020	
28. Phytoplankton	1.00	160.943	165.30		0.123	
29. Detritus	1.00				0.130	

Table 2. Balanced SD Ecopath model parameters of nine functional groups in the Okhotsk Sea ecosystem (1590,000 km²) for the 1980s.

Group name	Trophic level	Biomass (t·km ⁻² ·year ⁻¹)	Prod./biom. (year ⁻¹)	Cons./biom. (year ⁻¹)	Ecotrophic efficiency	Production / consumption
1. Phytoplankton	1.00	57.452	165.299		0.366	
2. Herbivorous plankton	2.00	197.484	8.025	31.545	0.779	0.254
3. Predatory plankton	3.20	72.327	4.174	17.461	0.773	0.239
4. Necton	3.37	22.069	0.678	3.448	0.604	0.197
5. Non-predatory zoobenthos	2.30	131.195	1.515	3.634	0.523	0.417
6. Predatory zoobenthos	3.30	13.459	1.033	6.869	0.167	0.150
7. Nectobenthos	3.61	3.145	0.440	5.520	0.441	0.080
8. Mammals and birds	3.68	0.322	0.195	2.932	0.000	0.067
9. Detritus	1.00	-	-	-	0.323	-

Table 3. Diet matrix of eleven functional groups in the Okhotsk Sea ecosystem for the 1980s period in the SD Ecopath model.

Prey	Predator						
	2	3	4	5	6	7	8
1. Phytoplankton	0.557						
2. Herbivorous plankton		0.822	0.701	0.299		0.036	0.400
3. Predatory plankton		0.171	0.225			0.036	
4. Necton			0.074			0.105	0.467
5. Non-predatory zoobenthos					1.000	0.659	0.133
6. Predatory zoobenthos						0.134	
7. Nectobenthos						0.029	
8. Mammals and birds							
9. Detritus	0.443	0.007		0.701			
10. Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 4a. Diet matrix of twenty-nine functional groups (1-13) in the Okhotsk Sea ecosystem (1590,000 km²) for the 1980s period in the NE Ecomod model.

Prey	Predator												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Baleen whales													
2. Toothed whales		0.001											
3. Sperm whales													
4. Pinnipeds		0.003											
5. Seabirds													
6. Walleye Pollock	0.064	0.081	0.012	0.126								0.027	
7. Juv. Pollock	0.065	0.081	0.013		0.600	0.006			0.005			0.028	
8. Pacific herring				0.124	0.025	0.005	0.005					0.022	
9. Salmon				0.311									
10. Capelin				0.005		0.050	0.100					0.053	
11. Pacific Sardine						0.010	0.015						
12. Other Gadidae				0.011									
13. Pleuronectidae		0.106										0.085	
14. Cottidae												0.025	
15. Other bottom fishes		0.053	0.050									0.001	0.057
16. Ammodytidae		0.053	0.050	0.011	0.025	0.010	0.001					0.001	
17. Myctophidae		0.162				0.013	0.010						
18. Bathylagidae						0.030	0.025					0.020	
19. Other mesopelagic fishes	0.050		0.025	0.286	0.106	0.018	0.020					0.008	
20. Crabs and shrimps	0.049	0.165					0.015		0.003			0.325	
21. Squids	0.143	0.246	0.849	0.127	0.053	0.039	0.023		0.007			0.033	
22. Jellyfish									0.006				
23. Carnivorous invertebrates							0.099	0.003				0.012	0.276
24. 2nd level benthos	0.054				0.001		0.007	0.008		0.034		0.159	0.638
25. Predatory zooplankton	0.253	0.046			0.188	0.370	0.271	0.796	0.697	0.416	0.017	0.051	0.019
26. Herbivorous zooplankton	0.243					0.450	0.409	0.184	0.281	0.55	0.120	0.134	
27. Phytobenthos													0.010
28. Phytoplankton	0.079										0.863		
29. Detritus		0.001	0.001		0.002			0.010				0.015	

Table 4b. Diet matrix of twenty-nine functional groups (14-26) in the Okhotsk Sea ecosystem for the 1980s period in the NE Ecopath model.

Prey	Predator												
	14	15	16	17	18	19	20	21	22	23	24	25	26
1. Baleen whales													
2. Toothed whales													
3. Sperm whales													
4. Pinnipeds													
5. Seabirds													
6. walleye Pollock	0.020												
7. Juv. Pollock	0.030							0.001	0.010				
8. Pacific herring		0.005						0.001					
9. Salmon													
10. Capelin	0.017	0.005						0.001					
11. Pacific Sardine													
12. Other Gadidae	0.030												
13. Pleuronectidae	0.240	0.020											
14. Cottidae	0.113												
15. Other bottom fishes	0.039	0.100											
16. Ammodytidae	0.001												
17. Myctophidae													
18. Bathylagidae	0.025	0.072											
19. Other mesopelagic fishes		0.152											
20. Crabs and shrimps	0.325	0.152					0.030	0.004	0.128				
21. Squids	0.022	0.051			0.004		0.020	0.003					
22. Jellyfish									0.008				
23. Carnivorous invertebrates	0.004		0.037	0.021	0.057		0.150						
24. 2nd level benthos	0.005	0.313	0.918			0.005	0.450	0.004		1.00			
25. Predatory zooplankton		0.020	0.005	0.152	0.571	0.905	0.050	0.970	0.139			0.172	
26. Herbivorous zooplankton	0.129			0.827	0.367	0.090	0.050	0.016	0.715			0.828	
27. Phytobenthos							0.050						
28. Phytoplankton											0.30		0.50
29. Detritus		0.111	0.040				0.20				0.70		0.50

As seen in Figure 1, the biomass pyramids of both models are roughly similar, as is the biomass distribution at trophic levels II and higher (Figure 2). The biomass of the trophic level I, however, is much lower in the SD model. The flow pyramid that is based on NE model exhibits a more acute angle than the flow pyramid of the SD model, indicating high transfer efficiency within the system. The volumes of each level of the flow pyramids are greater in the SD model compared to the NE model, indicating that the SD model exhibits more flow within a single trophic level. Figures 1 and 2 indicate that NE model contains higher amount of trophic levels than the SD model.

Table 5 also shows that the transfer efficiency is higher in the NE model (21.9%) than the SD model (6.2%). It also shows that Sea of Okhotsk exhibits a large proportion of flow originating from detritus (50% in the NE model and 33% in the SD model).

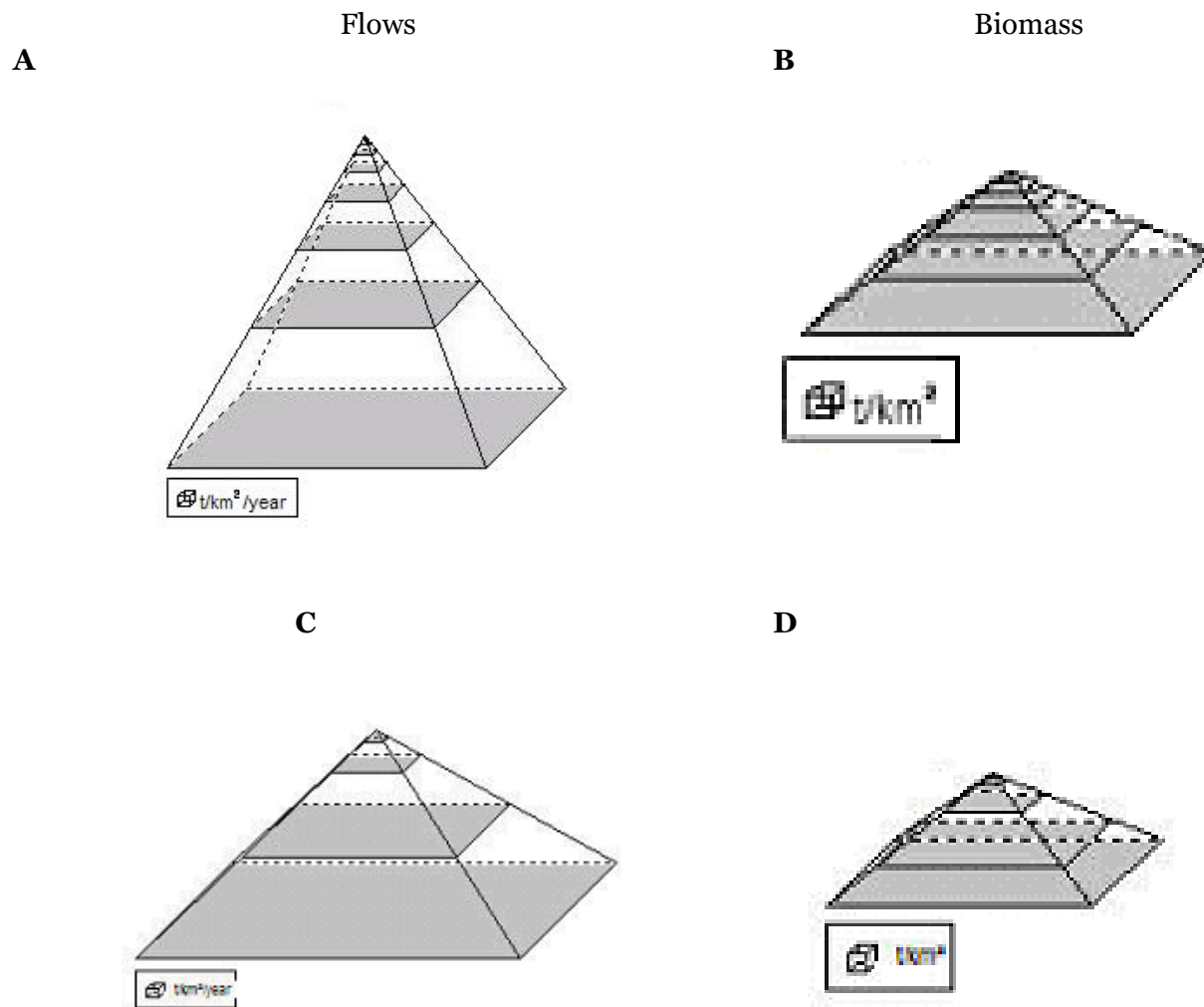
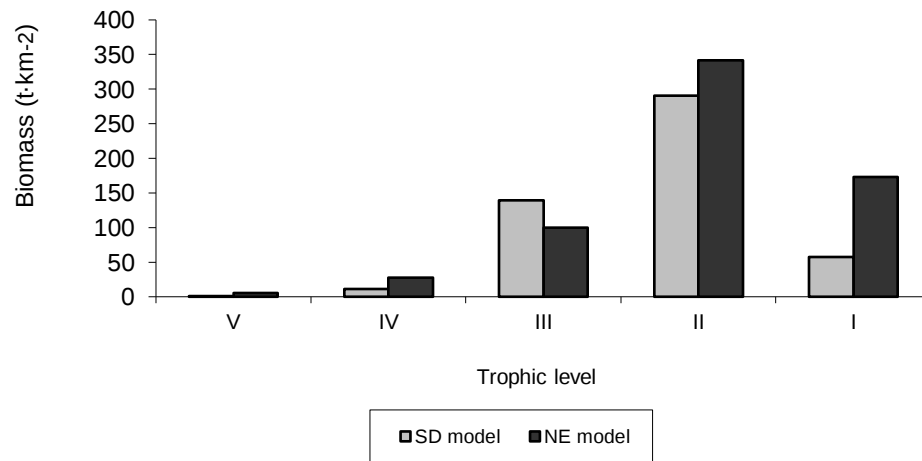


Figure 1. Trophic pyramids indicating the distribution of biomass and energy flow by trophic level (starting from the first-order consumers at trophic level II at the bottom of the pyramid) in the two models of the Sea of Okhotsk ecosystem for the 1980s; **A:** flow pyramid of NE model; **B:** biomass pyramid of NS model; **C:** flow pyramid of SD model; and **D:** biomass pyramid of SD model. Volume of the pyramid at a certain trophic level indicates the sum of all flows or biomass at that level. The angle of the pyramid is inversely proportional to the transfer efficiency of the system.

Table 5. Summary of trophic flow statistics in the two models of the Sea of Okhotsk ecosystem for the 1980s time period.

Feature	NE model (%)	SD model (%)
Proportion of total flow originating from detritus	50.0	33.0
Transfer efficiencies (calculated as geometric mean of data in TL 2-4)		
From primary producers	22.1	6.3
From detritus	21.7	6.1
Total	21.9	6.2

**Figure 2.** Biomass distribution by trophic levels (I-V) in the two models of the Sea of Okhotsk ecosystem. Height of the bars indicates the sum of biomass of all organisms at that trophic level

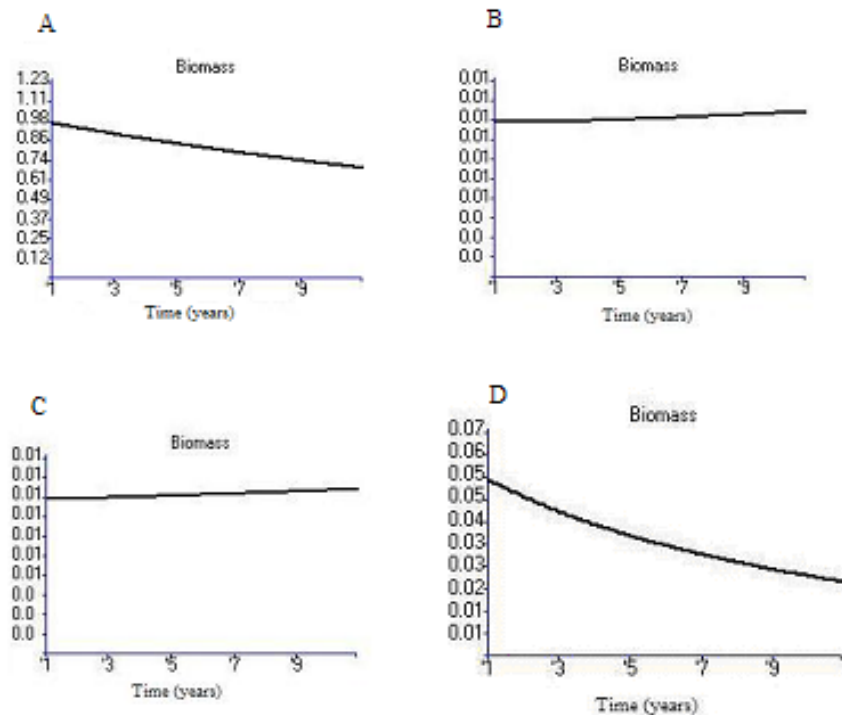


Figure 3. The effect of threefold increase in the fishing effort on the biomass of **A:** baleen whales; **B:** toothed whales; **C:** sperm whales; and **D:** pinnipeds. The results are based on the Ecosim simulation of the NE Okhotsk Sea model over the ten-year time period.

Figure 3 shows that threefold increase in the fishing effort caused a decrease in the biomass of baleen whales and pinnipeds. It also caused a slight increase in the biomasses of toothed and sperm whales.

Discussion

The purpose of this research was to create an Ecopath model of the Okhotsk Sea for the 1980s and to compare it with an already existing food web of the same region and period (Shuntov and Dulepova 1997).

Both flow pyramids (Figure 1) and transfer efficiency statistics (Table 5) indicate that the transfer efficiencies are higher in the NE model (21.9%) compared to the SD model (6.2%). One of the possible explanations for this is that there is a smaller number of functional groups and therefore greater number of species within a single functional group in the SD model. Because of this, the amount of trophic interactions in the system is greatly reduced. Even though an Ecopath model may accurately represent the flow of the biomass between the components of the system, it hides the multiple levels of prey-predator interactions that occur within a single functional group and clumps it under cannibalism. This may lead to an underestimation of the numbers of trophic levels in the system.

Since the NE model contains more functional groups than the SD model, it is capable of showing a more complex system of trophic interactions, resulting in a greater amount of trophic levels and greater transfer efficiency between the levels, compared to the older model.

It is interesting to note that biomass of zooplankton, non-predatory zoobenthos, and predatory zoobenthos as well as the P/B ratios of these functional groups are very similar in both models. One of the most visible differences between the two models, however, is that biomass of phytoplankton in NE model greatly exceeds that of a SD model. This difference could have resulted from the assumption that all bacterioplankton and

microzooplankton in the Okhotsk Sea are part of the microbial loop (Pomeroy 1974) and therefore can not be considered as part of the system. This may not be entirely true, since Markina and Chernyavskij (1984) estimate the production of the phytoplankton as 14,100 million t, but increase this number greatly to account for production of microphytoplankton. Latter estimation was used in order to calculate the P/B ratio for NE model. Shuntov and Dulepova (1997), however, estimate production of phytoplankton as 15,100 million t, which is closer to the first estimation done by Markina while it obviously does not account for the production of the microphytoplankton.

However, even if the above is true, the biomass distribution across the higher trophic levels is quite similar, as can be seen in Figures 1 and 2, indicating that the NE model does resemble the original SD model (1997).

It can also be seen in Figure 2 that the biomass of the first trophic level is actually smaller than the biomass of the second trophic level in both models. This seems counter-intuitive, as the biomass of the consumers is usually lower than the biomass of the producers. One of the potential explanations for this irregularity could be the very high turnover rate of phytoplankton in the Okhotsk Sea. This is indicated by an extremely high phytoplankton P/B ratio of 165.3 (Shuntov 1985). Additionally, both models indicate that a high proportion of flow originates from detritus, supporting the view that detritus plays a very important role in the Okhotsk Sea ecosystem (Sorokin et al. 1997). It is possible that the role of primary producers of the first trophic level in the Okhotsk Sea is less important than in the other ecosystems and some of the second trophic level animals are supported by the flow from detritus.

Figure 3 indicates that the threefold increase in fishing efforts caused a decrease in the biomass of the pinnipeds and baleen whales. This decrease could be explained by both the increase in direct mortality due to fishing, as well as the decrease of the prey due to increased fishing pressure.

This Ecopath simulation is an example of the many potential applications of this model of the Okhotsk Sea. This trophic mass-balance model takes into account the interactions between different components of the prey-predator food web and it could be useful in evaluating the extent of changes happening to the entire ecosystem.

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A PRELIMINARY REVIEW OF THE RECEPTION OF 'FISHING DOWN MARINE FOOD WEBS'*

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Abstract

Few studies have generated as much debate in academic circles and attracted as much public interest to degradation of marine ecosystems as the 1998 article “*Fishing down marine food webs*” by Daniel Pauly and colleagues in the journal *Science*. The present contribution characterizes the current state of this debate based on a review of studies published in 2016-2018 that cited this article, with emphasis on identifying those that supported and those which contradicted the *fishing down* concept. The survey yielded 323 articles authored by more than 1,500 researchers who supported this concept, while 235 authors challenged it. The articles examined covered almost all of the world's Large Marine Ecosystems and FAO Statistical Areas, and showed a considerable degree of international collaboration between research groups. The '*fishing down*' concept was primarily referenced in studies of marine ecosystems, notably coral reefs, but was also discussed in articles dealing with freshwater environments. About two thirds of the studies focused on community analyses, while almost a quarter focused on particular taxonomic groups, especially species of commercial interest. A majority of articles addressed various ecological aspects of marine and freshwater environments, followed closely by articles concerned with fisheries, both small-scale and industrial. Overall, the validity of the fishing down phenomenon was supported by 103 studies, while being contested by 26 articles.

Introduction

The exploitation of freshwater and marine ecosystems is an essential part of human civilization, with fisheries being recorded throughout history (Hu et al. 2009). Fisheries are still an important economic activity in many countries, as well as a crucial source of employment and income for hundreds of millions of people (Dyck and Sumaila 2010; FAO 2018; Teh and Sumaila 2011). Indeed, fisheries are essential for the subsistence of isolated and marginalized populations (Béné et al. 2010), because they provide an important, and in many cases, cheap source of animal protein (Kent 1997). Over time, the number of studies portraying a worrying picture of environmental degradation caused by a multitude of human interventions has escalated exponentially (Botsford 1997; Smith et al. 2006; Pandolfi et al. 2011; Costello et al. 2012; Pikitch 2012; Eriksen et al. 2014; Zeng et al. 2015). These studies look at the negative effects that are being felt in most ecosystems and that are occurring at pace that demands a clear effort from the scientific community, governments and the public.

The publication by Pauly et al. (1998s) titled '*Fishing down marine food webs*' is, with over 5,000 citations in Google Scholar (as of December 2019), one of the most cited papers in fisheries research (Stergiou and Christensen 2011; Branch and Linnell 2016). Its findings have been variously contested (Caddy et al. 1998; Branch et al. 2010; Banobi et al. 2011), and responses have been provided by the original authors, notably by its first author (www.fishingdown.org). Meanwhile, the number of publications reporting cases of 'fishing down' has grown over the years, including regions previously insufficiently studied (Pauly et al. 1998b; Pauly 2010; Liang and Pauly 2017; Liang and Pauly 2019; see also www.fishingdown.org).

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Few studies have generated as much debate in academic circles and generated as much public interest as '*fishing down*' (FD). Indeed, this article was able to attract the attention of scientists, policymakers and mass media to the point that it still is debated in the literature, many years after its publication.

The understanding of marine ecosystems has grown over the last decades (Claudet and Pelletier 2004; Liqueste et al. 2013; Guo and Wang 2019), a result of efforts to understand how biological and environmental elements interact with each other. The concept of Large Marine Ecosystems (Fanning et al. 2007; Sherman et al. 2009) and the growing use of Ecopath models to represent complex food webs and how fisheries and other human activities affect them (Pauly et al. 2000; Coll et al. 2009) have helped to elucidate the functioning of many small and larger ecosystems. However, these studies, along with field reviews, also showed that many gaps in knowledge still persist, even in ecosystems with multiple species of commercial interest (Essington 2007; Bevilacqua et al. 2016; Santos and Vianna 2018). While the scientific community has struggled to fill in these gaps, these efforts remain unequal, particularly in marine ecosystems bordering developing countries, since a long time series of reliable scientific data is required to address them properly.

The role of governments is crucial here, not only to support the acquisition of scientific knowledge on local and regional ecosystems by supporting the scientific community, but also to maintain essential long-term monitoring programs of environmental quality and fisheries, as well as recording landings from both small-scale and industrial fleets (Jacquet and Pauly 2008; Alfaro-Shigueto et al. 2010), while also being responsible for the pertinent legislation, and the management of natural resources. The running cost of these activities have also been highly unequal; even in developed countries, research efforts tend to be concentrated on the more profitable stocks, while many species with low or no commercial appeal are poorly studied (Johannes 1998; Jacquet and Pauly 2008). This becomes more perverse when considering tropical fisheries, due to the high diversity of species and the relatively low biomass of each, not to mention the overall scarcity of funds for research.

Finally, public awareness is required to guarantee that enough pressure can be exerted to push governments toward long-term solutions to environmental problems, as well as to generate interest for new researchers to join the scientific community and help with the development of more effective management of natural resources.

An interesting episode that demonstrates the impact of the *fishing down* concept occurred in the context of a study of the United Kingdom's fisheries. Following the initial publications of FD and of various studies, dealing with more local or regional cases (e.g., Pauly and Maclean 2003), a Royal Commission on Environmental Pollution (2004) was presented to the British Parliament which addressed the issue of fisheries as a source of environmental impact on the marine ecosystems, requiring legislators to participate and demand for the government to answer the challenges of sustainable and economically viable fisheries. While the proposals of the scientific community reached government policymakers, the media coverage was largely biased towards conservation, without considering promoting the equally necessary debate on the economic and social costs of a greater restriction of fisheries (Symes 2005). While the controversy may be perceived as favoring the fishing industry, the argument is valid since the restrictions imposed by legislators may have repercussions for employment, fish supply to markets and taxes to local authorities. On the other hand, ignoring the warnings from the scientific community may lead to the depletion of fish stocks and end up causing the same negative effects, through increasing costs of fisheries due to the fleet have to perform longer trips and diminished returns due to changes in the available stocks and the exploitation of species of lower value (Pauly 2009).

These and related considerations are all parts – often implicit – of the debates about FD and influenced how they unfolded over the years, and which part of the evidence, in different ecosystems, was considered. Does FD, initially based on the largely industrial fisheries statistics published by the Food and Agriculture Organization of

the United Nations (FAO), occur in artisanal fisheries in estuaries, whose diversity and concentration of juveniles are well-known? Does it occur in coral reefs fisheries? Does it occur in fisheries in coastal areas, or fisheries that exploit deep sea communities?

This study aims to answer these and related questions about FD. We examine the discussions that followed its publication, identify studies that support or contradict the notion of FD and characterize the current stage of the debate, 20 years after the publication that triggered it. Thus, this contribution updates and deepens previous citation analyses of this seminal paper, notably that in Stergiou and Christensen (2011).

Methods

The review was based on the articles that cited Pauly et al. (1998a). The survey was carried out based on Thomson Reuters' (ISI) Web of Science, which covers articles published by more than 10,000 indexed journals from 1945 to the present (Chadegani et al. 2013). This allowed retrieving all articles that cited Pauly et al. (1998a) from 1998 to the end of 2018. The search on the scientific platform was finalized in June 26th 2019. To be included, an article had to focus on fish and/or invertebrates and fisheries. Other taxonomic groups were excluded, as were land-based studies, and biological studies unrelated to fisheries (e.g., parasitism, taxonomic descriptions). Results were obtained from the *Web of Science Core Collection*, using the Cited Reference Search, which allowed recovering all literature that cited Pauly et al. (1998a), except for self-citations.

The results were then organized in a database which included the articles, or abstract in the few cases where the main text was not available. The studies were tagged as to their senior authors and co-authors, year of publication, journal, other publication details (incl. the impact factors of the journals, if any) and title. The institution of origin of each article was also recorded, as well as the country where the first author was based, along with the countries of the co-authors (which defined international partnerships or collaborations). The type of ecosystem covered were also identified, i.e., continental (freshwater), estuarine, marine and coral reefs, with combinations between classifications if the article treated more than one ecosystem type; the study areas were assigned to Large Marine Ecosystems (LME) and FAO statistical areas.

The entity that was the focus of a study was also recorded at the appropriate taxonomic level (species, genus, family), functional groups (large pelagics, small pelagics, demersal, etc.), or concerned with fish communities and/or exploited species.

The papers were analyzed by theme (ecology, biology, fishery, and pollution) and subtheme (fishery governance, fishery impact, diet, review, fishery production, functional group, etc.) to identify how FD is being researched and debated across scientific communities. The source of data (primary, secondary, modeled/simulated) was also recorded.

Finally, the opinion or conclusion of the authors for their studies and their position relative to the FD concepts was evaluated, and recorded as 'in favor', 'against' or 'neutral', with or without remarks.

In this contribution, the results presented are focused on the years 2016-2018 (Figure 1). This time period shows a slight even decline in the number of publications citing Pauly et al. (1998a), which suggest that most of the critique of FD and counterarguments have been presented and discussed by the scientific community. This offers an opportunity to observe how well the FD has fared after 20 years of scrutiny by local and regional research teams across a wide variety of marine and freshwater ecosystems.

Results

A total of 2,227 articles published from 1998 to 2018 were obtained from the Web of Science platform (Figure 1). The survey resulted in 385 articles published between 2016 and 2018, from which 15 were removed due to the participation of at least one of the authors of Pauly et al. (1998s), to remove all self-citations. Another 47 articles were removed for not being relevant for the debate, i.e., from fields of study unrelated to fisheries or marine biology. This triage process resulted in 323 valid studies left for analysis.

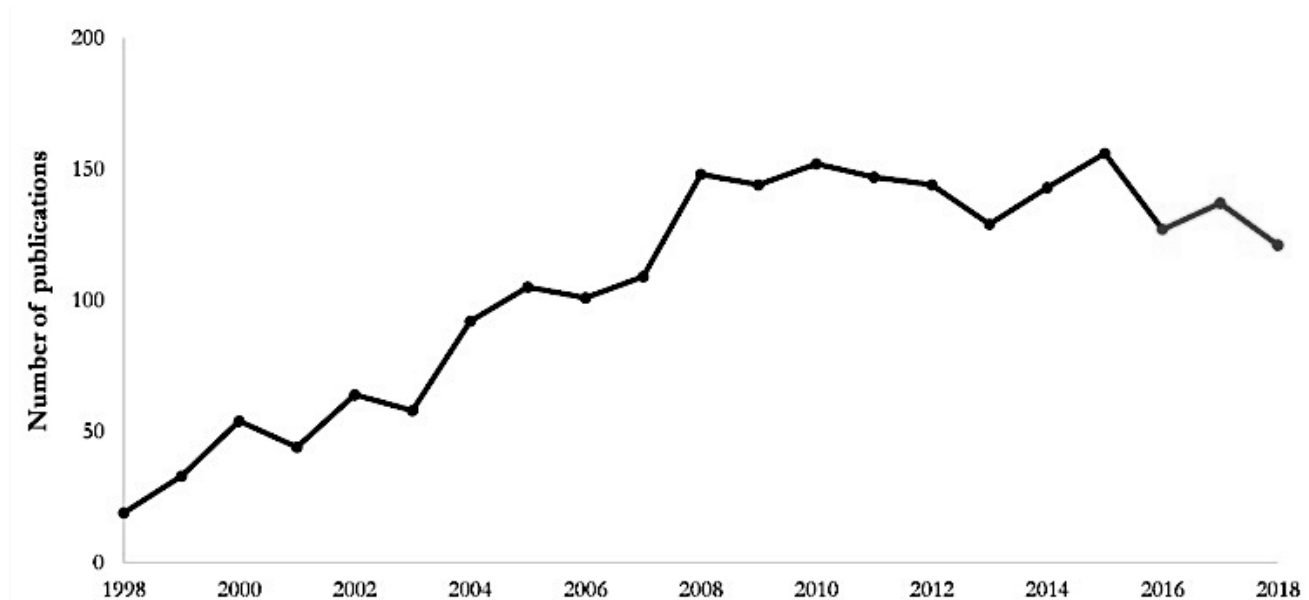


Figure 1. Number of articles considered herein that cited Pauly et al. (1998a). The articles published from 2016 to 2018 are the focus of this contribution.

Although this preliminary review covers only over a short and recent period (2016–2018), Table 1 still documents a total of 1,578 researchers publishing at least one article in this period, with eight authors participating in four studies. Noteworthy are researchers Marta Coll (8 studies), Chen Yong (7), and Elizabeth A. Fulton (5).

The articles produced were published in 146 journals (Table 2), with the most frequent being the *ICES Journal of Marine Science* (13), *PloS ONE* (12), *Ecological Indicators* (11), *Marine Policy* and *Ecological Modelling*, both with 10 studies, and *Scientific Reports* with 9. Based on the institution where the first author is affiliated, as mentioned at the time of publication, a total of 221 institutions were identified. The most prominent was James Cook University (Australia), where researchers participated in 10 studies, followed by the University of Guelph (Canada), with 5 articles, and 8 institutions from Canada, China, South Africa, Sweden, and the United States, with four studies each (Table 3).

Scientific institutions in the United States were responsible for the largest part of the published articles retrieved for this survey, with 77 studies of which 36% included co-authors from other institutions. Moreover, the United States, which published most of the studies on FD (Table 4), also showed up as the most recurrent partnership in articles published by other countries (Table 5 and 6). Australia, Canada, Brazil, China, and Spain were also major sources of studies that cited the original FD publication (with 33, 21, 19, 18 and 18 articles, respectively). The 10 leading countries when it comes to the number of studies, representing 71% of all three years surveyed, showed a mean of 54% in articles with international partnerships, but relevant among these are the United Kingdom, France, and Spain, whose studies had foreign co-authors in more than 80% of the

cases (88%, 86% and 83%, respectively). Overall, 50% of the publications were produced through international partnerships (i.e., 151 articles; Table 5).

Table 1. Participation of researchers on 323 articles that cited Pauly et al. 1998a), 2016 to 2018 (n=1,757).

Number of studies	Authorship
1	1444
2	111
3	13
4	Blanchard, JL; Bundy, A; Chen, XJ; Heymans, JJ; Lek, S; Ortiz, M; Ren, YP; Ding, Q
5	Fulton, EA
7	Chen, Y
8	Coll, M

Table 2. Journals in which 323 articles appeared that cited Pauly et al. (1998a), from 2016 to 2018 (n=146).

Number of articles	Journals
1	86
2	21
3	17
4	10
5	<i>Journal of Fish Biology;</i> <i>Fish and Fisheries; Acta Oceanologica Sinica</i>
8	<i>Ocean & Coastal Management; Frontiers in Marine Science; Fisheries Research</i>
9	<i>Scientific Reports</i>
10	<i>Marine Policy; Ecological Modelling</i>
11	<i>Ecological Indicators</i>
12	<i>PloS One</i>
13	<i>ICES Journal of Marine Science</i>

Table 3. Home institutions associated of the first author of 323 articles that cited Pauly et al. (1998a) from 2016 to 2018 (n=221).

Number of articles	Number of institutions
1	160
2	37
3	14
4	Ocean University of China; Shanghai Ocean University; Swedish University of Agricultural Sciences; University of British Columbia; University of California at San Diego; University of Cape Town; University of Florida; University of Queensland
5	University of Guelph
10	James Cook University

Table 4. Countries in which the first authors of 323 articles published from 2016 to 2018 that cited Pauly et al. (1998a), by number of articles. The numbers in brackets refer to the % of articles involving international cooperation (see also Table 5 and 6).

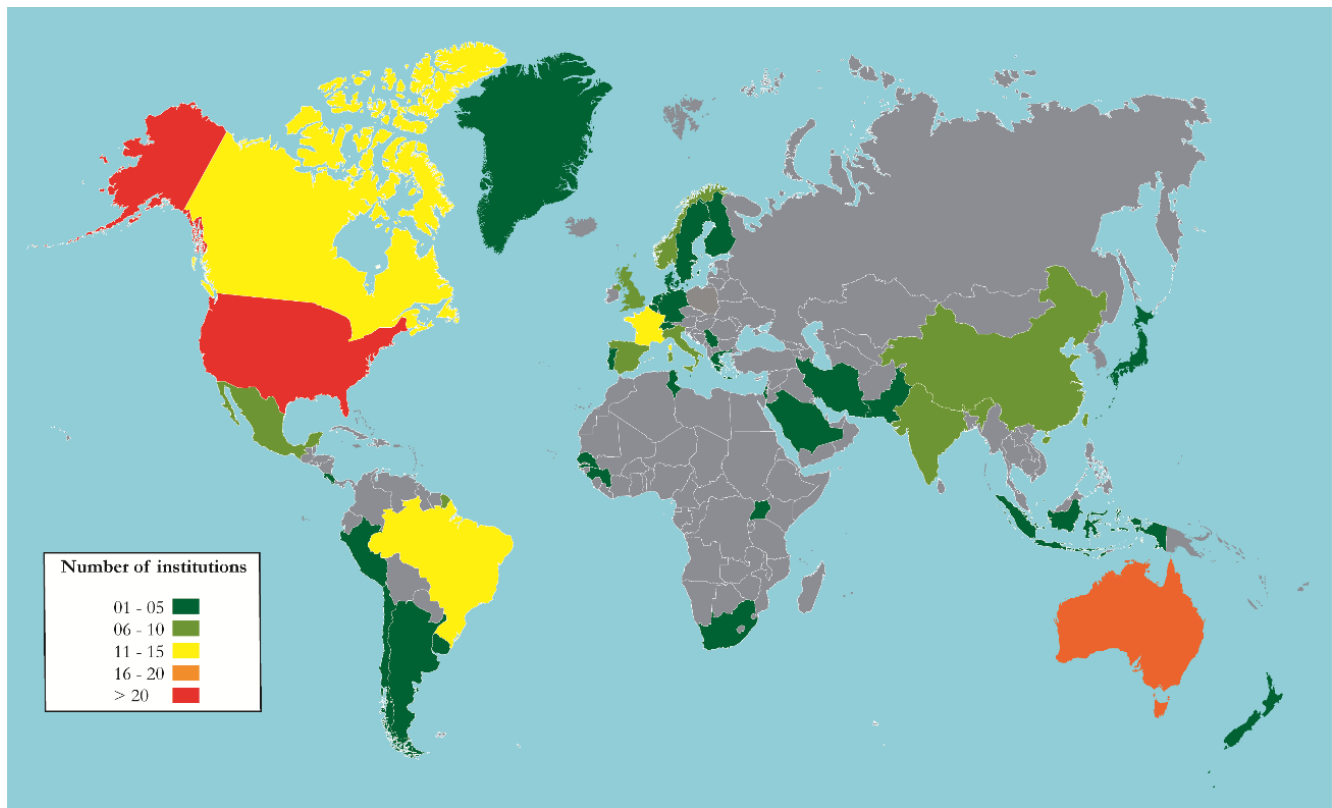
Main country	Number of studies	Main country	Number of studies
USA	77 (36)	Sweden	4 (75)
Australia	33 (46)	Netherlands	3 (33)
Canada	21 (29)	Indonesia	2 (0)
Brazil	19 (37)	Malta	2 (50)
China	18 (67)	New Zealand	2 (50)
Spain	18 (83)	Switzerland	2 (50)
France	14 (86)	Tunisia	2 (100)
Mexico	13 (54)	Uganda	2 (50)
United Kingdom	8 (88)	Uruguay	2 (50)
India	8 (12)	Saudi Arabia	1 (0)
Chile	7 (43)	Belgium	1 (0)
Italy	7 (0)	Cambodia	1 (100)
Norway	7 (86)	Costa Rica	1 (0)
Germany	6 (50)	Denmark	1 (0)
Portugal	6 (50)	Guinea	1 (100)
South Africa	4 (100)	Panama	1 (100)
Argentina	4 (50)	Pakistan	1 (0)
Finland	4 (25)	Peru	1 (0)
Greece	4 (0)	Kenya	1 (100)
Iran	4 (25)	Senegal	1 (100)
Israel	4 (25)	Serbia	1 (0)
Japan	4 (25)	Total	323

Table 5. Studies (2016 to 2018) citing Pauly et al. (1998a) with or without a partnership

Number of articles	Partnership (countries)	% of total
3	8	0.9
2	7	0.6
7	6	2.2
1	5	0.3
4	4	1.2
13	3	4.0
32	2	9.9
89	1	27.6
172	0	53.3
323	36	--

Table 6. International cooperation inherent in papers citing Pauly et al. (1998s), as reflected in the countries of their authors' institutions

Partner	Number of studies	Partner	Number of studies
USA	38	Mexico	7
United Kingdom	25	Cambodia	6
Canada	24	Netherlands	6
Australia	18	Chile	5
France	17	South Africa	5
Spain	17	Brazil	4
Denmark	10	Finland	4
Germany	9	Philippines	4
Italy	8	Portugal	4
Norway	8		

**Figure 2.** Home countries of the institutions from which the publications originated that cited Pauly et al. (1998a) from 2016 to 2018 (n=221).

The predominance of the United States was also observed in the total number of institutions whose researchers were the first authors of publication that cited Pauly et al. (1998a). Australia was the second major contributor (Figure 2), with researchers from 16 institutions participating in the debate. The three years' time window also revealed active research groups in Brazil, France, and Canada (14, 13, and 12 institutions, respectively).

Since their introduction in 1986, Large Marine Ecosystems (LME) have often been used to provide a context for an ecosystemic approach to the management of coastal and marine ecosystems and the sustainable development

of marine resources (Sherman and Hempel 2008; Pranovi et al. 2019). LME studies that mentioned or focused on FD have shown that a considerable research effort related to the Mediterranean Sea (28 articles published from 2016-2028), followed the Gulf of Mexico (15), Caribbean Sea (13), East and South Brazil Shelves (12 and 11, respectively), and North Sea (11) LMEs (Figure 3), with American and European LMEs receiving more emphasis than those of other regions.

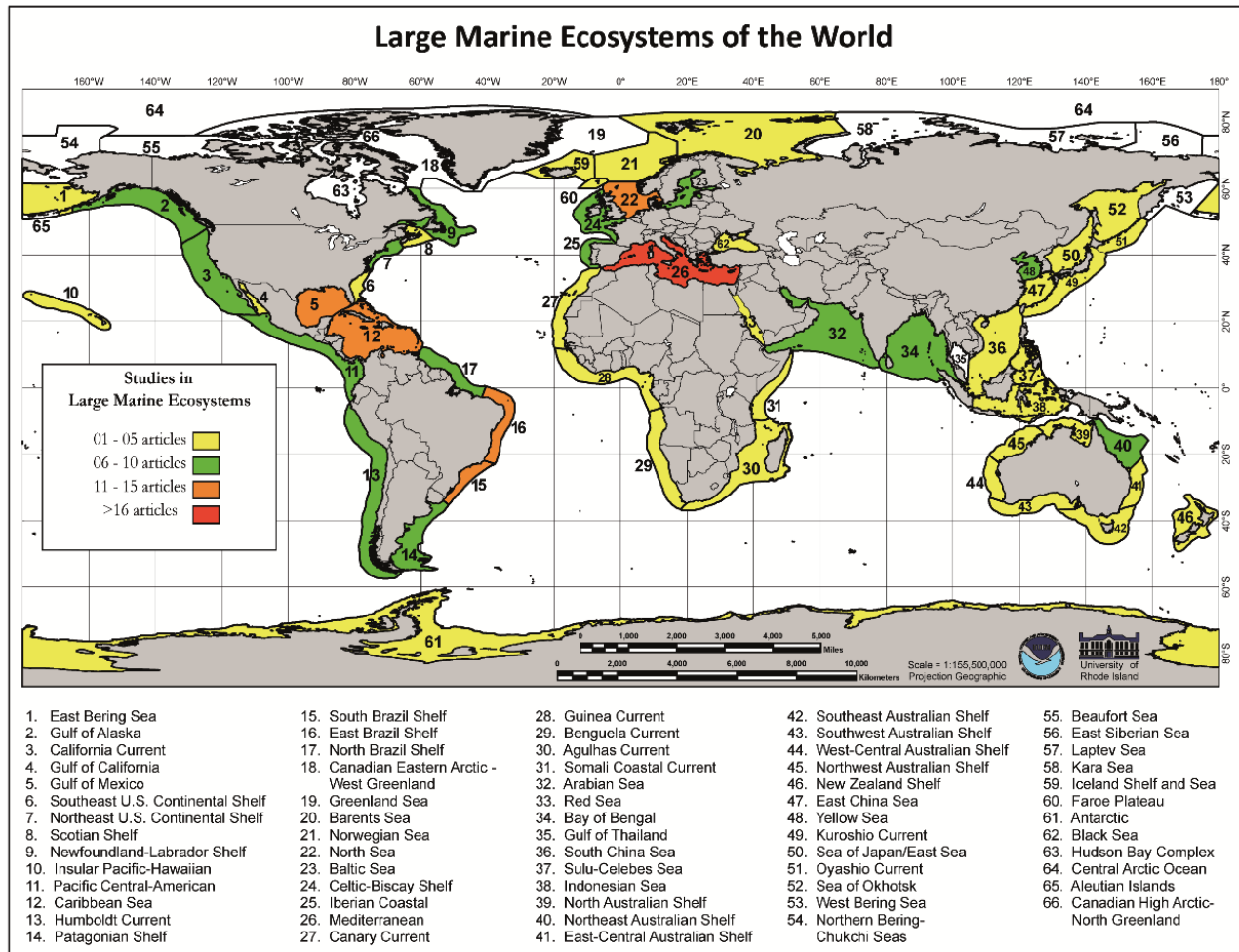


Figure 3. Large Marine Ecosystems studied in publications (2016-2018; n= 200) that cited Pauly et al. 1998a).

The coarser geography used by the Food and Agriculture Organization (FAO) to present the official fisheries statistics of its member states is also relevant here. Thus, Figure 4 shows that FD observed for the Western Central Pacific (32 studies in 2016-2018), including several island countries, and Eastern Central Pacific (23); FD was also studied in the Atlantic, with special emphasis to the Mediterranean Sea (29), Western Central Atlantic (25), Southwestern Atlantic (23), and Northeast Atlantic (22).

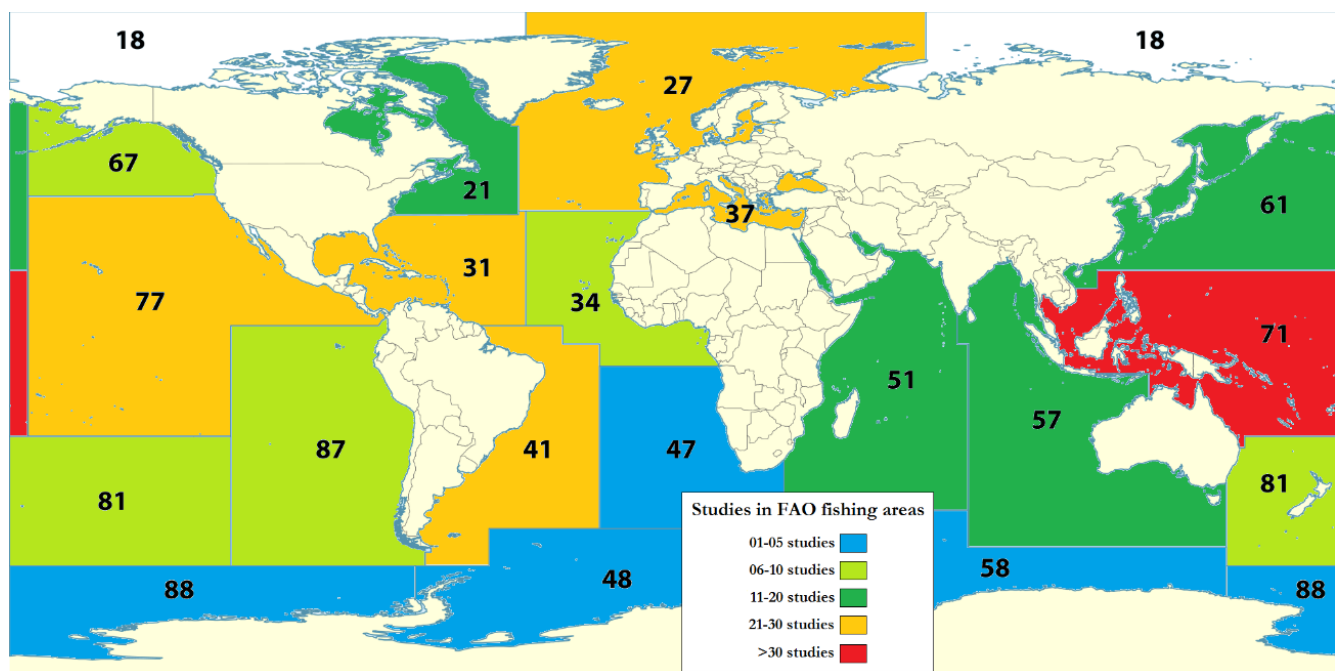


Figure 4. Heat maps of the number of publications (2016–2018) that cited Pauly et al. (1998a) by FAO Statistical Areas (n = 248).

FD was cited mainly in studies on marine ecosystems (67%), while also being mentioned in articles dealing with coral reefs, both in the Indo-Pacific and Atlantic Oceans. This applied to Asia (46% of 51 sampling sites), North America (21%), South America (19%), Africa (12%), and Australia (2%) (Figure 5A). The studies were predominantly aimed at studying broader aspects ecosystems, with 68% focusing on the animal communities of the ecosystem under study. Mostly, these studies touched on both the trophic and taxonomic structures of these communities, while nearly quarter of all studies focused on particular taxonomic groups, in particular those of commercial interest, such as tunas or sardines (Figure 5B).

A majority of studies addressed various ecological themes regarding marine and freshwater ecosystems, followed closely by articles concerned with fisheries, both small-scale and industrial (Figure 5C). A great diversity of topics was studied within these broad themes, with emphasis on understanding the complex nature of the trophic web in different ecosystems (35% of 323 studies). Also, these studies' literature documented serious attempts to identify the human impacts causing changes in marine environments (18%), and the many facets of fisheries (16%) (Figure 5D).

Finally, the *fishing down* concept was clearly supported by 103 articles, and clearly contested by 26 articles (Figure 6).

Discussion

This review covered only three out of 20 years of an ongoing debate on how much and how far fisheries activities affected the marine and freshwater in the manner described by Pauly et al. (1998a), i.e., by “*fishing down marine food webs*”. This concept explains the common decline in fisheries landings (e.g., Liang and Pauly 2017) and in the ecosystems (e.g., Liang and Pauly 2019) of large, high-trophic level species (HTL) and their gradual replacement by smaller, low-trophic level species (LTL) in waters exploited by modern industrial fisheries, as initially evidenced by the global landing statistic assembled by FAO (Pauly et al. 1998a) and subsequently confirmed in great detail by a large numbers of local, regional and global studies (see www.fishingdown.org).

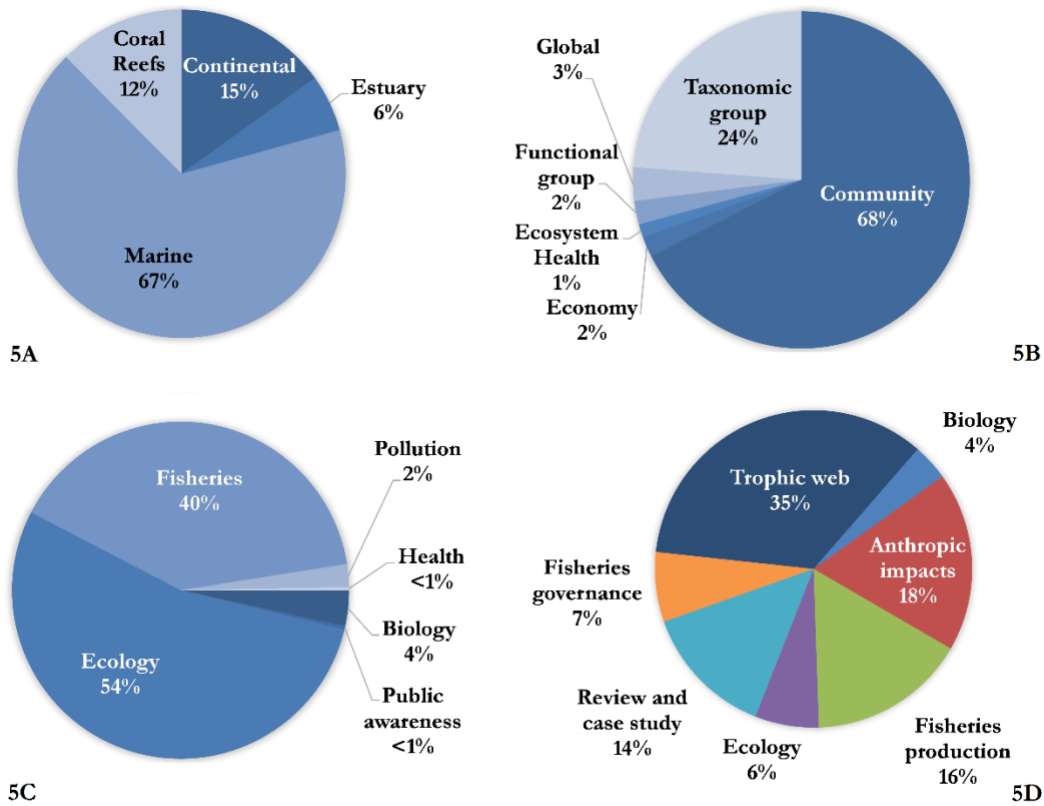


Figure 5. Ecosystems and topics examined in 323 publications, that cited the concept of “*Fishing down marine food webs*” (Pauly et al. 1998a), published from 2016 to 2018. **5A.** Environments; **5B.** Objects of study; **5C.** Themes; **5D.** Subthemes.

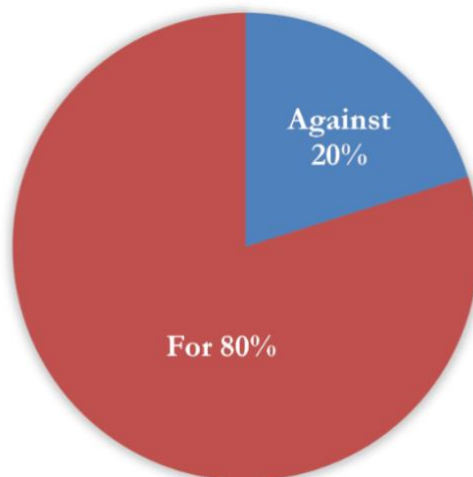


Figure 6. Acceptance vs. rejection of the “*fishing down*” concept of Pauly et al. (1998a), based on 129 articles published from 2016 to 2018 which took an explicit stand.

This present contribution identified over 1,500 scientists who published articles supporting the FD concept in 2016-2018, while 235 scientists debated its legitimacy based on their interpretation of local and regional fisheries. The debate took place mostly in prestigious publications, with high impact factors, something that reinforces the importance of the concept for the scientific community. While the participation of institutions from developed countries dominated the debate, the presence of developing countries was not ignored and numerous studies from data-limited regions of the world, including China, were available. Nonetheless, much effort is still needed to improve the knowledge of the marine ecosystems and its trends in trophic level occurring

in them from countries in South America, Africa, Southeast Asia, and the former Soviet Union. Also relevant to the debate, despite almost half of the studies showing some level of interactions between international scientific groups, is the fact that more international cooperation is required. This applies especially to new indicators of FD, capable of dealing with a wide variety of ecosystems, and the need to integrate data for fishing grounds and/or stocks and fisheries shared by different countries.

The FD concept was initially based on the analysis of time series of landing data; however, fisheries should not be viewed as the only source of data in the response of marine ecosystems to stressors. Thus, based on meticulous mesocosm experiments, Ullah et al. (2018) described how a synergic relation of global warming and ocean acidification may reduce the energy flow from producers to herbivores and higher trophic levels, mainly because of a collapse of biomass of major functional groups. Thus, while primary production increased due to a greater biomass of cyanobacteria, this surplus was converted to detritus, i.e., there was a shift towards a predominantly detritus-based ecosystem. Such “*energetic collapse*” scenario has the potential to affect the entire food web and lead to a collapse of higher trophic level groups (Ullah et al. 2018), including those already stressed by fishing pressure. Further, Ullah et al. (2018) demonstrated through their mesocosm experiments that the effects of global warming and acidification were distinct, with warming causing a reduction in energy flow, while acidification cause an increase in the biomass of cyanobacteria and detritus consumers.

Thus, the continuation of the current global warming and ocean acidification trends should have effects similar to FD, which is empirically verified (see, e.g., Cheung et al. 2013). While the idea anticipated the debate of the growing pressure of human activities in marine ecosystems, the literature has diversified to examine a plethora of new sources of impact and future scenarios now require much greater attention to the *precautionary principle* since all these combined impacts reduce the wiggle room for the sustainable management of fisheries.

A cautionary tale is described by Payne et al. (2016), who describe a worrying future should the levels of exploitation of natural resources and the impacts of human activities upon marine ecosystems continue to be high, or even increase. When these authors compared ecological traits and extinction events observed in marine vertebrate and mollusc genera, a consistent pattern was clear: large body sizes were a major trait associated with the extinction threat in modern oceans. This observation alone is critical when fisheries are considered, since the largest species and the largest individuals of commercial species are often more valued by the industry and consumers, and therefore targeted by fishers (Liang and Pauly 2019), with the reduction in size being a known pattern associated with overfishing (Haedrich and Barnes 1997; Jennings et al. 1998). This pattern was evaluated in an *Atlantis* model, which allows combining biophysical and fisheries data, based on five commercial fishes from the Southeast Australian coast, and Audzijonyte et al. (2013) reported a range of responses to fisheries and climate change, with the size of some species being strongly affected, while differences in other were negligible. The authors indicated that, while a size reduction was not seen in all evaluated species, the complexity of the trophic web must be taken into account to have a more precise picture of which populations would be affected most.

Zhang et al. (2016) agreed with the FD concept, but also highlighted the need for a re-evaluation of common tools of management, such as maximum sustainable yield (MSY). While the principle is to preserve the necessary biomass to allow the population to recover from the fishing pressure and still be available for fisheries in the following years, Zhang et al. (2016) warned about the problem of using single-species MSY in a multi-species context. Notably, they pointed out that the impact of different fishing gears may damage the fish populations in more ways than can be expressed by a single-species analysis. Added to this, natural fluctuations of other components of the trophic web may increase or decrease the biomass of a given population, due to greater predation, food restriction in the case of removal of prey populations. These challenges will require an

adaptation of current criteria and/or the development of new indicators (Bourdaud et al. 2016; Zhang et al. 2016).

In a thorough analysis of ecological indicators such as the Marine Trophic Index or MTI; Fishing in Balance Index or FiB; and the Expansion Factor or EF, presented in Bhathal and Pauly 2008) for the Mediterranean Sea, and covering 60 years' worth of catch data, Pennino et al. (2017) showed mostly convergent and complementary trends between all three indexes, describing an increase in the prevalence of capture of LTL over HTL species. Nonetheless, in recent years a divergent trend was seen in two groups of countries, with one continuing the previous trends, the second showing an increase in the landings of HTL species, which the authors attributed to an expansion of fishing areas due to modernization of small and large-scale fishing fleets, making available HTL stocks in unexplored areas (Pennino et al. 2017), an argument aligned with that of Kleisner et al. (2014) and Liang and Pauly (2017). The article also revealed two points that must be taken in consideration: 1, reliance on a single indicator will lead to an incomplete picture, especially when analyzing long time series, and 2, joint analyses of available ecological indicators should be attempted to avoid this trap (Pennino et al. 2017). Indicators, in any case, should be tested thoroughly before they can be used for fishery management (Shin et al. 2018).

Another point is that changes in the trophic levels of catches (i.e., in the MTI) in a given area can differ from those in adjacent regions, as is the case for the Black Sea when compared with the Eastern Mediterranean (Pennino et al. 2017; Tsikliras et al. 2015; Keskin and Pauly 2018). On a similar note, Angel et al. (2014) described a case where the excessive fishing pressure applied upon several commercial fish species provoked the collapse of their stocks, as could be expected, but also an increase of the biomass of jellyfishes, which increased their consumption of zooplankton, and thus reducing the prey biomass available to foraging species, which then prevented a recovery of HTL species (Angel et al. 2014).

Critiques of FD still occur, notably as part of a rejection of 'Malthusian scenarios' predicting a collapse of agriculture and fisheries. Thus, Asche and Smith (2018) claim that advances in technology and new management methods and regulations must not be ignored. Moreover, Malthusian scenarios still have not come to pass, and the worst-case scenarios for fisheries may too be too pessimistic, and thus unrealistic. Also, the use of bycatch reduction devices can mitigate the impact of fisheries in non-target species (Grubbs et al. 2018), with positive effect on their biomass and possibly their predators.

On the economic side, Sugiawan et al. (2017) developed an ambitious model based on catch data from 70 fishing countries between 1961 and 2010 which predicted how changes in economic factors affect the exploitation of marine resources. The resulting models showed a beneficial impact of economic growth on global marine fisheries, while increases in population density would lead to greater pressure on fish stocks. The model estimated precise annual income levels that would lead to declines in catch levels (3,827 USD per capita) and stock rebuilding (6,066 USD per capita). However, based on official estimates for 192 nations from the World Bank (2019), 70 countries are below the first value, while 92 are below the second. Thus, half of the countries would be below the economic growth that would lead to a decline in exploitation rates and rebuilding; this obviously doesn't take in consideration that per capita GDP does not necessarily reflect standards of living and ignore poverty-stricken areas within countries of medium and even high GDP. The precision of the model proposed by Sugiawan et al. (2017) is unrealistic, given the long-term problem of world fisheries: the quality of catch data, especially in developing and poor countries, and the accurate biomass estimates for fish population that are required for predictions of this sort.

As this review of the most recent years of the debate started by Pauly et al. (1998a) illustrates, the discussion on the extent of the FD phenomenon is still active. The multiple sources of impact that have been studied along

recent decades support a decline on the biomass of exploited fish populations, especially for HTL species (Pennino et al. 2017; Schmitter-Soto et al. 2018; Shin et al. 2018), in accordance with the findings of 20 years ago by Pauly et al. (1998a). Also, new studies on the impact of pollution and the consequences of bioaccumulation and biomagnification, the synergic relation of factors already stressing ecosystems with global warming, as well as ingestion of microplastics by marine animals reinforce the FD trends (Alava et al. 2017; Setälä et al. 2018).

Overall, studies from different scientific groups across the globe provide overwhelming support for *fishing down* in multiple ecosystems, despite the naysayers. However, many studies describe complex scenarios that may additional indicators to be able to cover a wide range of impacts and their consequences within the trophic web (Pennino et al. 2017; Shin et al. 2018), which will not be perceived if analyses are limited to catch data. After 20 years, “*fishing down marine food webs*” is still relevant and its warning ever more opportune, despite better data being gathered for many ecosystems and a wide variety of indicators being used. It is now up to us to expand Marine Protected Areas and use adequate fisheries management tools to attempt to reverse the trend toward impoverished marine food webs.

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SALMON AS GUIDE TO NOWHERE*

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Abstract

This review of the paper by M. Evans and L. Harris (2018. Salmon as Symbol, Salmon as Guide: what anadromous fish can do for thinking about island ecosystems and the globe. *Shima* 12: 1-14) was originally written following an invitation by the editor of *Shima, the International Journal of Research into Island Cultures*, but my submission was rejected because I could not take that delirious article seriously, although “it has been peer-reviewed”. I had not known that *Shima*, initially a neat niche journal, had been infected by postmodernism and succumbed, as have many journals, in the Humanities.

Introduction

One could think that a basic knowledge of salmon biology, ecosystem functioning, and the history of British Columbia, along with having lived in or visited some of the world’s major islands and archipelagos should be enough to enable me to assess the article of Evans and Harris (2018) titled “Salmon as symbol, salmon as guide: What anadromous fish can do for thinking about island ecosystems and the globe” (SSSG), but it is not so. One also needs to be able to penetrate the thickets of what might be called “French theory” – also known as postmodernism – and the empty pronouncements of authors such as the ubiquitous Bruno Latour, and the more obscure Deleuze, Guattari and Co. (see Sokal and Bricmont 1998).

Predictably, one encounters the word “paradigm” in the first paragraph, perhaps as a marker that what follows is going to be serious stuff. Then, an author is cited who stresses that “the relations between islands occurs at sea”, which reminded me of Donald Trump, who, in the aftermath of hurricane Maria in 2017, informed an amazed world that “Puerto Rico is an island surrounded by water.”

And down we go.

It goes downhill from there – Bruno Latour steps in, with an “actor-network theory” (Latour 2005), which links humans, animals, landscapes, and rocks as equal participants, or “actants” into “assemblages”, i.e., “multiplicities of semiotic, material and social flows with no assumptions of what human-non-human entities might be included” (whatever that means), and which, apparently, some people take seriously.

What follows are seven more pages of random prose of this type and even good old Jean Paul Sartre and his *Critique of Dialectical Reason* is evoked, but we shall not drown in it, and seek refuge on some island of clarity, with rivers where actual salmon may thrive. Unfortunately, the single exhibit in SSSG is a map of the distribution of Chinook salmon populations in the upper Columbia River, far away from any island or archipelago.

So, we must find our way back into the text, i.e., wade through vignettes with salmon-related factoids. One tells us of salmon in Hawai’i, where the fish acquired through a complex trade relationship and consumed, thus

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linking Hawai'i and the Pacific Northwest. And the point is? Then we go to New Zealand, where introduced Atlantic salmon did not thrive, but trout did. So what?

Only when we get to the introduction of Atlantic salmon to the British Columbia do we get into potentially interesting territory. But even here, the factual elements are well known: Atlantic salmon (*Salmo salar*) is, in B.C., an introduced species, with all that it implies for competition with various species of Pacific salmon (*Oncorhynchus* spp.), intensified by a form of intensive culture which is bound to cause environmental problems (Brill and Pauly 2004; Morton and Williams 2003; Morton *et al.* 2017).

Conclusions?

Thus, it is only after 10 pages of largely meaningless wordage that do we finally get to what may be the point of the paper: that before contact and colonization, the First Nations of the Columbia River Basin were successfully managing the Pacific salmon that they had access to, in contrast to the present. This is certainly a valid point, but why the verbiage that preceded this claim? (This claim, incidentally is not substantiated, although it could have been straightforwardly done).

What is the lesson in all this? One could be that this author, a fisheries scientist, is too dense to understand the fine points of a paper applying contemporary concepts of sociology and anthropology to a set of issues that go way above his head. Or, and this would be really sad, SSSG is another case of trivialities being jargonified until they appear to be conveying deep insights.

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MARINE BIODIVERSITY ASSESSMENTS

PALAU MARINE BIODIVERSITY IN FISHBASE AND SEALIFEBASE*

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Abstract

The marine biodiversity of Palau was documented using two global databases FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). Much of the island's biodiversity are reef-associated and found in the neritic zone. Mapping the distribution of pelagic organisms found in Palau showed that the waters surrounding the main island Babeldaob and some of the smaller islands further south of it, Fana and Sonsorol, have the highest biodiversity of pelagic fishes, a finding that supports the setting up of marine reserves around the main islands.

Introduction

The Republic of Palau is composed of 12 inhabited islands and 700+ islets, a cluster of islands in the westernmost part of Oceania and part of the Caroline Island group. The main island group, including Babeldaob, Koror, Peleiu, Angaur, Kayangel, Ngeruangel, and the Rock Islands, with the six isolated islands (Helen Reef, Tobi, Merir, Pulo Anna, Sonsorol, and Fana) that lie 339 to 599 km to the southwest Babeldaob, comprise the 604,253 km² EEZ that envelops Palauan waters. Although Babeldaob, the second largest island in Micronesia after Guam, is the biggest island in the Palauan chain, the country's capital and largest population is located on Koror (Golbuu et al. 2005).

The Palau archipelago has the most diverse coral fauna in Micronesia, with a high density of tropical marine habitats comparable to other geographic areas around the world. In addition to coral reefs, mangroves, and seagrass beds, Palau has more than 70 marine lakes, several algal beds, mud basins, current-swept lagoon bottoms, rich tidal channels, and anoxic basins within the rock islands, many of which contain hard corals and associated fauna and flora. This high concentration of marine lakes makes Palau a unique biological treasure (Golbuu et al. 2005; Marino et al. 2008). Its coral diversity is said to be comparable to that of the Philippines, Indonesia, and Australia (Golbuu et al. 2005). Previous estimates of its coral diversity ranges from 385 species belonging to 66 genera (Randall 1995) to 425 species belonging to 78 genera (Maragos et al. 1994), to even as high as 625 species (Golbuu et al. 2005). However, the most recent estimate by NOAA (2015) pegs the total species of corals at around 400, with none being endemic to the island. The archipelago also boasts of a diverse assemblage of fish and other invertebrates (Bauman et al. 2004; Golbuu, et al. 2005). Estimates suggest that reef fish in Palau may be well over 1,500 species (Myers 1999; Winterbottom 2004; Bauman et al. 2004) and other than scleractinian corals, an estimated 200 species of cnidarians are also found in its waters (Bauman et al. 2004). Marine sponges are estimated to be more than 300 species, although the total fauna may be as high as 500 if small and burrowing species are included (Kelly-Borges and Valentine 1995; Bauman et al. 2004; Golbuu et al. 2005). Estimates of other invertebrate groups are not so comprehensive, but suggest that there are about 2,000 species of invertebrates found in the area. However, endemism is low among Palauan marine organisms

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but difficult to estimate because many groups are not well documented (Bauman et al. 2004; Golbuu, et al. 2005).

This study investigates species diversity in the waters of Palau by establishing some major features of the archipelago's marine biodiversity (expressed as a map of habitat preferences) using ecological data from the global information systems FishBase (www.fishbase.org) for fishes and SeaLifeBase (www.sealifebase.org) for other marine vertebrates and invertebrates. In addition, the exploitation of marine species is discussed based on catch data from the *Sea Around Us* (www.seaaroundus.org).

Materials and Methods

Information on the distribution (geographically referenced occurrence of marine species) and ecology (habitats and depth ranges) of species occurring in Palau were obtained from scientific literature and online checklists and resources. These were encoded in two global species information systems, FishBase and SeaLifeBase and the resulting number of species by taxon was compared with estimates from Bauman et al. (2004) and Golbuu et al. (2005).

Distribution data from FishBase and SeaLifeBase were used with AquaMaps (www.aquamaps.org) to obtain probabilities of occurrence by grids of half degree cells for each of the pelagic species identified in Table 1. Here, we assume that cells filled with probabilities represent 'preferred' (or 'suitable') habitats according to the logic presented in Reygondeau et al. (2014). Then, following Reygondeau et al. (2013), these probabilities were assumed to be analogous to the proportional abundances as used in the estimation of Simpson's index of heterogeneity ($SI=1/\sum p_i^2$), i.e., the weighted mean of the proportional abundances of species occurring in a given cell (see Peet 1974). We refer to this as the Habitat Preference Index (HPI), estimated for each half degree cell, and mapped to show the evenness of the composition of pelagic species 'preferring' a given half-degree latitude and longitude cell within the Palau EEZ. HPI values approaching 1 represent cells with a high number of species 'preferring' those habitats, while HPI values approaching 0 represent cells with a low number of species preferring those habitats.

The time series trends of habitat preferences of exploited pelagic and demersal marine fish species were obtained using a slightly different approach. Preference of species for habitats, as defined in Palomares et al. (2015; Filter 5: Habitat preference)¹, were obtained using species ecology data in FishBase and SeaLifeBase. Species habitat indices ($HI_{spp} = \text{number of habitat where species is present} / \text{total number of habitats defined}$) were weighted by the volume of the catch (metric tonnes) obtained from the reconstructed marine fisheries catch data presented in Lingard et al. (2011)¹. The average annual $HI_{catch} = (HI_{spp} * Catch_{spp}) / \text{Total Annual Catch}$ was then plotted over the 1950–2010 period of reconstructed marine fisheries catches. This metric tests the change in species composition of the catch by following the behavior of the habitat index of the species in the catch. Presumably, spatial expansion (to offshore pelagic resources) and/or diversification to more reachable, and thus available, demersal resources, will be reflected in the habitat index of species in the catch. Thus, expansion of a fishery to exploit large pelagic species offshore is indicated by a decrease in HI values (towards zero) and the opposite (towards one) reflects diversification of target species, presumably demersal or reef-associated species which occur in a wide variety of habitats.

¹ http://www.seaaroundus.org/catch-reconstruction-and-allocation-methods/#_Toc421534362

¹ See the Sea Around Us data for Palau here: <http://www.seaaroundus.org/data/#/eez/585?chart=catch-chart&dimension=taxon&measure=tonnage&limit=10>

Results and Discussion

Data from around 220 references for fishes² and over 620 references for marine vertebrates and invertebrates³ were used to gather distribution, biological, and ecological data for over 3,400 species, i.e., 43% finfishes, 19% mollusks, 14% cnidarians (mostly corals), 8% crustaceans (mostly decapods), 2% chordates, and the rest being other groups dominated by echinoderms and algae, the bulk of which are found in neritic waters, or at depths of 0-100 m (Table 3; Figures 1A-1B). Of these, 21 species were identified as endemics and more than 1,000 species are classified as endangered (457 fishes, 32 sharks/rays, 23 marine mammals, 20 seabirds, 6 reptiles, and 476 invertebrates; see Figure 1C). Biodiversity profiles created for other islands (Easter Islands, Pitcairn, Kermadec, French Polynesia and New Caledonia) shows that Palau has mid-level endemism in comparison (see Table 2). Our results echo the conclusions of Veron et al. (2015), in that endemism is highest in and around the Coral Triangle region and that it decreases further out the south Pacific region. Although, as the same study has indicated, this may be a reflection of the amount of research done favoring the Coral Triangle area.

Habitat preference indices were estimated for 53 pelagic species with AquaMaps data (Table 1), made up of 28% dolphins, 25% bony fishes, 15% sharks, 13% mollusks, 11% whales, 4% hydrozoans, and 1 species each of sea turtle and crocodile. Resulting HPI values ranged between 0.07-0.2 for fish species and 0.09-0.18 for 5 whale, 16 dolphin, 10 decapod, and 4 cephalopod species. Figures 2A-2B present the map of HPI values showing a clear trend of 'preference' for the main island Babeldaob and some of the smaller islands further south, Fana and Sonsorol, hosting most of the reef-associated and demersal species. The HPI ranges also suggest that for any one half-degree cell in the archipelago, an average of over 15 pelagic fish species may occur, and within the area of high diversity, i.e., Babeldaob, that average may go as high as 20 species.

The time series of marine fisheries catches from Lingard et al. (2011), re-expressed in this study as Figure 3 (upper panel) show the dominance (64%) of skipjack tuna (*Katsuwonus pelamis*) throughout the time series. Yellowfin tuna (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) make up 25% of the catch. These catches are mostly by foreign fishing fleets, which pay their way to fish in Palau waters, dominated by Japan (34% of total catches), with the USA (18%), Taiwan (10%), and Papua New Guinea (8%) following suit. Palau itself fishes only 6% of the annual fisheries catches coming from its waters. These target species, as we can assume from Figure 2A, are most likely caught in the northern part of the archipelago. The trend in the annual habitat index of the catch shows that species preferring pelagic habitats (small to large-sized tunas, cephalopods, sharks and rays; HI range of 0.20 to 0.33) increased in the early years to 1980 and started declining from then onwards. This suggests that the pelagic fisheries expanded from near-shore to offshore habitats, undoubtedly encouraged by the establishment of the American processing facility in Koror (see Lawson 1991) in the 1960s. The decline in the HI values is most likely associated with the shutting down of this facility in the early 1980s, suggesting that operations probably were then limited to offshore fleets exploiting large pelagic tunas which are found only in the upper 200 m of the water column (see Nichols 1991).

In conclusion, the maps in Figures 2A and 2B show a clear pattern of high pelagic species diversity around the main island cluster, possibly the biomass that is largely exploited by foreign fishing fleets. This robust pattern suggests that this area is a prime candidate for setting up a marine reserve, which currently is the focus of the Palauan government (Golbuu et al. 2005; Friedlander et al. 2014).

² See the FishBase checklist of the marine fishes of Palau here:

http://www.fishbase.org/Country/CountryChecklist.php?what=list&trpp=50&c_code=585&csub_code=&cpresence=Reported&sortby=phylo&ext_CL=on&ext_pic=on&vhabitat=saltwater

³ See the SeaLifeBase checklist of the marine vertebrates and invertebrates of Palau here:

http://www.sealifebase.org/Country/CountryChecklist.php?what=list&trpp=50&c_code=585&csub_code=&cpresence=Reported&sortby=alpha2&ext_CL=on&ext_pic=on&vhabitat=all2

Table 1. List of pelagic species with AquaMaps data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) used in the habitat preference index analyses presented in Figures 2A-2B. These represent 2% of the species in Table 2, i.e., species reportedly occurring in the waters of Palau.

Phylum	Order	Class	Family	Genus	Species	Author	Habitat
Chordata	Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>acutorostrata</i>	Lacépède, 1804	pelagic
				<i>Balaenoptera</i>	<i>borealis</i>	Lesson, 1828	pelagic
				<i>Balaenoptera</i>	<i>physalus</i>	(Linnaeus, 1758)	pelagic
				<i>Balaenoptera</i>	<i>musculus</i>	(Linnaeus, 1758)	pelagic
				<i>Megaptera</i>	<i>novaeangliae</i>	(Borowski, 1781)	pelagic
			Delphinidae	<i>Steno</i>	<i>bredanensis</i>	(Cuvier, 1828)	bathypelagic
				<i>Stenella</i>	<i>longirostris</i>	(Gray, 1828)	pelagic
				<i>Stenella</i>	<i>attenuata</i>	(Gray, 1846)	pelagic
				<i>Stenella</i>	<i>coeruleoalba</i>	(Meyen, 1833)	pelagic
				<i>Delphinus</i>	<i>delphis</i>	Linnaeus, 1758	pelagic
				<i>Lagenodelphis</i>	<i>hosei</i>	Fraser, 1956	pelagic
				<i>Grampus</i>	<i>griseus</i>	(Cuvier, 1812)	pelagic
				<i>Peponocephala</i>	<i>electra</i>	(Gray, 1846)	pelagic
				<i>Globicephala</i>	<i>macrorhynchus</i>	Gray, 1846	pelagic
				<i>Orcinus</i>	<i>orca</i>	(Linnaeus, 1758)	pelagic
			Kogiidae	<i>Kogia</i>	<i>breviceps</i>	(Blainville, 1838)	pelagic
				<i>Kogia</i>	<i>sima</i>	(Owen, 1866)	pelagic
			Physeteridae	<i>Physeter</i>	<i>macrocephalus</i>	Linnaeus, 1758	pelagic
			Ziphiidae	<i>Ziphius</i>	<i>cavirostris</i>	Cuvier, 1823	pelagic
				<i>Mesoplodon</i>	<i>densirostris</i>	(Blainville, 1817)	pelagic
	Crocodylia	Reptilia	Crocodylidae	<i>Crocodylus</i>	<i>porosus</i>	Schneider, 1801	pelagic
	Testudines		Cheloniidae	<i>Chelonia</i>	<i>mydas</i>	(Linnaeus, 1758)	pelagic
	Carcharhiniformes	Elasmobranchii	Carcharhinidae	<i>Carcharhinus</i>	<i>longimanus</i>	(Poey, 1861)	pelagic-oceanic
				<i>Prionace</i>	<i>glauca</i>	(Linnaeus, 1758)	pelagic-oceanic
			Sphyrnidae	<i>Sphyrna</i>	<i>lewini</i>	(Griffith & Smith, 1834)	pelagic-oceanic
				<i>Sphyrna</i>	<i>mokarran</i>	(Rüppell, 1837)	pelagic-oceanic
				<i>Sphyrna</i>	<i>zygaena</i>	(Linnaeus, 1758)	pelagic-oceanic

Table 1. (Continued) List of pelagic species with AquaMaps data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) used in the habitat preference index analyses presented in Figures 2A-2B. These represent 2% of the species in Table 2, i.e., species reportedly occurring in the waters of Palau.

Phylum	Order	Class	Family	Genus	Species	Author	Habitat
	Lamniformes	Elasmobranchii	Alopiidae	<i>Alopias</i>	<i>pelagicus</i>	Nakamura, 1935	pelagic-oceanic
			Lamnidae	<i>Isurus</i>	<i>oxyrinchus</i>	Rafinesque, 1810	pelagic-oceanic
	Orectolobiformes	Elasmobranchii	Rhincodontidae	<i>Rhincodon</i>	<i>typus</i>	Smith, 1828	pelagic-oceanic
	Perciformes	Actinopterygii	Carangidae	<i>Decapterus</i>	<i>macarellus</i>	(Cuvier, 1833)	pelagic-oceanic
			Coryphaenidae	<i>Coryphaena</i>	<i>equiselis</i>	Linnaeus, 1758	pelagic-oceanic
			Echeneidae	<i>Phtheichthys</i>	<i>lineatus</i>	(Menzies, 1791)	pelagic-oceanic
			Gempylidae	<i>Gempylus</i>	<i>serpens</i>	Cuvier, 1829	pelagic-oceanic
			Istiophoridae	<i>Istiophorus</i>	<i>platypterus</i>	(Shaw, 1792)	pelagic-oceanic
				<i>Tetrapturus</i>	<i>angustirostris</i>	Tanaka, 1915	pelagic-oceanic
			Scombridae	<i>Acanthocybium</i>	<i>solandri</i>	(Cuvier, 1832)	pelagic-oceanic
				<i>Katsuwonus</i>	<i>pelamis</i>	(Linnaeus, 1758)	pelagic-oceanic
				<i>Thunnus</i>	<i>alalunga</i>	(Bonnaterre, 1788)	pelagic-oceanic
				<i>Thunnus</i>	<i>albacares</i>	(Bonnaterre, 1788)	pelagic-oceanic
				<i>Thunnus</i>	<i>obesus</i>	(Lowe, 1839)	pelagic-oceanic
				<i>Odontanthias</i>	<i>borbonius</i>	(Valenciennes, 1828)	pelagic-oceanic
			Xiphiidae	<i>Xiphias</i>	<i>gladius</i>	Linnaeus, 1758	pelagic-oceanic
Cnidaria	Hydrozoa	Narcomedusae	Aeginidae	<i>Solmundella</i>	<i>bitentaculata</i>	(Quoy & Gaimard, 1833)	pelagic
		Trachymedusae	Rhopalonematidae	<i>Amphogona</i>	<i>apsteini</i>	(Vanhoeffen, 1902)	pelagic
Mollusca	Cephalopoda	Octopoda	Argonautidae	<i>Argonauta</i>	<i>argo</i>	Linnaeus, 1758	pelagic
		Teuthida	Ctenopterygidae	<i>Ctenopteryx</i>	<i>sicula</i>	(Verany, 1851)	bathypelagic
			Histioteuthidae	<i>Histioteuthis</i>	<i>hoylei</i>	(Goodrich, 1896)	pelagic
			Octopoteuthidae	<i>Taningia</i>	<i>danae</i>	Joubin, 1931	pelagic-oceanic
			Ommastrephidae	<i>Sthenoteuthis</i>	<i>oualaniensis</i>	(Lesson, 1830)	pelagic
			Onychoteuthidae	<i>Onychoteuthis</i>	<i>banksii</i>	(Leach, 1817)	pelagic
			Thysanoteuthidae	<i>Thysanoteuthis</i>	<i>rhombus</i>	Troschel, 1857	pelagic

Table 2. Comparison of SeaLifeBase and FishBase (March 2015) coverage of French Polynesia and its archipelagos marine biodiversity with literature and online sources. Marine biodiversity of Easter, Pitcairn, Kermadec Islands and New Caledonia islands are also presented. Note that SeaLifeBase contains more species than most of the review from other sources. (Nat = Native, End = Endemic).

Taxon	Easter Isl		Pitcairn Isl		Kermadec Isl		French Polyn		New Caled		Palau		Palau species from literature and online sources
	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	
Arthropoda	222	4	50	2	273	29	1108	5	2362	21	283	3	-
Brachiopoda			1		1		9		17		3		>249 [Crustaceans, Bauman, et al. (2004)].
Bryozoa	2				200	2	1		34		2		-
Chaetognatha							4		6		4		-
Chordata	51		58		64		165		407	1	186		-
Ascidacea					4		84		302		126		-
Appendicularia									4				>100 [Golbuu, et al. (2005); Bauman, et al. (2004)].
Aves	31		35		47		56		52		28		-
Mammalia	15		21		9		22		27		23		-
Sea turtles	4		2		3		3		5		4		12 [Bauman, et al. (2004)].
Sea snakes	1				1				15	1	2		4 [Bauman, et al. (2004)].
Crocodyles											1		2 [Bauman, et al. (2004)].
Cnidaria	60	1	89		56	1	184	1	871		489	16	1 [Bauman, et al. (2004)].
Porifera	19		8		27		17		246	10	88		625 [Golbuu, et al. (2005)], >600 [Bauman, et al. (2004)], 400 hard corals & 300 soft corals [NOAA, 2015].
Echinodermata	28	1	56		92	26	33		358	1	160		>300 [Bauman, et al. (2004)].
Foraminifera	30		8		10	2	1		424		11		21 [Golbuu, et al. (2005)].
Mollusca	221	16	294		452	50	967	6	1767	2	662	1	-
Marine worms									357				185 [Golbuu, et al. (2005)]; 423 species [Palau National Environmental Protection Council (2015)].
Annelida	43				27		6		264		23		>70 [Bauman, et al. (2004)].
Echiura									1				-
Platyhelminthes									70		19		-
Nematoda									8				-
Sipuncula					5		7		2		3		-
Phoronida									5				-
Kinorhyncha									3				-
Hemichordata									3				-
Sagenista					1				1		4		-
Nemertea	1												-
Rotifera	1												-
Gastrotricha							1						-
Gnathostomulida							9						-
Algae													259 [Bauman, et al. (2004)].
Dinophyta							4				1		-
Ochrophyta	24	3	2		12		4		5		26		-
Chlorophyta	31		1		13		17		11		82		-

* 400 Scleractinia, >200 other Cnidarians

† 185 Opisthobranchs, 1 Nautilus, 206 gastropods, 7 giant clams, 24 bivalves

Table 2. (Continued) Comparison of SeaLifeBase and FishBase (March 2015) coverage of French Polynesia and its archipelagos marine biodiversity with literature and online sources. Marine biodiversity of Easter, Pitcairn, Kermadec Islands and New Caledonia islands are also presented. Note that SeaLifeBase contains more species than most of the review from other sources. (Nat = Native, End = Endemic).

Taxon	Easter Isl		Pitcairn Isl		Kermadec Isl		French Polyn		New Caled		Palau		Palau species from literature and online sources
	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	
Chlorophyta	31		1		13		17		11		82		-
Rhodophyta	61	6			19		13		1		96		-
Tracheophyta									1		7		-
Cyanobacteria	1						1				16		-
Placozoa											1		-
Not assigned (Plantae)									1				-
TOTAL non-fish	795	31	567	2	125	110	2551	12	686	35	2166	20	
Pisces from FishBase	193	12	346	2	242	6	892	12	2348	5	1548	1	

Table 3. Number of marine species reportedly occurring in the waters of Palau grouped by higher taxa and geometric mean depth (m) available in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). There are almost 3,500 species reported for Palau, i.e., 43% finfishes, 19% mollusks, 14% cnidarians (mostly corals), 8% crustaceans (mostly decapods), 2% chordates, and the rest being other groups dominated by echinoderms and algae. This account is in no way complete, however, as recent expeditions are continuously identifying species new to science from the region. A list of the more than 840 published sources used to assign species to the Palau can be obtained from the FishBase and SeaLifeBase online search pages.

Geometric mean depth (m)	100	200	1000	6000
Marine mammals	18	1	3	1
Seabirds	28			
Marine reptiles	7			
Bony fishes	1473	24	4	1
Sharks and rays	30	1	1	
Crustaceans	270	3	14	
Mollusks	645	3	12	2
Echinoderms	155	1	4	
Corals	383	2	1	
Other inverts	394	8	1	0

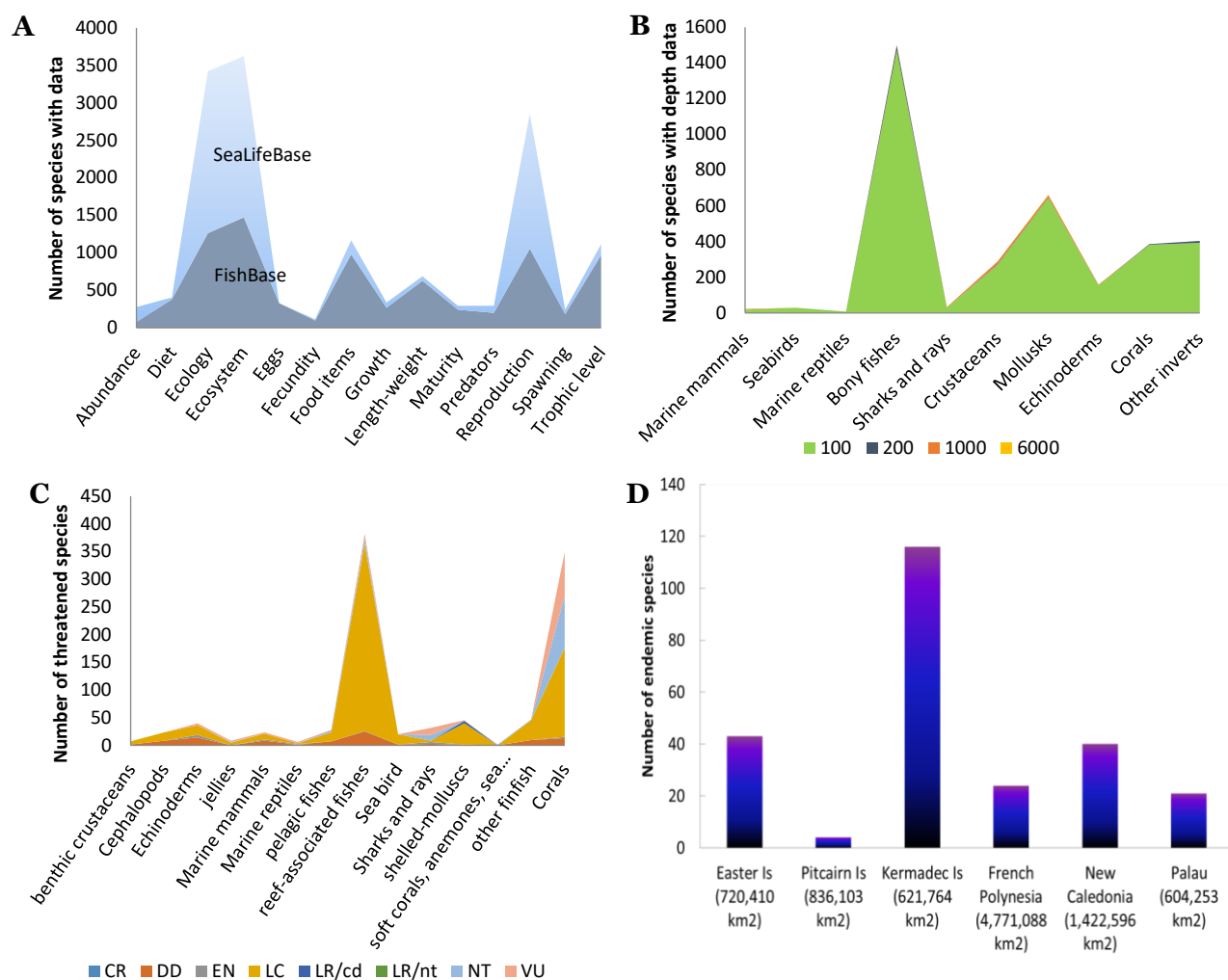


Figure 1. Comparative data on the marine biodiversity of Pacific Islands; **A:** Data currently available in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) for about 3,500 marine species occurring in New Caledonia based on about 840 published sources; **B:** Number of species by taxa by depth for about 3,500 species with depth data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org); **C:** The threatened species (according to the IUCN version of 2015) occurring in French Polynesia make up more almost 29% of the over 3,500 species gathered for this study in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). Fishes, sharks and rays make up half of this, and the other half is dominated by corals, decapods, cephalopods, gastropods, seabirds and marine mammals; **D:** Number of endemic species by country with more or less the same EEZ area in the Pacific region.

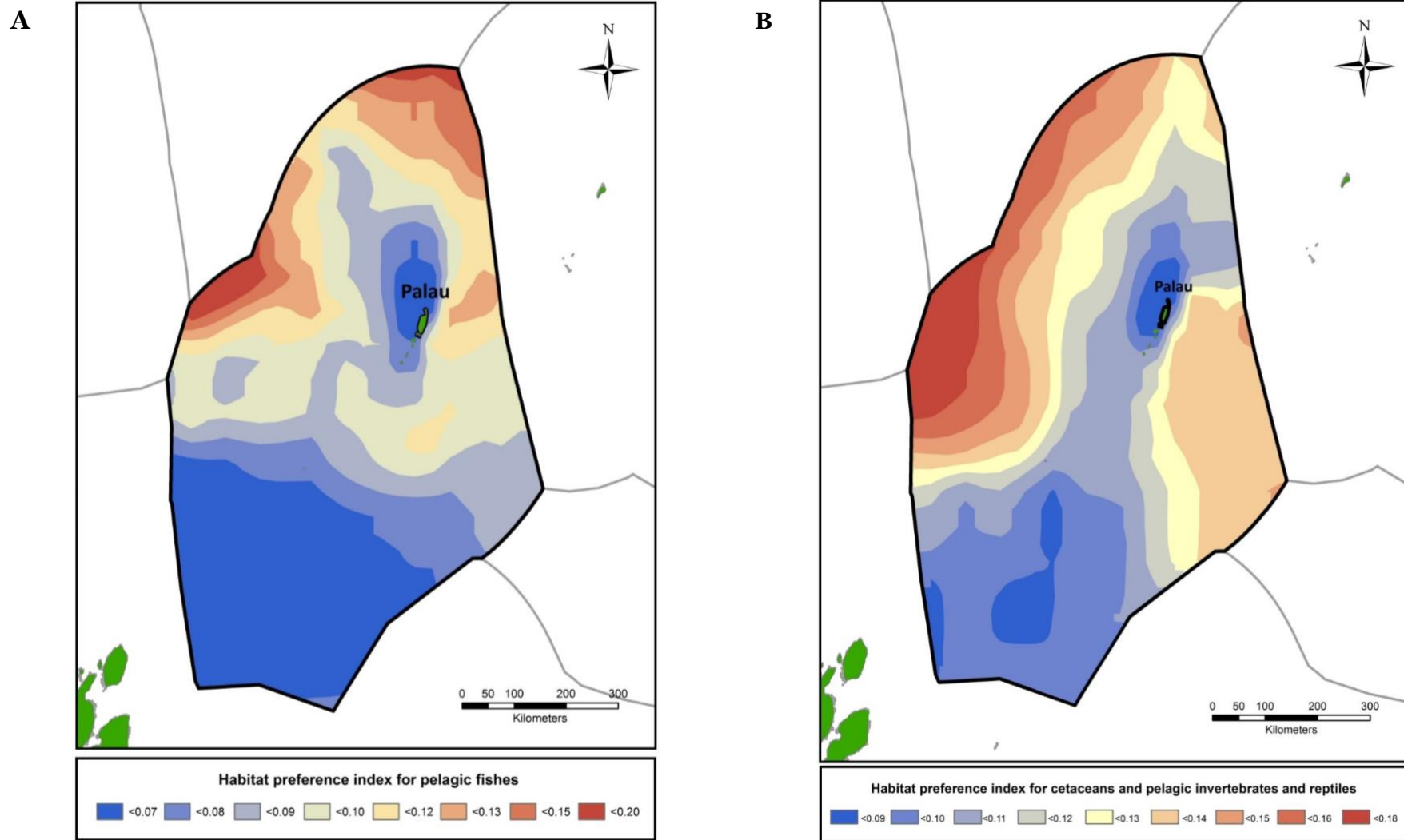


Figure 2. Distribution of the habitat preference index (HPI) in Palau; **A:** 21 fish species; **B:** 21 species of whales and dolphins, etc.

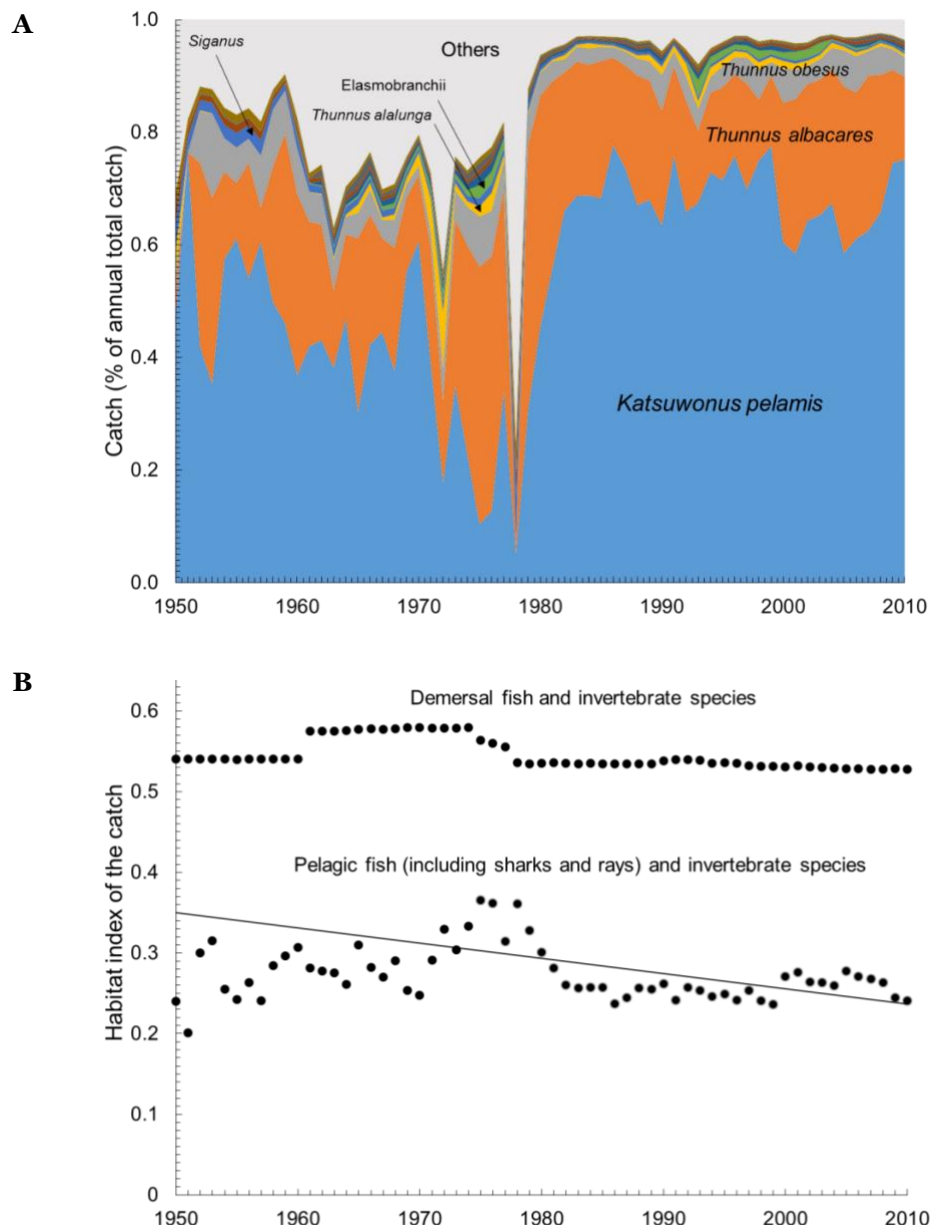


Figure 3. Time series indicators marine species exploitation in Palau, based on data extracted from the *Sea Around Us* database (www.seaaroundus.org); **A:** Catches (expressed as % of annual total) showing dominance of *Katsuwonus pelamis*, skipjack tuna; **B:** Trend in annual averages of habitat index weighted by the catch of demersal and pelagic species. A strong decline in HI values, notably in pelagic species, indicates a shift of the fishery towards the more lucrative large pelagic species.

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THE MARINE BIODIVERSITY OF THE POLAR SEAS IN FISHBASE AND SEALIFEBASE*

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Abstract

The polar seas are generally ice-covered waters with highly seasonal weather conditions, temperature, formation and extent of sea ice. To date, more than 8,000 marine species are estimated to occur in these waters (5,782 – Arctic; >8,200 – Antarctic). A collaboration with the Alfred-Wegener-Institut resulted in a preliminary list of marine species in the polar seas (7,710 species), collated from published documentation and made available via FishBase and SeaLifeBase. This list includes 533 species of bony fishes, 10 sharks, 17 rays, 208 vertebrates (whales, dolphins and sea birds), and at least 6,816 invertebrates and 114 plant species. This report includes the polar sea species list, their marine ecoregions, and an overview of available data on ecology, life history, and population dynamics.

Introduction

The polar seas are divided between the northern (Arctic) and southern (Antarctic) hemispheres. The Arctic, defined as latitudes from 66.5° of the equator, from the high Arctic to the sub Arctic parts of Canada, Greenland and Faroe Islands, Finland, Iceland, Norway, Russia, Sweden, and the United States, including associated marine areas (AMAP 2018), covering an area of about 14 million km² in winter and 7 million km² in summer (Thomas and Dieckmann 2010). The Antarctic “*extends south of the Polar Front to the coasts of the Antarctic continent*” with a total area of ~34.8 million km² (Griffiths 2010). These areas have a variety of habitats for marine species such as sea ice, hot vents, cold seeps, and continental shelves that can reach depths of more than 5,000 m (Griffiths 2010; Michel 2013). The threats facing the Arctic and Antarctic are numerous (Bennet et al. 2015) and to meet them, a good knowledge of their biodiversity is essential.

A project that aims to improve the coverage of the marine biodiversity of the polar seas in FishBase and SeaLifeBase was initiated through funding from the Alfred-Wegener-Institut (AWI). An inventory of available information on marine species in the polar seas was started in January 2018. This document reports on the progress of this project for the period January 2018-September 2019, with work highlights for the third quarter of 2019.

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Materials and Methods

Data were acquired from an extensive repository of scientific literature notably from *Antarctic Science*, *Journal of Ichthyology*, *Polar Biology*, Google Scholar, Google Books, and Web of Science were searched using keywords such as “polar sea”, “polar marine biodiversity”, “Arctic”, and “Antarctic” among others. References were also searched and grouped based on the composition of the circumpolar Arctic (i.e., Arctic General, Barents Sea, Beaufort Sea, Chukchi Sea, East Siberian Sea, Greenland Sea, Iceland Sea, Kara Sea, Laptev Sea, Northern Bering Sea, Norwegian Sea, Northwest Atlantic-Greenland, and White Sea), and the Antarctic. As of September 2019, about 765 references were provided by partners (e.g., Dr Todd Miller from NOAA, Dr Thomas Brey from AWI, Dr Wolf Arntz, FishBase and SeaLifeBase teams) on distribution, trophic ecology, abundance, life history, trophic ecology, and reproduction of species occurring in the polar seas.

Taxonomic data were validated against the World Register of Marine Species (WoRMs; www.marinespecies.org) and Catalogue of Life (CoL; www.catalogueoflife.org). Specific data on non-fish species were extracted and encoded into SeaLifeBase (www.sealifebase.org), a FishBase-like global biodiversity database on marine metazoans (except fish) of the world, while specific data on fish species were encoded in FishBase (www.fishbase.org), the global biodiversity information system on fishes of the world. These two global information systems work hand in hand to provide comprehensive data coverage on polar species for which data can be obtained.

Results and Discussion

A total of 975 references were used in FishBase (n=151) and SeaLifeBase (n=824) to assign fish and other marine metazoans to the polar seas. Figure 1 summarizes the types of references used with mainly 50%-59% from peer-reviewed journals; 46% of the references for fish came from book and book chapters, while the other sources for non-fish were from reports (13%), internet sources (11%), book/book chapters (11%), and the remaining (6%) from theses, database, compilations, and proceedings. This indicates the availability of references based on relevance on the World Wide Web, i.e., books for fishes, and journals for non-fish species. Eight references composed of regional checklists and books accounted for 75% of the 573 fish species recorded in FishBase, i.e., Andriyashev et al. (1995; 38%), Coad (2018; 32%), Miller (1993; 32%), Neilsen et al. (1992; 26%), Coad (1995; 24%), Quast et al. (1972; 21%) and Robins et al. (1991; 18%) covering more than 100 species per reference. Other references covered 10 to 100 fish species (30%), and the rest covered less than 10 species (65%). In SeaLifeBase, 95% of the 6,449 metazoan (non-fish) species were accounted for by three online databases validated by experts, i.e., Bisby et al. (2005; 55%), WoRMs (40%), and Rosenberg (2009; 18%), suggesting a good taxonomic quality of our compilation. Geographic validation was accounted for by references covering 10 to 920 species (241 references), and the rest with only 1-9 species per reference (580 references).

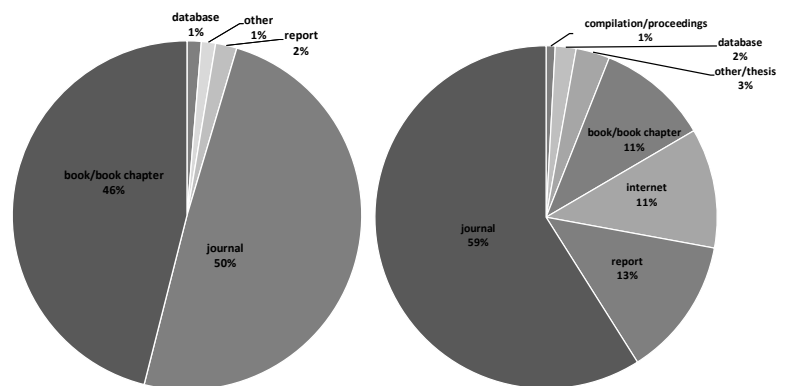


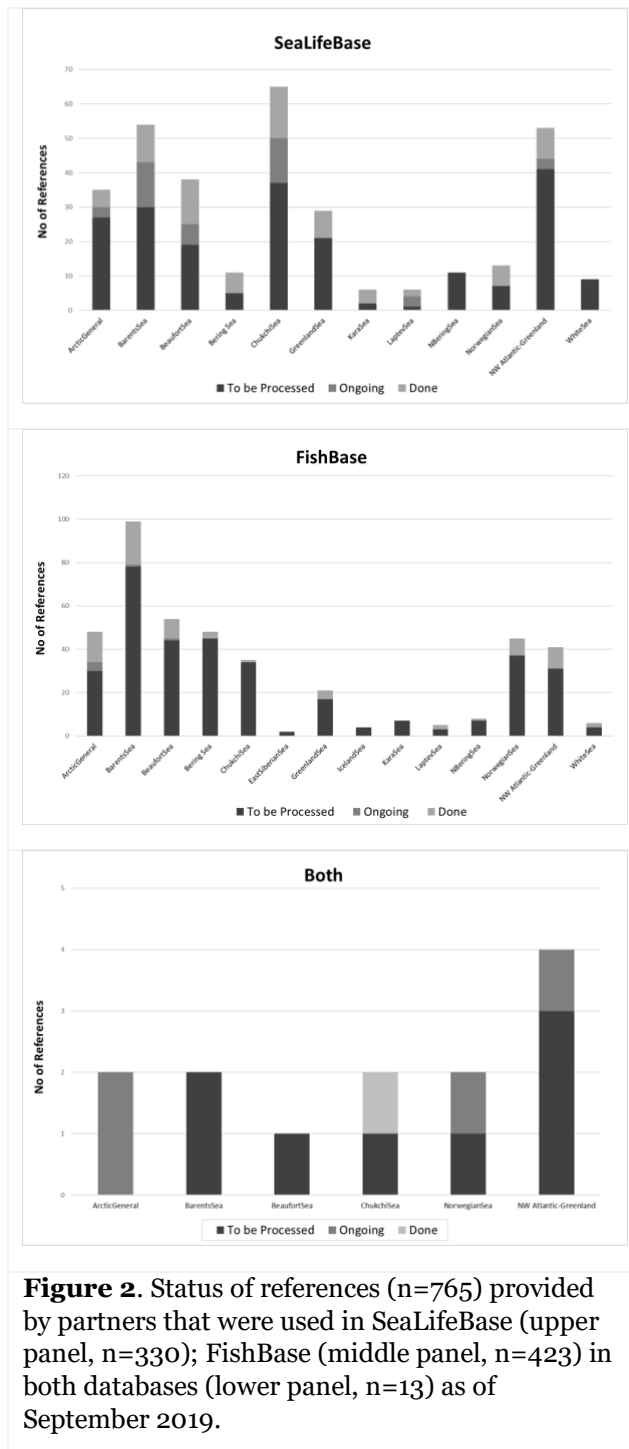
Figure 1. Left panel: Types of references (n=151) so far used in FishBase (for fish species; n=572) to assign species to the polar seas. Right panel: Types of references used (n=824) in SeaLifeBase (for non-fish metazoans; n=7138) to assign species to the polar seas. Data from September 2019 versions of FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org).

These statistics include the work done for the ongoing effort which started in January 2018 with an initial count of 6,105 marine species (fish–522; non-fish–5,583) assigned to the Polar Regions, using 697 references. Figure 2 shows the current status of references done and being processed from the pool of literature provided by partners (765 references). As of September 2019, 20% (79 SeaLifeBase; 74 FishBase; 1 Both) were fully exhausted, 7% (41 SeaLifeBase; 6 FishBase; 4 Both) ongoing (i.e., used for distribution but processing is ongoing for other information, i.e., ecology, abundance, life history, and population dynamics), and the remaining 73% (210 SeaLifeBase; 343 FishBase; 8 Both) are still to be processed (see Appendix A for the detailed count of references per topic in each area).

In 21 months of encoding, 1,555 non-fish marine metazoans were added to SeaLifeBase, while 50 fish species were added to FishBase, which increased FishBase and SeaLifeBase coverage to 7,710 marine species (fish–572; non-fish–7,138) assigned to the polar seas and thus available for species list queries. Based on estimates from the literature, Acanthocephala (23), Chaetognatha (23), and Ctenophora (16), Foraminifera (252), Gastrotricha (8), Hemichordata (10), Mollusca (1,715), Platyhelminthes (132), Sipuncula (21) probably have the most complete coverage in SeaLifeBase (Figure 3). Polar sea fish species coverage (Pisces–572) in FishBase are nearly complete (Figure 3). Other taxonomic groups are largely incomplete, while some do not have available estimates.

There are also 36 marine ecoregions in the polar seas, and through this work, a total of 5,615 marine species (fish–243; non-fish–5372) were assigned to these ecoregions (see Appendix B).

This project increased the data coverage of both databases, see Table 1.



1 List of species by ecosystem: 1) Antarctica: fishes (https://fishbase.ca/trophicEco/FishEcoList.php?ve_code=259), other vertebrates and invertebrates (https://www.sealifebase.ca/TrophicEco/FishEcoList.php?ve_code=259); 2) Arctic: fishes (https://fishbase.ca/trophicEco/FishEcoList.php?ve_code=1205), other vertebrates and invertebrates (https://www.sealifebase.ca/TrophicEco/FishEcoList.php?ve_code=1205); 3) All other species list queries by marine ecoregion is also available on Fishbase (<https://fishbase.ca>) and SeaLifeBase (<https://www.sealifebase.ca>).

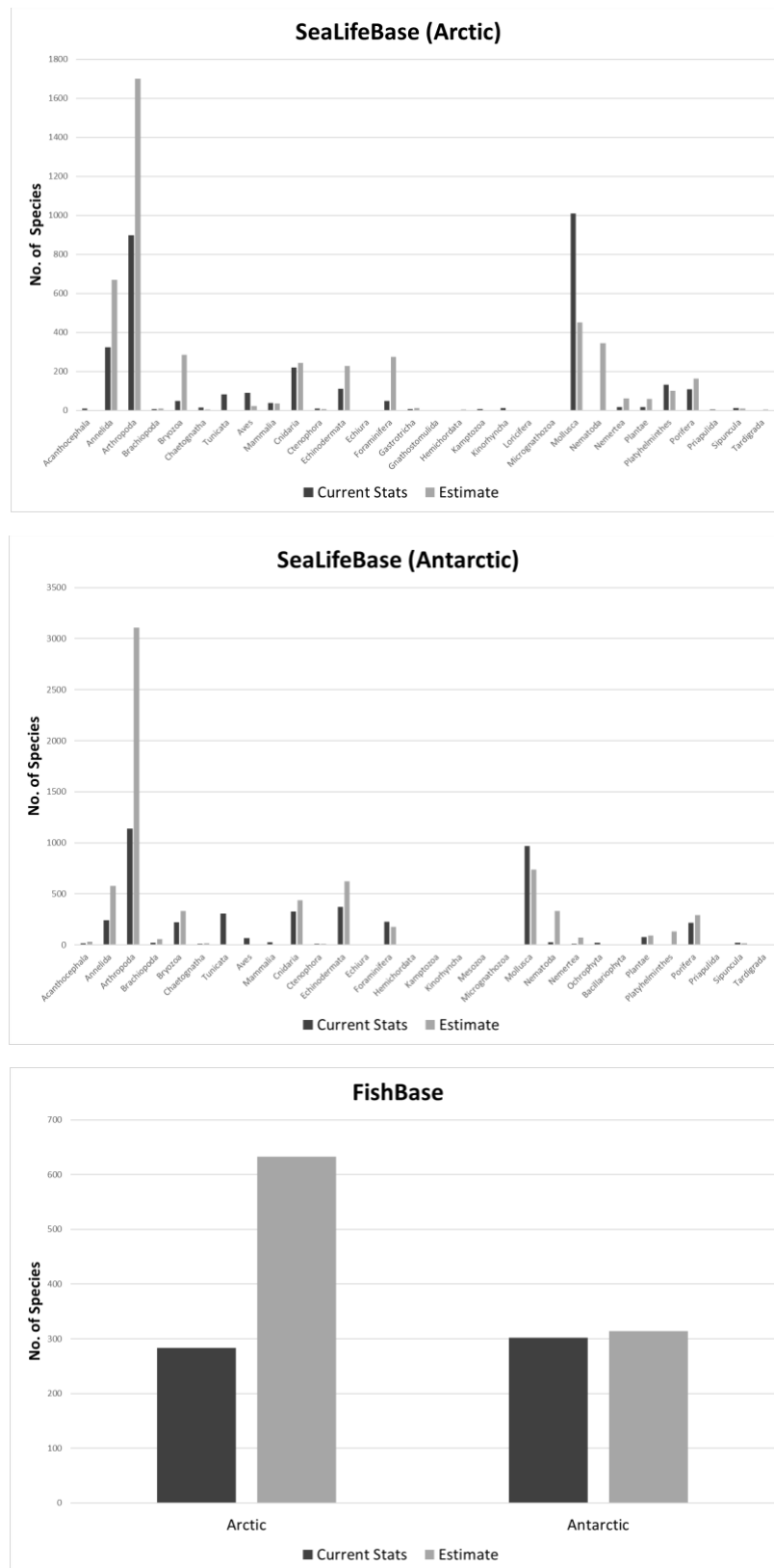


Figure 3. Number of species assigned to the Arctic (upper panel) and the Antarctic (middle panel) in SeaLifeBase and in FishBase (lower panel) compared with their publication estimates by species group as of September 2019.

Third Quarter of 2019 Highlights

Aside from the continuous encoding of data from references provided by our partners, during the third quarter of 2019, focus was given to increasing common names for polar species in FishBase and SeaLifeBase. Here are the details of the 2019 third quarter outputs:

- 1) Data on polar seas species common names increased by 4%, 326 records for 226 species using 18 references in SeaLifeBase and 17%, 167 records for 135 species using 4 references in FishBase. At present, the total count of common names for polar seas species in both databases is 9,881 (SLB–8,738 common names for 1,846 species; FB–1,143 common names for 521 species). Additional common names will be provided by our collaborator Todd Miller from NOAA. He is currently corresponding with collaborators for common names in Russian and from native (First Nation) people in the Arctic. This will be incorporated into the database in the 4th quarter report.
- 2) During the reporting period, the following were performed under AquaMaps:
 - Occurrence point data for non-fish species were received from GBIF; processing of occurrence cells in preparation for computing species environmental envelopes (HSPEN) for non-fishes completed; generation of probabilities of species occurrence (HSPEC) and mapped data completed. Implementation/uploading of latest maps in aquamaps.org on-going.
 - Evaluation ongoing for (1) inclusion of dissolved oxygen (bottom layer) as additional predictor of distribution for deep water species ongoing; (2) effect of observed/real dataset (Bio-ORACLE) on current/present distribution; and (3) holes in species richness maps in polar and gyre regions (current/2050). Collaborated with AWI on algorithm to detect faulty maps. These will be among the priorities for the upcoming map review and editing process, along with maps for crucial species groups (e.g., corals, highly commercial species), and species that are potential winners and losers due to climate change by year 2050.

Table 1. Data available for polar sea species in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) as of September 2019.

Data	FishBase (572 sp)	SeaLifeBase (7138 sp)
Ecology	422 records	6942 records
Depth Range	544 records	3801 records
Distribution	728 records	7168 records
Reproduction	241 records	5939 records
Growth	1211 records for 156 species	1433 records for 186 species
Max Lengths	721 records for 249 species	682 records for 364 species
Food Items	7104 records for 359 species	7488 records for 519 species
Diet	1031 records for 164 species	414 records for 106 species
Abundance	429 records for 124 species	2838ords for 140 species

- 3) With respect to item 1 of the contract (Provision of FishBase/SeaLifeBase/AquaMaps data through their web-based interfaces and through a mirror server at AWI web portals; notably at the Helmholtz Institute for Functional Marine Biodiversity at the University Oldenburg or HIMFB web portal, in the context of knowledge transfer to the public), this is no longer pursued as per meeting of Thomas Brey with Nina Garilao in November 2018. The AWI IT department is not yet amenable to hosting any of the mirrors. Dr. Brey received for HIFMB the physical copies of the FishBase and SeaLifeBase mirrors that are now in the August 2019 version. This is the third update for the year, the others were done in February and April.

Conclusion and Recommendations

The results presented here indicate good progress in increasing the coverage of Polar species in FishBase and SeaLifeBase. We are keeping abreast with new literature focusing on the region using Google Alerts for new publications. The challenge is to keep up with the encoding pace as new information becomes available to assure their inclusion in FishBase and SeaLifeBase updates, notably for newly described species or revisions of known taxonomic groups, which may require the splitting of or combination of data for species undergoing such revisions. This affects the species count for polar seas as well as lists of species by taxonomic group, by country, and by ecosystems.

We note some data processing challenges when information provided by partners do not match the FishBase and SeaLifeBase database conventions (e.g., growth and length-weight data which need further processing). Some of these data may not be usable, and thus, require further data mining, e.g., for life traits. As for species assignment in marine ecoregions, a process was developed and in execution to ensure that all polar seas species are assigned to their corresponding marine ecoregion.

Finally, partnership with institutions that may have biodiversity data, and/or additional information that can contribute towards the completion of key data for the polar seas is actively pursued, with the help of current partners.

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Appendix A. Number of references available per ecosystem in the polar seas per topic. Diet, growth, and reproduction (some numbers pertaining to “ongoing” studies were omitted).

SEALIFEBASE									
Ecosystem	Dist_abun_size_freq			Diet studies		Growth		Reproduction	
	Total Refs	Ongoing	Done	Total Refs	Done	Total Refs	Done	Total Refs	Done
Arctic General	31	2	4	1	1				
Barents Sea	44	11	6	6	4	3	1	1	
Beaufort Sea	24	6	4	8	5	6	2		
Bering Sea	4			7	5				
Chukchi Sea	48	12	4	13	4	3	1	1	1
East Siberian Sea									
Greenland Sea	19			3	2	6	1	1	1
Iceland Sea									
Kara Sea	7	4							
Laptev Sea	6	3	2						
NBering Sea	9			2					
Norwegian Sea	7			2	2	3	3	1	1
NW Atlantic-Greenland	32		2	14	6	6		1	1
White Sea	9								
SLB	240	38	22	56	29	24	8	3	4

FISHBASE

Ecosystem	Dist_abun_size_freq			Diet studies		Growth		Reproduction	
	Total Refs	Ongoing	Done	Total Refs	Done	Total Refs	Done	Total Refs	Done
Arctic General	34	4	9	2		4	2	8	2
Barents Sea	50	1	11	20	2	14	2	15	5
Beaufort Sea	31	1	3	13	4	8	1	2	1
Bering Sea	18		2	10		18		2	2
Chukchi Sea	26			6	1	3			
East Siberian Sea	2								
Greenland Sea	11		1	7				3	3
Iceland Sea	4								
Kara Sea	4			2		1			
Laptev Sea	3					2	2		
NBering Sea	5			2		1	1	1	1
Norwegian Sea	12			8		16	2	10	6
NW Atlantic-Greenland	17		3	11		8	2	6	6
White Sea	5	1	1			1	1		
	222	7	30	81	7	76	13	47	26

Appendix B. Number of species assigned to each marine ecoregion in the polar seas based on September 2019 versions of FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org).

Marine Ecoregions	FishBase	SeaLifeBase
Amundsen/Bellingshausen Sea	1	72
Antarctic Peninsula	1	90
Baffin Bay - Davis Strait	123	824
Beaufort Sea - continental coast and shelf		907
Beaufort-Amundsen-Viscount Melville-Queen Maud		15
Bouvet Island		136
Chukchi Sea	35	619
Crozet Islands		379
East Antarctic Dronning Maud Land		23
East Antarctic Enderby Land		54
East Antarctic Wilkes Land		108
East Greenland Shelf	3	106
East Siberian Sea	39	94
Heard and Macdonald Islands		276
High Arctic Archipelago		21
Hudson Complex		108
Kara Sea	35	158
Kerguelen Islands		1624
Lancaster Sound		11
Laptev Sea	44	485
North and East Barents Sea		798
North and East Iceland		31
North Greenland		465
Northern Labrador		11
Northern Norway and Finnmark		118
Peter the First Island		18
Prince Edward Islands		238
Ross Sea	5	37
South and West Iceland		45
South Georgia	2	481
South Orkney Islands		823
South Sandwich Islands		352
South Shetland Islands	2	672
Weddell Sea	50	625
West Greenland Shelf	3	124
White Sea	10	171

NEW CALEDONIA'S MARINE BIODIVERSITY IN FISHBASE AND SEALIFEBASE*

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Abstract

For the last 60 years, New Caledonia has been the subject of numerous biodiversity studies, which facilitated the review of the islands' marine biodiversity. The over 13,300 scientific contributions (1898-2015) used in this review resulted in a species list which now contains 2,348 fishes, and >6,800 non-fish species (35% arthropods; 26% molluscs; 13% cnidarians; 6% foraminiferans; 6% chordates - 306 tunicates, 52 seabirds, 27 dolphins and whales, 5 sea turtles, and 15 sea snakes; 6% sponges, marine worms and algae; and 5% echinoderms). These species lists and the associated information on ecology and biology are available via FishBase and SeaLifeBase.

Introduction

The archipelago of New Caledonia, in the Southwest Pacific, has an EEZ covering 1.4 million km², a shelf area of 63,159 km² (*Sea Around Us* 2015) and a total land area of 18,275 km² (CIA 2015). It has one main island, Grand Terre, which is surrounded by the second largest barrier reef in the world, and three provinces, the Northern and Southern Province the main island, and the Loyalty Islands to its east, with the larger islands surrounded by smaller islands (McKenna et al. 2011). Marine life in these islands is supported by enclosed lagoons, barrier reefs, coral reefs, seagrass beds and mangroves, hosting a rich marine fauna that put New Caledonia on the World Heritage list in 2008 (McKenna et al. 2011).

Payri and Richer de Forges (2007) report on an inventory of the marine fauna of New Caledonia, drawing on taxonomic analyses based on bone and shell fragments from as early as 1774, and which was validated and extended by more recent date surveys. Faunal inventories in New Caledonia conducted from the 1900s focused on the ecology of coral reef fauna leaving a gap for species found in external reef slopes beyond depths of 40 metres. In spite of this, Payri and Richer de Forges (2007) was able to list more than 9000 marine species as being described by the time this contribution was written.

This study examines the diversity of marine species occurring in New Caledonia, using the distribution and ecological information from the global information systems, FishBase (www.fishbase.org) for fishes, and SeaLifeBase (www.sealifebase.org) for marine invertebrates and tetrapods (marine mammals and reptiles, and sea birds). It also attempts to establish areas where large pelagic species are likely to occur within the New Caledonian EEZ, given that it has recently been declared 'marine park' which already contains numerous smaller protected marine areas (Wood 2007). This information might be useful, notably if combined with information on siltation and destruction of offshore coral reef areas due to nickel mining, given that New Caledonia has the largest known deposit of nickel in the world (McGinley 2011; McKenna et al. 2011).

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Materials and Methods

Scientific contributions (from online checklists and resources) explicitly mentioning the occurrence of species in New Caledonia were obtained and data on the distribution (geographically referenced occurrences) and ecology (habitats and depth ranges) from these sources were encoded into global information systems, i.e., FishBase and SeaLifeBase. The resulting number of species by taxon encoded in FishBase and SeaLifeBase were compared with those in Payri and Richer de Forges (2007) and other publications with reports on the marine biodiversity of New Caledonia.

Distribution data from FishBase and SeaLifeBase were used in Aquamaps (www.aquamaps.org) to obtain probabilities of occurrence for each of the commercially important species identified in Table 1. Here we assume that cells with non-zero probabilities represent ‘preferred’ (or ‘suitable’) habitats according to the logic presented in Reygondeau et al. (2014). Then, following Reygondeau et al. (2013), these probabilities were assumed to be analogous to the proportional abundances as used in the estimation of Simpson’s index of heterogeneity ($SI=1/\Sigma p_{i2}$), i.e., the weighted mean of the proportional abundances of species occurring in a given cell (see Peet 1974). We refer to this as the Habitat Preference Index, estimated for each half degree cell, and mapped to show the evenness of the composition of pelagic species ‘preferring’ a given half-degree latitude and longitude cell within the New Caledonian EEZ. HPI values approaching 1 represent cells with high numbers of species ‘preferring’ those habitats, while HPI values approaching 0 represent cells with low numbers of species preferring those habitats.

The time series trends of habitat variability of exploited pelagic and demersal marine fish species were obtained using a slightly different approach. Preference of species for habitats, defined in Palomares et al. (2015; Filter 5: Habitat preference)¹, were obtained from species ecology data in FishBase and SeaLifeBase. Species habitat indices ($HI_{spp} = \text{number of habitat where species is present} / \text{total number of habitats defined}$) were weighted by the volume of the catch (metric tonnes) obtained from the reconstructed marine fisheries catch data presented in Harper et al. (2009). The average annual $HI_{catch} = (HI_{spp} * \text{Catch}_{spp}) / \text{Total Annual Catch}$ was then plotted over the 1950-2010 period of reconstructed marine fisheries catches published in the *Sea Around Us* database for New Caledonia (see Harper et al. 2009)². This metric tests the change in species composition of the catch by following the behavior of the habitat index of the species in the catch. Presumably, spatial expansion (to offshore pelagic resources) and/or gradual diversification to more available demersal resources, will be reflected in the habitat index of species in the catch. Thus, expansion of a fishery to exploit large pelagic species offshore is indicated by a decrease in HI values (towards zero) and the opposite (towards one) reflects diversification of target species, presumably demersal or reef-associated species which occur in a wide variety of habitats.

Results and Discussion

Data from more than 6,900 references for fishes³ and 6,400 references for marine vertebrates and invertebrates⁴ were used to gather distribution, biological and ecological data for about 2,348 fishes, and more than 6,800 non-fish species i.e., 35% arthropods; 26% mollusks; 13% cnidarians; 6% foraminiferans; 6% chordates - 306 tunicates, 52 seabirds, 27 dolphins and whales, 5 sea turtles, and 15 sea snakes; 6% sponges, marine worms and algae; and 5% echinoderms, 74% of these species are found in neritic waters, or depths of 0-100 m (Table 2; Figures 1A-1B). Of these, 40 species were considered endemic (52% Annelida, 25% Porifera, 13% Pisces, and 5%

¹ http://www.seaaroundus.org/catch-reconstruction-and-allocation-methods/#_Toc421534362

² <http://www.seaaroundus.org/data/#/eez/540?chart=catch-chart&dimension=taxon&measure=tonnage&limit=10>

³ See FishBase checklist of New Caledonian marine fishes here:

http://www.fishbase.org/Country/CountryChecklist.php?what=list&trpp=50&c_code=540&csub_code=&cpresence=Reported&sortby=phylo&ext_CL=on&ext_pic=on&vhabitat=saltwater

⁴ See SeaLifeBase checklist of New Caledonian marine vertebrates and invertebrates here:

http://www.sealifebase.org/Country/CountryChecklist.php?what=list&trpp=50&c_code=540&csub_code=&cpresence=Reported&sortby=alpha2&ext_CL=on&ext_pic=on&vhabitat=all2

each Mollusca, Echinodermata and Reptilia) (Table 3; Figure 1D). Endemism for marine species in New Caledonia was found to be less than 5% by IUCN (2003), thus confirming the number of endemic species we found based on available literature. This placed New Caledonia (40 species) third, after Easter Island (43 species) and Kermadec Island (116 species) in the Pacific for marine endemism.

We also used the inventory by Payri and Richer de Forges (2007) as a baseline for the number of species known in New Caledonia. Our study was able to treat 14 out of 16 marine groups included in their study (see Table 2). Note that due to limited time, the chapters on Bryozoa (407 species), and Algae (443 species) were not treated. In spite of this, we were able to increase Payri and Richer de Forges (2007) estimated number of species occurring in New Caledonia by 631 species for 9 of the groups treated (Arthropoda-317, Ascidiacea-12, Mammalia-2, Cnidaria-87, Porifera-97, Echinodermata-101, Phoronida-1 and sea turtles-1) with the use of additional references.

Discrepancies were encountered, i.e., of 446 species (Aves-3, Mollusca-384, and marine worms-59), 108 species have not been formerly described in the taxonomic literature, e.g., species epithets quoted as 'sp.', 'cf' or '?' (86 mollusks and 22 marine worms). Such cases do not follow the FishBase/SeaLifeBase taxonomic format and were thus not encoded. We were able to find taxonomic descriptions for 424 foraminiferan species formerly quoted as above using other references, thus reducing the unencodable records for this group to 162 species, while 15 sea snake species remained without species epithets and thus unencodable.

More than 700 references were used to assign species to New Caledonia, 25% of which were taxonomic contributions with descriptions of new species, alluding to a high rate of new species being discovered and/or being recently described (see Payri and Richer de Forges 2007). This implies to a lack of more detailed biological and ecological data for these recently described species, and which could be considered as 'data gaps'. In spite of this, New Caledonia still has the largest number of known marine species compared to other Pacific islands (see Table 3).

Protecting this rich biodiversity are 15 MPAs established around the archipelago (Wood 2007). The effectivity of these MPAs was presented by Wantiez et al. (1997) who observed an increase in the relative abundance and species richness in the region. IUCN (2015) identified 2 Critically Endangered species, 20 Endangered, 141 Vulnerable, 145 Near Threatened, and 864 (66% of species listed under the IUCN Red List) species of Least Concern.

HPI values were estimated for 121 pelagic species with AquaMaps data (Table 1), made up of 50% bony fishes, 10% dolphins, 9% whales, 12% sharks, 8% molluscs, 7% decapod crustaceans, 4% chaetognaths, 2 tunicates, and 1 species each of annelid, pycnogonid, and sea turtle. These ranged between 0.01-0.07 for fish species and 0.03-0.08 for 11 whales, 12 dolphins, 10 mollusks, 9 decapod crustaceans, 5 chaetognaths, 2 tunicates and, 1 annelid, pycnogonid and sea turtle species. Figures 2A-2B indicate a trend of 'preference' for the western part of New Caledonia, i.e., Chesterfield/Bellona Plateau, one of the main reef areas of New Caledonia, supported by five guyots, and hosts reef-associated species (Kulbicki 2007, Pelletier 2007). These results suggest that the preferred habitats of pelagic marine species which occur in New Caledonia are in areas outside of established MPAs.

The time series trend of the catches within the New Caledonian EEZ, indicate a change from large catches of tuna (*Thunnus albacares* and *T. alalunga*) and reef-associated species (emperors, Family Lethrinidae and groupers, Family Serranidae) to large catches of small pelagics (Family Scombridae) and other demersal species (sea cucumbers, mullets, and snappers; Figure 3; upper panel). The HI values for 25 fish species, 2 invertebrates and 60 higher taxonomic groups, i.e., less disaggregated groups (HI range of 0.35-0.40 for pelagic habitats and 0.50-

0.54 for demersal habitats) show a slight increasing trend when weighted by the catch (Figure 3; lower panel), basically emulating the catch trends.

The New Caledonia fisheries consist of (now) domestic tuna fishery fleets, and equally important coastal artisanal, recreational, and subsistence fisheries (Harper et al. 2009). The exploitation of large tuna species by the industrial and recreational fleets and the gradual change to smaller and near-shore pelagic species (for example, *Scomberomorus commerson*; see Dalzell et al. 1996) is reflected in the slightly increasing HI values of the catch of pelagic species. On the other hand, continued exploitation by the artisanal and subsistence fisheries, for example, of sea cucumbers (see Harper et al. 2009), is reflected in the higher HI values of the catch of demersal species. This behavior seems to suggest an increasing diversification of target species, i.e., of species which are found in a wide range of habitats both pelagic and demersal (or in reef areas). However, the superimposed trend in the regional marine trophic index for New Caledonia (see Kleisner et al. 2015)⁵ suggests a decrease in the trophic level of the catch from the 3.74 high in 1960 to the 3.2 low in 2010. This suggests that in spite of the increase in catches and in the variety of target species, this diversification targets more low-trophic level species. This leads to the conclusion that the highly endemic and diverse New Caledonian marine ecosystem is also experiencing the now well-known phenomenon of ‘fishing down the food web’ (see Pauly et al. 1998).

In summary, our study shows that most of the commercially important pelagic species occur in areas which are not protected by MPAs and that the New Caledonian catches are now tending towards smaller and lower trophic level species, in spite of the sustained catches of large tuna species. Thus, the highly endemic and diverse marine ecosystem of the New Caledonian archipelago should benefit from the establishments of no-take zones within the newly declared ‘Parc national de la mer de corail’, that will protect commercially exploited high-trophic level species.

⁵ See also <http://www.seaaroundus.org/data/#/eez/540/marine-trophic-index> and <http://www.seaaroundus.org/doc/Methods/MTIMethod/Method-MTI-FiB-RMTI-New-June-15-2015.pdf>

Table 1. List of pelagic species with AquaMaps data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) used in the habitat preference index analyses presented in Figures 2A-wB. These represent the commercially important species reportedly occurring in New Caledonia waters from Sea Around Us. (Hab= Habitat; P= Pelagic; BP= Bathypelagic; PO= Pelagic-Oceanic).

Order	Class	Family	Genus	Species	Author & Year	Hab
Aciculata	Polychaeta	Chrysopetalidae	<i>Bhawania</i>	<i>goodei</i>	Webster, 1884	P
Decapoda	Malacostraca	Aristeidae	<i>Aristaeopsis</i>	<i>edwardsiana</i>	(Johnson, 1867)	BP
Decapoda	Malacostraca	Aristeidae	<i>Aristeus</i>	<i>virilis</i>	(Bate, 1881)	BP
Decapoda	Malacostraca	Benthescymidae	<i>Benthescymus</i>	<i>investigatoris</i>	Alcock & Anderson '99	BP
Decapoda	Malacostraca	Oplophoridae	<i>Acanthephyra</i>	<i>curtirostris</i>	Wood-Mason, 1891	BP
Decapoda	Malacostraca	Oplophoridae	<i>Acanthephyra</i>	<i>eximia</i>	Smith, 1884	P
Decapoda	Malacostraca	Oplophoridae	<i>Oplophorus</i>	<i>gracilirostris</i>	Milne-Edwards, 1881	BP
Decapoda	Malacostraca	Palaemonidae	<i>Thaumastocaris</i>	<i>streptopus</i>	Kemp, 1922	P
Decapoda	Malacostraca	Penaeidae	<i>Funchalia</i>	<i>taaningi</i>	Burkenroad, 1940	P
Decapoda	Malacostraca	Penaeidae	<i>Funchalia</i>	<i>villosa</i>	(Bouvier, 1905)	BP
Pantopoda	Pycnogonida	Colossendeidae	<i>Colossendeis</i>	<i>macerrima</i>	Wilson, 1881	BP
Not assigned	Not assigned	Krohnittidae	<i>Krohnitta</i>	<i>pacifica</i>	(Aida, 1897)	P
Not assigned	Not assigned	Pterosagittidae	<i>Pterosagitta</i>	<i>draco</i>	(Krohn, 1853)	P
Not assigned	Not assigned	Sagittidae	<i>Ferosagitta</i>	<i>robusta</i>	(Doncaster, 1902)	P
Not assigned	Not assigned	Sagittidae	<i>Flaccisagitta</i>	<i>enflata</i>	(Grassi, 1881)	P
Not assigned	Not assigned	Sagittidae	<i>Flaccisagitta</i>	<i>hexaptera</i>	(d'Orbigny, 1836)	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>acutorostrata</i>	Lacépède, 1804	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>edeni</i>	Anderson, 1879	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>borealis</i>	Lesson, 1828	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>physalus</i>	(Linnaeus, 1758)	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>musculus</i>	(Linnaeus, 1758)	P
Cetacea	Mammalia	Balaenopteridae	<i>Balaenoptera</i>	<i>bonaerensis</i>	Burmeister, 1867	BP
Cetacea	Mammalia	Delphinidae	<i>Delphinus</i>	<i>delphis</i>	Linnaeus, 1758	P
Cetacea	Mammalia	Delphinidae	<i>Feresa</i>	<i>attenuata</i>	Gray, 1874	P
Cetacea	Mammalia	Delphinidae	<i>Globicephala</i>	<i>macrorhynchus</i>	Gray, 1846	P
Cetacea	Mammalia	Delphinidae	<i>Lagenodelphis</i>	<i>hosei</i>	Fraser, 1956	P
Cetacea	Mammalia	Delphinidae	<i>Orcinus</i>	<i>orca</i>	(Linnaeus, 1758)	P
Cetacea	Mammalia	Delphinidae	<i>Peponocephala</i>	<i>electra</i>	(Gray, 1846)	P
Cetacea	Mammalia	Delphinidae	<i>Stenella</i>	<i>longirostris</i>	(Gray, 1828)	P
Cetacea	Mammalia	Delphinidae	<i>Stenella</i>	<i>attenuata</i>	(Gray, 1846)	P
Cetacea	Mammalia	Delphinidae	<i>Stenella</i>	<i>coeruleoalba</i>	(Meyen, 1833)	P
Cetacea	Mammalia	Delphinidae	<i>Steno</i>	<i>bredanensis</i>	(Cuvier, 1828)	BP
Cetacea	Mammalia	Delphinidae	<i>Tursiops</i>	<i>truncatus</i>	(Montagu, 1821)	P
Cetacea	Mammalia	Delphinidae	<i>Tursiops</i>	<i>aduncus</i>	(Ehrenberg, 1833)	BP
Cetacea	Mammalia	Kogiidae	<i>Kogia</i>	<i>breviceps</i>	(Blainville, 1838)	P
Cetacea	Mammalia	Kogiidae	<i>Kogia</i>	<i>sima</i>	(Owen, 1866)	P
Cetacea	Mammalia	Physeteridae	<i>Physeter</i>	<i>macrocephalus</i>	Linnaeus, 1758	P
Cetacea	Mammalia	Ziphiidae	<i>Mesoplodon</i>	<i>densirostris</i>	(Blainville, 1817)	P
Cetacea	Mammalia	Ziphiidae	<i>Ziphius</i>	<i>cavirostris</i>	(Cuvier, 1823)	P
Copelata	Appendicularia	Oikopleuridae	<i>Oikopleura</i>	<i>longicauda</i>	(Vogt, 1854)	P
Copelata	Appendicularia	Oikopleuridae	<i>Stegosoma</i>	<i>magnum</i>	(Langerhans, 1880)	P
Testudines	Reptilia	Cheloniidae	<i>Chelonia</i>	<i>mydas</i>	(Linnaeus, 1758)	P
Octopoda	Cephalopoda	Argonautidae	<i>Argonauta</i>	<i>argo</i>	Linnaeus, 1758	P
Spirulida	Cephalopoda	Spirulidae	<i>Spirula</i>	<i>spirula</i>	(Linnaeus, 1758)	P
Teuthida	Cephalopoda	Histioteuthidae	<i>Histioteuthis</i>	<i>hoylei</i>	(Goudrich, 1896)	P
Teuthida	Cephalopoda	Octopoteuthidae	<i>Taningia</i>	<i>danae</i>	Joubin, 1931	PO
Teuthida	Cephalopoda	Ommastrephidae	<i>Eucleoteuthis</i>	<i>luminosa</i>	(Sasaki, 1915)	P
Teuthida	Cephalopoda	Ommastrephidae	<i>Hyaloteuthis</i>	<i>pelagica</i>	(Bosc, 1802)	P
Teuthida	Cephalopoda	Ommastrephidae	<i>Sthenoteuthis</i>	<i>oualaniensis</i>	(Lesson, 1830)	P
Teuthida	Cephalopoda	Onychoteuthidae	<i>Onychoteuthis</i>	<i>banksii</i>	(Leach, 1817)	P
Teuthida	Cephalopoda	Thysanoteuthidae	<i>Thysanoteuthis</i>	<i>rhombus</i>	Troschel, 1857	P
Vampyromorphida	Cephalopoda	Vampyroteuthidae	<i>Vampyroteuthis</i>	<i>infernalis</i>	Chun, 1903	P
Anguilliformes	Actinopterygii	Derichthyidae	<i>Nessorhamphus</i>	<i>danae</i>	Schmidt, 1931	BP
Anguilliformes	Actinopterygii	Derichthyidae	<i>Nessorhamphus</i>	<i>ingolfianus</i>	(Schmidt, 1912)	BP
Anguilliformes	Actinopterygii	Nemichthyidae	<i>Avocettina</i>	<i>infans</i>	(Günther, 1878)	BP
Anguilliformes	Actinopterygii	Nemichthyidae	<i>Nemichthys</i>	<i>scolopaceus</i>	Richardson, 1848	BP
Anguilliformes	Actinopterygii	Serrivomeridae	<i>Stemonidium</i>	<i>hypomelas</i>	Gilbert, 1905	BP
Aulopiformes	Actinopterygii	Alepisauridae	<i>Alepisaurus</i>	<i>brevirostris</i>	Gibbs, 1960	BP
Aulopiformes	Actinopterygii	Alepisauridae	<i>Alepisaurus</i>	<i>ferox</i>	Lowe, 1833	BP
Aulopiformes	Actinopterygii	Evermannellidae	<i>Coccorella</i>	<i>atlantica</i>	(Parr, 1928)	BP
Aulopiformes	Actinopterygii	Evermannellidae	<i>Evermannella</i>	<i>indica</i>	Brauer, 1906	BP
Aulopiformes	Actinopterygii	Evermannellidae	<i>Odontostomops</i>	<i>normalops</i>	(Parr, 1928)	PO

Marine and Freshwater Miscellanea II

Table 1. (continued) List of pelagic species with AquaMaps data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) used in the habitat preference index analyses presented in Figures 2A-wB. These represent the commercially important species reportedly occurring in New Caledonia waters from Sea Around Us. (Hab= Habitat; P= Pelagic; BP= Bathypelagic; PO= Pelagic-Oceanic).

Order	Class	Family	Genus	Species	Author & Year	Hab
Aulopiformes	Actinopterygii	Giganturidae	<i>Gigantura</i>	<i>indica</i>	Brauer, 1901	BP
Aulopiformes	Actinopterygii	Omosudidae	<i>Omosudis</i>	<i>lowii</i>	Günther, 1887	BP
Aulopiformes	Actinopterygii	Paralepididae	<i>Lestidiops</i>	<i>indopacifica</i>	(Ege, 1953)	BP
Aulopiformes	Actinopterygii	Paralepididae	<i>Macroparalepis</i>	<i>affinis</i>	Ege, 1933	BP
Aulopiformes	Actinopterygii	Paralepididae	<i>Magnisudis</i>	<i>indica</i>	(Ege, 1953)	BP
Aulopiformes	Actinopterygii	Paralepididae	<i>Stemonosudis</i>	<i>elegans</i>	(Ege, 1933)	BP
Aulopiformes	Actinopterygii	Scopelarchidae	<i>Benthalbella</i>	<i>infans</i>	Zugmayer, 1911	BP
Aulopiformes	Actinopterygii	Scopelarchidae	<i>Scopelarchoides</i>	<i>danae</i>	Johnson, 1974	BP
Beloniformes	Actinopterygii	Exocoetidae	<i>Cheilopogon</i>	<i>atrisignis</i>	(Jenkins, 1903)	PO
Beloniformes	Actinopterygii	Hemiramphidae	<i>Euleptorhamphus</i>	<i>viridis</i>	(van Hasselt, 1823)	PO
Beryciformes	Actinopterygii	Anoplogastridae	<i>Anoplogaster</i>	<i>cornuta</i>	(Valenciennes, 1833)	BP
Beryciformes	Actinopterygii	Diretmidae	<i>Diretmus</i>	<i>argenteus</i>	Johnson, 1864	BP
Beryciformes	Actinopterygii	Trachichthyidae	<i>Hoplostethus</i>	<i>atlanticus</i>	Collett, 1889	BP
Beryciformes	Actinopterygii	Trachichthyidae	<i>Paratrachichthys</i>	<i>tralli</i>	(Hutton, 1875)	BP
Cetomimiformes	Actinopterygii	Cetomimidae	<i>Cetostoma</i>	<i>regani</i>	Zugmayer, 1914	BP
Cetomimiformes	Actinopterygii	Rondeletidae	<i>Rondeletia</i>	<i>loricata</i>	Abe & Hotta, 1963	BP
Gadiformes	Actinopterygii	Bregmacerotidae	<i>Bregmaceros</i>	<i>japonicus</i>	Tanaka, 1908	PO
Gadiformes	Actinopterygii	Macrouridae	<i>Bathygadus</i>	<i>spongiceps</i>	Gilbert & Hubbs, 1920	BP
Gadiformes	Actinopterygii	Macrouridae	<i>Coryphaenoides</i>	<i>striatus</i>	Barnard, 1925	BP
Gadiformes	Actinopterygii	Moridae	<i>Gadella</i>	<i>brocca</i>	Paulin & Roberts, 1997	BP
Lampriformes	Actinopterygii	Lampridae	<i>Lampris</i>	<i>guttatus</i>	(Brünnich, 1788)	BP
Lampriformes	Actinopterygii	Trachipteridae	<i>Zu</i>	<i>cristatus</i>	(Bonelli, 1819)	BP
Lophiiformes	Actinopterygii	Ceratiidae	<i>Cryptopsaras</i>	<i>couesii</i>	Gill, 1883	BP
Lophiiformes	Actinopterygii	Gigantactinidae	<i>Gigantactis</i>	<i>vanhoeffeni</i>	Brauer, 1902	BP
Lophiiformes	Actinopterygii	Linophrynidae	<i>Haplophryne</i>	<i>mollis</i>	(Brauer, 1902)	BP
Myctophiformes	Actinopterygii	Myctophidae	<i>Taaningichthys</i>	<i>bathophilus</i>	(Tåning, 1928)	BP
Myctophiformes	Actinopterygii	Myctophidae	<i>Benthoema</i>	<i>fibulatum</i>	(Gilbert & Cramer, 1897)	BP
Myctophiformes	Actinopterygii	Neoscopelidae	<i>Neosopelus</i>	<i>macrolepidotus</i>	Johnson, 1863	BP
Osmeriformes	Actinopterygii	Alepocephalidae	<i>Photostylus</i>	<i>pycnopterus</i>	Beebe, 1933	BP
Osmeriformes	Actinopterygii	Opisthoproctidae	<i>Opisthoproctus</i>	<i>grimaldii</i>	Zugmayer, 1911	BP
Perciformes	Actinopterygii	Bramidae	<i>Brama</i>	<i>myersi</i>	Mead, 1972	PO
Perciformes	Actinopterygii	Carangidae	<i>Decapterus</i>	<i>macarellus</i>	(Cuvier, 1833)	PO
Perciformes	Actinopterygii	Champsodontidae	<i>Champsodon</i>	<i>guentheri</i>	Regan, 1908	BP
Perciformes	Actinopterygii	Coryphaenidae	<i>Coryphaena</i>	<i>equiselis</i>	Linnaeus, 1758	PO
Perciformes	Actinopterygii	Echeneidae	<i>Phtheichthys</i>	<i>lineatus</i>	(Menzies, 1791)	PO
Perciformes	Actinopterygii	Gempylidae	<i>Gempylus</i>	<i>serpens</i>	Cuvier, 1829	PO
Perciformes	Actinopterygii	Howellidae	<i>Howella</i>	<i>brodiei</i>	Ogilby, 1899	BP
Perciformes	Actinopterygii	Scombridae	<i>Thunnus</i>	<i>alalunga</i>	(Bonnaterre, 1788)	PO
Perciformes	Actinopterygii	Scombridae	<i>Thunnus</i>	<i>albacares</i>	(Bonnaterre, 1788)	PO
Perciformes	Actinopterygii	Scombridae	<i>Thunnus</i>	<i>obesus</i>	(Lowe, 1839)	PO
Perciformes	Actinopterygii	Xiphiidae	<i>Xiphias</i>	<i>gladius</i>	Linnaeus, 1758	PO
Saccopharyngiformes	Actinopterygii	Eurypharyngidae	<i>Eurypharynx</i>	<i>pelecanaoides</i>	Vaillant, 1882	BP
Stephanoberyciformes	Actinopterygii	Melamphidae	<i>Melamphaes</i>	<i>danae</i>	Ebeling, 1962	BP
Stomiiformes	Actinopterygii	Gonostomatidae	<i>Cyclothone</i>	<i>acclinidens</i>	Garman, 1899	BP
Stomiiformes	Actinopterygii	Phosichthyidae	<i>Ichthyococcus</i>	<i>ovatus</i>	(Cocco, 1838)	BP
Stomiiformes	Actinopterygii	Sternoptychidae	<i>Valenciennellus</i>	<i>tripunctulatus</i>	(Esmark, 1871)	BP
Stomiiformes	Actinopterygii	Stomiidae	<i>Astronesthes</i>	<i>indicus</i>	Brauer, 1902	BP
Tetraodontiformes	Actinopterygii	Triacanthodidae	<i>Triacanthodes</i>	<i>intermedius</i>	Matsuura & Fourmanoir '84	BP
Zeiformes	Actinopterygii	Grammicolepididae	<i>Grammicolepis</i>	<i>brachiusculus</i>	Poe, 1873	BP
Zeiformes	Actinopterygii	Parazenidae	<i>Cyttopsis</i>	<i>rosea</i>	(Lowe, 1843)	BP
Carcharhiniformes	Elasmobranchii	Carcharhinidae	<i>Carcharhinus</i>	<i>longimanus</i>	(Poe, 1861)	PO
Carcharhiniformes	Elasmobranchii	Carcharhinidae	<i>Prionace</i>	<i>glauca</i>	(Linnaeus, 1758)	PO
Carcharhiniformes	Elasmobranchii	Sphyrnidae	<i>Sphyrna</i>	<i>lewini</i>	(Griffith & Smith, 1834)	PO
Carcharhiniformes	Elasmobranchii	Sphyrnidae	<i>Sphyrna</i>	<i>mokarran</i>	(Rüppell, 1837)	PO
Lamniformes	Elasmobranchii	Alopiidae	<i>Alopias</i>	<i>pelagicus</i>	Nakamura, 1935	PO
Lamniformes	Elasmobranchii	Lamnidae	<i>Isurus</i>	<i>oxyrinchus</i>	Rafinesque, 1810	PO
Lamniformes	Elasmobranchii	Pseudocarchariidae	<i>Pseudocarcharias</i>	<i>kamoharai</i>	(Matsubara, 1936)	PO
Orectolobiformes	Elasmobranchii	Rhincodontidae	<i>Rhincodon</i>	<i>typus</i>	Smith, 1828	PO
Squaliformes	Elasmobranchii	Dalatiidae	<i>Isistius</i>	<i>brasiliensis</i>	(Quoy & Gaimard, 1824)	BP

Table 2. Number of marine species reportedly occurring in New Caledonia waters by higher taxa and geometric mean depth (m) available in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). There are over 6,500 species reported for New Caledonia, i.e., 34% finfishes, 23% crustaceans (mostly decapods), 17% mollusks, 9% cnidarians (mostly corals), 2% chordates, and the rest being other groups dominated by echinoderms and algae. This account is in no way complete, however, as recent expeditions are continuously identifying species new to science from the region. A list of the more than 13,000 published sources used to assign species to New Caledonia can be obtained from the FishBase and SeaLifeBase online search pages.

Geometric mean depth (m)	100	200	1000	4000	6000	Subtotal
Marine mammals	19	1	3	1		24
Seabirds	52					52
Reptiles	19					19
Bony fishes	1817	91	287	47		2242
Sharks and rays	47	5	22	2		76
Crustaceans	815	108	522	77		1522
Mollusks	929	52	161	22	1	1143
Echinoderms	223	6	18	4		251
Corals	468	8	79	3		558
Other inverts	424	27	137	43		631

Table 3. Number of species by taxa and island groups available from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). New Caledonia species accounts are compared with available estimates from published literature of similar islands in the same broad biogeographic region, the Kermadecs has the highest number of reported endemic species, followed by New Caledonia. (Nat = Native, End = Endemic).

Taxon	Easter Is		Pitcairn Is		Kermadec Is		French Poly		Palau		New Caled		New Caledonia species from literature and online sources
	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	Nat	End	
Arthropoda	222	4	50	2	273	29	1108	5	283	3	2362	21	2043 [Payri, et al. (2007)].
Brachiopoda			1		1		9		3		17		4 [Payri, et al. (2007)].
Bryozoa	2				200	2	1		2		34		407 [Payri, et al. (2007)].
Chaetognatha							4		4		6		-
Chordata	51		58		64		165		186		407	1	389 [Payri, et al. (2007)].
Ascidacea					4		84		126		302		290 [Payri, et al. (2007)].
Appendicularia											4		-
Aves	31		35		47		56		28		52		55 [Payri, et al. (2007)].
Mammalia	15		21		9		22		23		27		25 [Payri, et al. (2007)].
Sea turtles	4		2		3		3		4		5		4 [Payri, et al. (2007)].
Sea snakes	1				1				2		15	1	15 [Payri, et al. (2007)].
Crocodyles									1				-
Cnidaria	60	1	89		56	1	184	1	489	16	871		784 [Payri, et al. (2007)].
Porifera	19		8		27		17		88		246	10	149 [Payri, et al. (2007)].
Echinodermata	28	1	56		92	26	33		160		358	1	257 [Payri, et al. (2007)].
Foraminifera	30		8		10	2	1		11		424		585 [Payri, et al. (2007)].
Mollusca	221	16	294		452	50	967	6	662	1	1767	2	2151 [Payri, et al. (2007)].
Marine worms											357		416 [Payri, et al. (2007)].
Annelida	43				27		6		23		264		-
Echiura											1		-
Platyhelminthes									19		70		-
Nematoda											8		-
Sipuncula					5		7		3		2		-
Phoronida											5		4 [Payri, et al. (2007)].
Kinorhyncha											3		-
Hemichordata											3		-
Sagenista					1				4		1		-
Nemertea	1												-
Rotifera	1												-
Gastrotricha							1						-
Gnathostomulida							9						-

Table 3. (Continued) Number of species by taxa and island groups available from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). New Caledonia species accounts are compared with available estimates from published literature of similar islands in the same broad biogeographic region, the Kermadecs has the highest number of reported endemic species, followed by New Caledonia. (Nat = Native, End = Endemic).

Algae													443 [Payri, et al. (2007)].
Dinophyta							4		1				-
Ochrophyta	24	3	2		12		4		26		5		-
Chlorophyta	31		1		13		17		82		11		-
Rhodophyta	61	6			19		13		96		1		-
Tracheophyta									7		1		-
Cyanobacteria	1						1		16				-
Placozoa									1				-
Not assigned (Plantae)											1		-
TOTAL non-fish	795	31	567	2	1252	110	2551	12	2166	20	6866	35	
Pisces from FishBase	193	12	346	2	242	6	892	12	1520	1	2348	5	

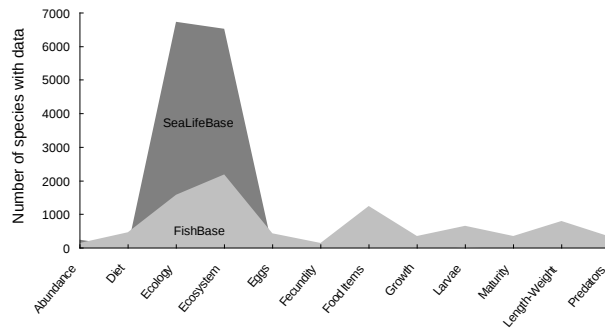
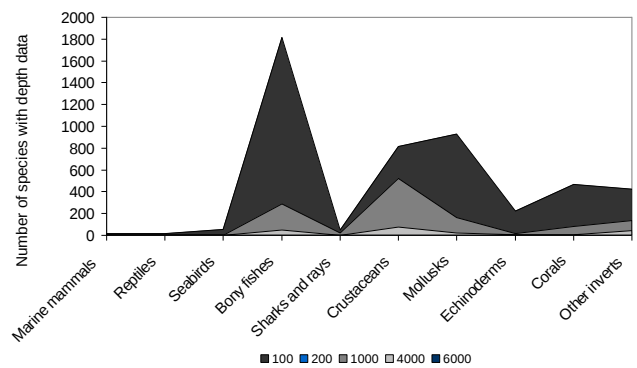
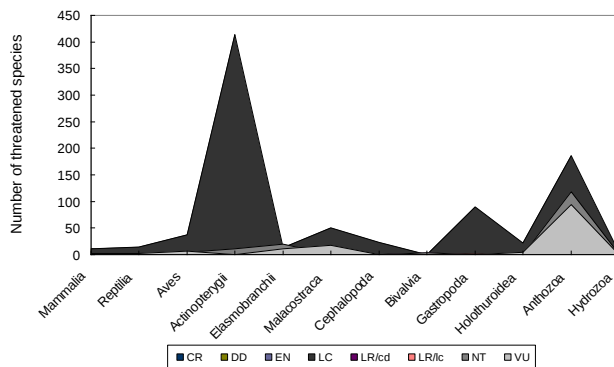
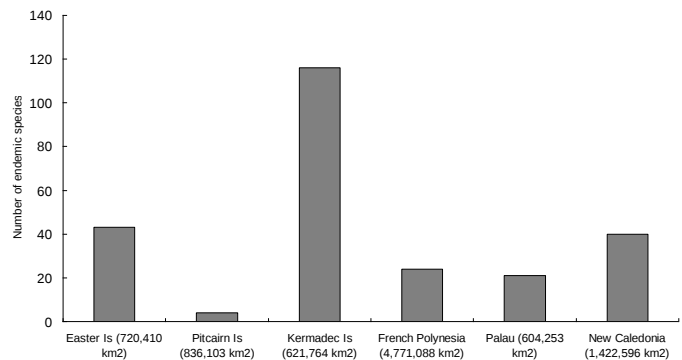
A**B****C****D**

Figure 1. Marine Biodiversity of New Caledonia and other Pacific region; **A:** Data currently available in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) for over 9,200 marine species occurring in New Caledonia based on about 13,300 published sources.; **B:** Number of species by taxa by depth for over 6,500 species with depth data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org); **C:** The threatened species (according to the IUCN version of 2015) occurring in French Polynesia make up more almost 14% of the over 9,200 species gathered for this study in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). Fishes, sharks and rays make up half of this, and the other half is dominated by corals, decapods, cephalopods, gastropods, seabirds and marine mammal; **D:** Number of endemic species by country with more or less the same EEZ area in the Pacific region.

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PEOPLE MATTER(S)

PROFESSOR GOTTHILF HEMPEL'S 90TH BIRTHDAY*

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Abstract

This brief contribution presents an English translation followed by the original German text of the short speech given by the author on behalf of the graduate students of Professor Dr. Gotthilf Hempel on April 4, 2019, at the celebration of his 90th birthday in Bremen's City Hall. A list of the doctoral theses supervised by Professor Hempel is appended.

Introduction

On April 4, 2019, an event was held in Bremen's City Hall to celebrate the 90th birthday of Professor Gotthilf Hempel (https://en.wikipedia.org/wiki/Gotthilf_Hempel; Figure 1).

This contribution presents the short speech the author gave on behalf of Professor Hempel's many graduate students (Figure 2; also see Appendix), first in an English translation, then in the original German.

English translation

Ladies and Gentlemen:

In addition to science and institute-building, Professor Hempel has had many students. There have been some 70 doctoral students and uncounted MSc students. That's a whole lot. I am here to speak on their behalf. Although I am now an old man, I was young once, and Professor Hempel was both my MSc and doctoral supervisor.



Figure 1. Professor Gotthilf Hempel with one of his former doctoral students, Dr. Cornelia Nauen (Photo: David Grémillet)

I asked some of my former classmates about their experiences with Professor Hempel and each shared with me a different story. And then, I understood: Professor Hempel, my supervisor, was like my mother (I have seven siblings in France): she gave each one of us a different part of her person, depending on who we were and what we needed.

And so, it was with Professor Hempel: He gave us each what corresponded to us and what we needed.

For my part, I needed a way out of Europe. And so, Professor Hempel asked his colleagues in Africa if they would take on one of his students. This is how I came to spend my fourth semester in Ghana, where I was able to do the fieldwork for my MSc before I had the equivalent of a Bachelor's degree.

I started writing scientific articles rather early on – and many of these papers ended up in the *Berichte der Wissenschaftlichen Kommission für Meereskunde*, of which he was the editor.

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After I graduated, Professor Hempel even smuggled me into the then GTZ, now GIZ, although even then I did not exactly fit the image of a German development expert.

And when things went wrong in Indonesia, he came to Jakarta to find what was going on. My boss there came drunk to the meeting, which made it possible to resolve the misunderstanding, and enabled me to start my doctoral studies.

Here again, I received Professor Hempel's full support, although what I wrote in my dissertation was quite heavy and remains controversial even now.

It's been 40 years - and we've managed to stay in touch and help each other. For example, if he is still producing a book, I am ordered to write a chapter. Of course, I do that (Figure 3).

And when I turned 60 and my friends made a celebration of it, Professor Hempel came 'all the way' to Vancouver, Canada, where I now live and work.

So, it was clear that I would come here to thank you, Professor Hempel, for your dedication to all your students, and express my thanks for all that you have done for me.

Deutsche Originalfassung

Meine Damen und Herren,
Neben Wissenschaft und Institutsgründungen, hat Professor Hempel viele Studenten betreut. Etwa 70 Doktoranden waren es, und ungezählte Diplomanden. Das ist eine ganze Menge. Ich soll sie hier vertreten: zwar bin ich jetzt auch ein alter Mann; aber ich war mal jung, und Professor Hempel war mein Diplom- und Doktorvater.

Ich habe einige meiner damaligen Mitstudenten gefragt, und alle gaben mir verschiedene Geschichten. Und da verstand ich: Professor Hempel, mein Doktorvater war wie meine Mutter (ich habe 7 Geschwister in Frankreich): Sie gab jeder und jedem von uns einen anderen Teil ihrer Person, je danach was wir waren und brauchten.

Und so war es mit Professor Hempel: es gab jedem von uns das was uns entsprach und wir brauchten.

Für meinen Teil brauchte ich ein Weg aus Europa. So fragte Professor Hempel seine Kollegen in Afrika ob sie einen seiner Studenten aufnehmen würden – und so kam in meinem vierten Studiensemester nach Ghana, wo ich die Feldarbeit für mein Diplom machen konnte bevor ich ein Vordiplom hatte.

Ich fing ziemlich früh an, wissenschaftliche Artikel zu schreiben, und so landeten mehrere meiner Aufsätze in die Berichte der Wissenschaftlichen Kommission für Meereskunde, von denen er der Herausgeber war.

Als ich mein Diplom hatte, hat Professor Hempel mich sogar in die damalige GTZ, jetzt GIZ, hineingeschmuggelt, obwohl ich schon damals dem Bilde eines deutschen Entwicklungshelfers nicht gerade entsprach.



Figure 2. Daniel Pauly thanking Professor Hempel on April 4, 2019, Bremen City Hall.

Und als einiges in Indonesien schief ging, kam er nach Jakarta um zu finden was geschehen war. Mein Chef dort kam betrunken zu dem Treffen, was es möglich machte, das Misverständnis zu lösen, und es mir ermöglichte, meine Doktorarbeit anzufangen.

Hier wieder bekam ich Professor Hempel's volle Unterstützung, obwohl das, was ich in meiner Doktorarbeit schrieb, ziemlich starker Tobak was, und jetzt immer noch umstritten ist.

Vierzig Jahre ist es her – und wir haben es fertig gebracht, in Kontakt zu bleiben, und uns gegenseitig zu helfen. Zum Beispiel, wenn er ein Buch produziert, werde ich noch beordert ein Kapitel zu schreiben. Selbstverständlich tue ich das.

Und als ich 60 Jahre alt wurde, und mein Freunde einer Feier daraus machten, kam Professor Hempel "all the way" nach Vancouver, Kanada, wo ich jetzt lebe und arbeite.

So war es klar dass ich hier kommen würde um Ihnen, Professor Hempel, meinen Dank für Ihr Engagement für alle Ihre Studenten auszusprechen, sowie mein Dank für alles das was Sie für mich getan haben.

Appendix

Doctoral theses supervised by Professor Hempel. (Courtesy of Dr. Werner Ekau, Leibniz-Zentrum für Marine Tropenforschung, University of Bremen), by completion year (1969 to 1993).¹

1969

- Hartmann, J.: Verteilung und Nahrung des Ichthyoneustons im subtropischen Nordostatlantik. Diss., Univ. Kiel, 189 S.
 Rosenthal, H.: Schwimmleistung und Nahrungssuche bei den Larven des Herings *Clupea harengus* L. Diss., Univ. Hamburg, 127 S.
 Stehmann, M.: Vergleichend morphologische und anatomische Untersuchungen zur Systematik der nordeuropäischen Rochen der Familie Rajidae. Diss., Univ. Kiel, 193 S.

1970

- Arntz, W. E.: Das Makrobenthos der Kieler Bucht im Jahr 1968 und seine Ausnutzung durch die Kliesche (*Limanda limanda* L.). Diss., Univ. Kiel, 167 S.
 Schopka, S. A.: Vergleichende Untersuchungen zur Reproduktivität am Hering (*Clupea harengus* L.), Kabeljau (*Gadus morhua* L.) und Seehasen (*Cyclopterus lumpus* L.) in NO-Atlantischen Gewässern. Diss., Univ. Kiel, 134 S.
 Weikert, H.: Verteilung und Tagesperiodik des Evertabratenneuston im subtropischen Nordostatlantik. Diss., Univ. Kiel, 170 S.

1971

- Ehlebracht, J.: Stoffliche Veränderungen während des Reifezyklus' in Ovarien von Herbst- und Frühjahrsheringen (*Clupea harengus* L.) der westlichen Ostsee. Diss., Univ. Kiel, 109 S.
 Schnack, D.: Vergleichende Untersuchungen zur Nahrungsökologie von Heringslarven. Diss., Univ. Kiel, 124 S. 1972.
 Ali Khan, J.: Distribution and abundance of fish larvae in the Gulf of Aden and in the waters off the coast of W. Pakistan in relation to the environment. Diss., Univ. Kiel, 191 S.

¹ This list may be incomplete, and omits the many 'Diplom' theses (equivalent to MSc theses), for example the author's 'Diplom' thesis, Pauly, D. 1973. Ökologische und fischereiliche Untersuchung einer kleinen west-afrikanischen Lagune [Investigations on the ecology and fishery of a small West African Lagoon; in German, with English summary], Diplomarbeit, Kiel University, 89 p.



Figure 3. One of many books edited by G. Hempel, and in which he got the author to participate.

- Grosch, U. A.: Die Abwasserbelastung der Untertrave in den Jahren 1968, 1969 und der Einfluss der Abwässer auf das Makrobenthos des Aestuars. Diss., Univ. Kiel, 153 S.
- Kühnhold, W. W.: Untersuchungen über die Toxizität von Rohölextrakten und -emulsionen auf Eier und Larven von Dorsch und Hering. Diss., Univ. Kiel, 174 S.
- Pommeranz, T.: Der Einfluß von Wellenschlag und Licht auf die Eier der Scholle *Pleuronectes platessa* L. Diss., Univ. Kiel, 152 S.
- 1974**
- Boysen, H. o.: Quantitative Untersuchungen am Hyperbenthos der Kieler Bucht. Diss., Univ. Kiel, 205 S.
- Ehrich, S.: Die Fische der Großen Meteorbank. Eine Untersuchung des Biotops Große Meteorbank aus ichthyologischer Sicht. Diss., Univ. Kiel, 213 S.
- Link, G.: Untersuchungen über Chemismus und Zooplankton der Untereider. Diss., Univ. Kiel, 150 S.
- 1975**
- John, H.-Ch.: Untersuchungen am oberflächennahen Ichthyoplankton des mittleren und südlichen Atlantischen Ozeans. Diss., Univ. Kiel, 186 S.
- Möller, H.: Der Einfluß von Temperatur und Salzgehalt auf Entwicklung und Verbreitung von Fischparasiten. Diss., Univ. Kiel, 108 S.
- Wörner, F.: Untersuchungen an drei Myctophidenarten *Benthosema glaciale* (Reinhardt, 1837) *Ceratoscopelus maderensis* (Lowe, 1839) und *Myctophum (M.) punctatum* Rafinesque, 1810 aus dem Nordwestafrikanischen Auftriebsgebiet im Frühjahr 1972. Diss., Univ. Kiel, 136 S.
- 1976**
- Inyang, M.: A study of the Baltic palaemonid shrimp, *Palaemon adspersus* var. *fabricii* (Rathke) in Kiel Bay. Diss., Univ. Kiel 113 S.
- 1977**
- Schulze-Wiehenbrauck, H.: Laborversuche über den Einfluss von Besatzdichte und Wasserbelastung auf *Tilapia zillii* und *Cyprinus carpio* (Pisces). Diss., Univ. Kiel, 135 S.
- 1978**
- Nauen, C. E.: Populationsdynamik und Ökologie des Seesterns *Asterias rubens* L. in der Kieler Bucht. Diss., Univ. Kiel, 216 S.
- 1979**
- Alheit, J.: Die Stellung der Fische im Ökosystem einer subtropischen Lagune Bermudas. Diss., Univ. Kiel, 136 S.
- Kils, U.: Schwimmverhalten, Schwimmleistung und Energiebilanz des antarktischen Krills, *Euphausia superba*. Diss., Univ. Kiel, 71 S.
- Palsson, O. K.: Zur Biologie juveniler Gadiden (Gruppen Oll) in isländischen Gewässern. Diss., Univ. Kiel, 74 S.
- Pauly, D.: Gill size and temperature as governing factors in fish growth: A generalization of Bertalanffy's growth formula. Diss., Univ. Kiel, 156 S.
- 1980**
- Damm, U.: Langfristige Veränderungen in der Verbreitung von Nordseefischen, untersucht durch Korrelations- und Varianzanalyse. Diss., Univ. Kiel, 145 S.
- Kock, K.- H.: Fischereibiologische Untersuchungen an drei antarktischen Fischarten: *Champscephalus gunnari* Lönnberg, 1905, *Chaenocephalus aceratus* (Lönnberg, 1906) und *Pseudochaenichthys georgianus* Norman, 1937 (Notothenioidei, Channichthyidae). Diss., Univ. Kiel, 218 S.
- Nieland, H.: Die Nahrung von Sardinen (*Sardina pilchardus* Walbaum), Sardinellen (*Sardinella aurita* Valenciennes; *Sardinella eba* Valenciennes) und Maifischen (*Ethmalosa fimbriata* Bowdich) vor der Westküste Mrikas. Diss., Univ. Kiel, 137 S.
- Rau, N.: Hydrography and biological properties, and the fishery in the harbor area of Cebu City, Philippines. Diss., Univ. Kiel, 107 S.
- Rumohr, H.: Der „Benthosgarten“ in der Kieler Bucht. Experimente zur Bodentierökologie. Diss., Univ. Kiel, 195 S.
- Wosnitza-Mendo Aguilar, C. (1980): Zur Populationsdynamik und Ökologie von *Tilapia rendalli* (Blgr.) im Lago Sauce (Peru). Diss., Univ. Kiel, 147 S.
- 1981**
- Schöfer, W.: Untersuchungen über den Einfluss von Petrolkohlenwasserstoffen (Öl) auf die Fortpflanzung von Fischen. Diss., Univ. Kiel, 87 S.
- 1982**
- Hubold, G.: Zur Laichökologie der südwestatlantischen Sardelle *Engraulis anchoita* (Hubbs und Marini, 1935). Diss., Univ. Kiel, 161 S.
- Nawa, I.: An ecological study of the Cross River estuary. Diss., Univ. Kiel, 163 S.

1983

- Bußmann, B.: Untersuchungen zur Bestandstrennung beim Blauen Wittling (*Micromesistius poutassou*, Risso 1810) im Nordost-Atlantik. Diss., Univ. Kiel, 121 S.
- Klages, N.: Der nordische Krill *Meganyctiphanes norvegica* (M. Sars) - Nahrung und ernährungsethologische Aspekte. Diss., Univ. Kiel, 104 S.
- Lopes, P.: Distribution and abundance of ichthyoplankton in the upper 250 m of the equatorial central Atlantic. Diss., Univ. Kiel, 132 S.
- Macias, E.: Study on the migration of postlarval shrimp of the genus *Penaeus*, from the Pacific Ocean to the lagoon complex Caimanero-Huizache, State of Sinaloa, Mexico. Diss., Univ. Kiel, 87 S.
- Reck, G.: The coastal fisheries in the Galapagos Islands, Ecuador. Description and consequences for management in the context of marine environmental protection and regional development. Diss., Univ. Kiel, 231 S.

1985

- Kellermann, A.: Zur Biologie der Jugendstadien der Notothenioidei (Pisces) an der Antarktischen Halbinsel. Diss., Univ. Kiel, 228 S.
- Marschall, H.-P.: Untersuchungen zur Funktionsmorphologie und Nahrungsaufnahme der Larven des Antarktischen Krills, *Euphausia superba* Dana. Diss., Univ. Kiel, 99 S.
- Wolff, M.: Fischerei, Ökologie und Populationsdynamik der Pilgermuschel *Argopecten purpuratus* (L.) im Fischereigebiet von Pisco (Peru) unter dem Einfluß des El Niño 1982/83. Diss., Univ. Kiel, 113 S.
- Zarkeschwari, N.: Fische als Fischräuber, dargestellt an der Nahrung demersaler Fische der Nordsee. Diss., Univ. Kiel, 141 S.

1986

- Boysen-Ennen, E. (1986): Zur Verbreitung von Gemeinschaften des Meso- und Makrozooplanktons im sommerlichen Oberflächenwasser der Weddell See (Antarktis). Diss., Univ. Kiel, 171 S.
- Reinke, M.: Zur Bewegungs- und Nahrungsphysiologie der Tunikaten *Salpa thompsoni* (Antarktis) und *Salpa fusiformis* (Mittelmeer). Diss., Univ. Kiel, 152 S.
- Siegel, V.: Untersuchungen zur Biologie des antarktischen Krills, *Euphausia superba*, im Bereich der Bransfield Straße und angrenzender Gebiete. Diss., Univ. Hamburg, 237 S.

1987

- Gutt, J.: Zur Verbreitung und Ökologie der Seegurken (Holothuroidea, Echinodermata) in der Weddell See (Antarktis). Diss., Univ. Kiel, 175 S.
- Lohmeyer, U.: Bestandskundliche Untersuchungen der Bodenfische des östlichen Indischen Ozeans im vorgelagerten Schelf der Inseln Sumatra, Java und Bali. Diss., Univ. Kiel, 138 S.
- Piatkowski, U.: Zoogeographische Untersuchungen und Gemeinschaftsanalysen am epipelagischen Makroplankton im Bereich der Antarktischen Halbinsel und der Weddell See. Diss., Univ. Kiel, 197 S.
- Schwarzbach, W.: Die Fischfauna der östlichen und südlichen Weddell-See: Geographische Verbreitung, Nahrung und trophische Stellung der Fischarten. Diss., Univ. Kiel, 137 S.
- Voß, J.: Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos der Weddellsee. Diss., Univ. Kiel, 189 S.

1988

- Ekau, W.: Ökomorphologie nototheniider Fische aus dem Weddellmeer, Antarktis. Diss., Univ. Kiel, 189 S.
- Hagen, W.: Zur Bedeutung der Lipide im antarktischen Zooplankton. Diss., Univ. Kiel, 169 S.
- Piepenburg, O.: Zur Zusammensetzung der Bodenfauna in der westlichen Framstraße. Diss., Univ. Kiel, 152 S.

1989

- Diel, S.: Zur Lebensgeschichte dominanter Copepodenarten (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*) in der Framstraße. Diss., Univ. Kiel, 149 S.

1990

- Mumm, N.: Zur sommerlichen Verteilung des Mesozooplanktons im Nansen Becken, Nordpolarmeer. Diss., Univ. Kiel, 216 S.

1991

- Kunzmann, A.: Blood physiology and ecological consequences in Weddell Sea fishes (Antarctica). Diss., Univ. Kiel, 79 S.

1992

- Wöhrmann, A.P.A.: Gefrierschutz bei Fischen der Polarmeere. Diss., Univ. Kiel, 94 S.

1993

- Dorrien, C. F. von: Zur Ökologie und Respiration einiger arktischer Bodenfische. Diss., Univ. Kiel, 101 S.
- Kurbjewit, F.: Reproduktion und Lebenszyklen dominanter Copepodenarten aus dem Weddellmeer (Antarktis). Diss., Univ. Bremen, 236 S.

MARINE BIODIVERSITY: A HUMANIST PERSPECTIVE*

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Abstract

This contribution is based on an invited talk given to the Royal Society of Canada in Victoria on November 26, 2015, as part of their symposium on *Marine Biodiversity: Indispensable Resources, Unprecedented Opportunities*. It offers a humanist perception on the importance of marine biodiversity for society.

Introduction

Glory be to God for dappled things
For skies of couple-colour as a brindled cow;
For rose-moles all in stipple upon trout that swim...
All things counter, original, spare, strange;
Whatever is fickle, freckled (who knows how?)...

That is a part of Hopkins' paean to biodiversity in all its mystery. We know biodiversity is important, and we know bits of why, but not everything. Today, as humanist and geographer, I am going to focus on three people-parts of the complex issues around marine biodiversity: (1) why it should matter to people, (2) what the arts have to teach us, and (3) society and marine biodiversity.

Why biodiversity should matter to people

The sea and those fishing communities that dwell upon its shores are a very precious part of our world, our history and, it would follow, our psyche. There is something fascinating about the sea - we go and sit beside it on holiday, some of us as eco-tourists, some to fish for recreation; some of us paddled as children in rock pools in the inter-tidal zone, and became ecologists or marine biologists when we grew up - or poets, or philosophers. In the Christian Bible, the waters are among the very first things that God creates, separating land and sea and creating the shore. Many other belief systems (including natural science in its evolutionary mode) speak with reverence of the ocean as progenitor of humanity in some way or another.

In all those ways, and more, the ocean is fundamental to life on this planet, but its marine life is being hugely exploited and its biodiversity wantonly damaged by us. This is happening without enough understanding of the long-term consequences of our actions. So, we ended up recently missing the beautiful sea stars of this coast, grieving the beached dead humpback caught in fishing nets, or the cry of the seagull as one nears the harbour.

Such damage did not, of course, happen overnight. There has been a long war between certain kinds of economies and marine diversity. European explorers brought environmental depredation with them to North America. Indeed, when John Cabot returned from his 'discovery' of Newfoundland, he reported that the fish on the Grand Banks were so thick in the water, one could have walked on them... and thus started the attack on the Grand Banks marine ecosystem that has resulted in the commercial extinction today of cod, flounder, Greenland

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halibut, and redfish. One scholar commented of America that “to those, / who followed Columbus / ...the New World seemed incredible / because of the natural endowments.... / The men of Henry Hudson’s *Half Moon* were temporarily disarmed / by the fragrance of the New Jersey shore, / while ships running farther up the coast / occasionally swam through large beds of floating flowers /.... Had they been other than they were / they might have written a new mythology here. / As it was / they took inventory”/.

At root, this kind of attitude stems from the old perception that we are somehow outside of nature, with ‘dominion’ over it. The ocean in this view of things provides us with ‘ecosystem services’ – its purpose is to service the wants (not needs – *wants*) of humankind. That kind of utilitarian thinking fails to consider more complex and nuanced ways of thinking about oceans and their biodiversity - thinking that takes into account a wider human picture.

Issues of food security (being sure people have enough to eat) are vital; so is environmental integrity – because without it, our foodstuffs by land and seas become threatened and we become food insecure. The philosopher John Locke thought the deep to really be as boundless as the poets call it: but now we know better, for its fish are dying, its waters polluted, its beauty despoiled, and its coastal settlements in crisis. With the disruption of marine food webs that is currently underway, there is a sense in which marine creatures are also becoming food insecure. For their sake and ours, then, it has become urgent that we try to understand how biodiversity in our oceans functions – and how healthy it is. Oceans are, after all, a key part of the biosphere that sustains us and every other living thing on this planet, without which none of us can survive.

Our environment, including all those wonderful marine creatures, has evolved over time to generate biodiversity that is the best guarantee against uncertain conditions. Where adaptation has been insufficient, species have died out: variation is fundamental to flexibility and hence to successful adaptation. That is a demonstration lesson in sustainability for humans also. The warning signs that things may be amiss are always felt first at the local scale – by people who notice that the herring spawn on kelp is very scarce this year, by fishers who see fewer fish species and smaller fish in their nets, by tourist operators who worry that the Great Barrier Reef is dying, by people round the shores of the Indian Ocean who know that there are fewer fish and fewer kinds of fish, because the mangrove swamps have been destroyed and the spawning habitat for several species have disappeared with them.

The importance of the sea as reflected in poetry, art and theatre

Those who live from the sea rely on its biodiversity for foodstuffs and employment, but people don’t just use the ocean, economically speaking. We don’t just ‘take inventory’. We sing songs about the sea and its shores, in many languages, and we write poetry and novels about it and its importance for human beings. Listen:

“... the sea is all about us;
The sea is the land’s edge also, the granite
Into which it reaches, the beaches where it tosses
Its hints of earlier and other creation:
The starfish, the horseshoe crab, the whale’s backbone...
It tosses up our losses, the torn seine,
The shattered lobsterpot, the broken oar
And the gear of foreign dead men. The sea has many voices,
Many gods and many voices.”

(T.S. Eliot: “The Dry Salvages”).

Those voices are social, historical, cultural, spiritual and psychological, not just geo-bio-chemical and economic, and they are important. We are fascinated by the deep waters of the oceans of this, the blue planet. Musicians know it and show it through for example:

Sibelius Symphonies, especially 1 and 2 or Mendelssohn's "Fingal's Cave"; folk songs from all over the globe, like "Caller Herrin" or "Farewell tae Tarwathie" (whales) or "Let me Fish off Cape St Mary's" (cod and capelin); or pop music such as "La mer" or even Ringo Starr's "Octopus' Garden".

Playwrights know it:

Full fathom five my father lies
Of his bones are corals made
Those are pearls that were his eyes
Nothing of him that remains
But hath suffered a sea change
Into something rich and strange...

Marine biodiversity is exactly that.

Maritime First Nations know this. They have a rich cultural history, spirituality and resource use practice that cannot be pulled apart, but is truly holistic. The B.C. First Nations' Nlhakap'amu story of the Old One reminds them that the creator (however you or I might wish to understand that word) caused "all kinds of birds and fish to appear, to which he gave names, and ascribed to them certain positions and functions". And he said to the people "Where you see fish jump, there you will find water to drink ... It will quench your thirst, and keep you alive".

There it is, in a nutshell: biodiversity, food security and thus the need for careful stewardship. We have a huge amount to learn from Aboriginal peoples in terms of understanding how to behave inside nature, as stewards, not just top predators.

Society and marine biodiversity

As a society, it is important that we look at the linkages between marine creatures in all their complexity and ourselves in all our complexity, and see their wellbeing as our responsibility. To do that, we need to identify the underlying *values* in the choices we have made about managing various parts of the environment, including fisheries, over time and through a variety of institutions ranging from community to nation (and, by implication, beyond). All the time we need to hold in mind our status as top predator, a status that has become increasingly powerful over time, as technological inventions and innovations have rendered us more and more capable of ecosystem destruction.

At issue here is the health of natural resources, human communities, cultures and ways of life. We need to be aware of ecosystem justice, to recognise that -- while we have the right to use our environment as a necessary resource for our survival as a species -- we must also accept the concurrent responsibility to not abuse that right by taking more than we need and more than an ecosystem can sustain without undue damage. A similar logic holds for marketplace activity — businesses have a right to maintain themselves as viable entities... but not if that destroys the rights of communities of local people and local resources, by inflicting such environmental damage that marine biodiversity becomes endangered.

Responsible behaviour that protects marine biodiversity is enshrined in the UN's "precautionary principle", a cautious approach that advocates behaving in the way *least* likely to cause damage, even if that means doing less

than we might, because we know we are dealing with situations where our knowledge is inadequate and our understanding therefore quite uncertain and far from perfect.

The difficulties lie, not in establishing such a principle (the United Nations has already done this), but in interpreting and applying it *justly* and, in terms of our focus here today, in a way that protects biodiversity. We need some humility here and to humility, I would add Kant's ethical imperative, which reminds us that it is *not* enough merely to avoid the misuse of others because that still leaves us thinking it is okay to use them as instruments toward the satisfactions of our own desires, wants, needs.

The ethics involved are indeed complicated, as we found out when preparing the book, published in 2000, that considered ethics and fisheries management in Canada. We called it *Just Fish* (Coward, Ommer and Pitcher 2000). It was the first publication to look at this issue, and it involved fishers, academics, First Nations, and others. It spoke about the fairness (or otherwise) of the distribution of wealth from our exploitation of the environment, and the fairness (or otherwise) of our management regulations, which should allow ordered (not disordered, or out of balance) harvesting of its wealth.

It is not easy to convince governments, firms, and powerful people to restore damaged parts of the various ecosystems that are involved. Nor is it easy to be *creative and fair* about the ways in which we do, or could, share our knowledge about these natural systems. But this is what ecosystem justice is all about - the idea that an ecosystem represents a community of inter-dependent members, who all have a legitimate dependency on the smooth functioning of the system. It recognizes - for example - marine fisheries as being prosecuted by humans within the bounds of an understanding of the sea and all its creatures and their habitats as a fragile, interdependent, finite system.

The UN Millennium Assessment's authors know the importance of this marine biodiversity. Our politicians and others need to know it too. It would help if they, and we, understand that we don't have all the answers but:

- One of the most important considerations in thinking about human food security is the health of marine ecosystems – for which biodiversity is essential;
- We have the right to use our oceans as a necessary resource; the concurrent responsibility is that we not abuse that right by taking more than we need;
- Who 'we' are here is a tricky problem, and one that has to be faced. Whose food base are we responsible for? Local coastal peoples? The metropolitan and inland populations of the country? Hungry people in the developing world?
- What 'need' is, is also problematic: Is it the need of a large firm to survive and to make profits, thereby keeping local people employed? Is it the need of a small firm to do that, thereby keeping employment and possibly also local capital functioning? Are the two antithetical?

Moreover, communities which have survived in a particular place for a substantial period of time, which have a set of established customary rights to resources in that place, have the right to continued survival ... If that survival is not threatened by natural alterations driven by climate change and ocean acidification in the environment (what we might call an 'act of God and society') leading to collapsed coral reefs or coastlines damaged by storm surges and other such 'natural disasters' resulting in a concomitant serious loss of marine biodiversity.

Because the world is uncertain, we need some version of the precautionary principle to guide our behaviour. Science is essential but it cannot tell us all we need to know about the world and its complexities and variabilities. That is where those who are most dependent on a particular local healthy ecosystem can help, and will do the best job of taking care of it. People whose lives depend on coastal resources are the best people to

protect our coasts. Of course, they need guidance and specialist knowledge from government agencies and others, but that should be taken in combination with their own detailed understanding of their own particular part of the coastal ecosystem. They are (we need to remember) invested in the local in a way that the blue-water footloose fleets of industrial nations are not. The principle of adjacency and that of 'precaution' need to be fundamental to resource management policy.

Some implications of what I have been saying

We need, then, the kind of compelling insight into the future of our societal delusions about 'nature as merely resource'. Promoting marine biodiversity as an essential part of the survival of us in our planetary home is one of the things the humanities can provide. We can touch hearts and minds, on canvas, on stage, through film, stories, books, and poetry. Cross-discipline metaphors are very rich. Think of marine food security – that's biodiversity in action. Think of cultural keystone species – what cod means to Newfoundlanders; salmon to BC First Nations; buffalo to the Cree; caribou to the Inuit. Think about cultural diversity and other hybrids like it, because that is a kind of ideas diversity – and the richer the diversity, the more inherent integrity the knowledge system possesses. And that will help us explain - to politicians, managers, and non-coastal folk - why marine diversity is so important to marine life, to cultural life, to society, and to this planet.

The truth -- as some few people have argued passionately for decades – is that we all – in the humanities, social sciences, marine sciences, and local experts - need to come together to effectively generate such attitude change. Only this can we save our oceans and marine life in all its diversity.

Anne Michaels once described history as a kind of slow cataclysm. She warned that it “stalks before it strikes”. This is especially true of the recent history of marine biodiversity. Evolutionary and biological processes are slow: Species shrink, fade, become endangered...and then - unless COSEWIC and other initiatives can protect them - become extinct. But these and their habitats are things we cannot afford to lose. They embody so much of complexity and flexibility – they are a metaphor for resilience and adaptive innovation. In an age of increasing uncertainty, they provide us with a lesson we cannot afford either to ignore or to destroy.

Tides rise and fall ... but tidal waves wash out our villages and shorelines; waters warm ... and grow cooler, and that affects both the fish and other living things in the ocean and, in turn, affects us. As stewards of this planet's marine life, we would do well to remember the wisdom of Cormac McCarthy:

“This is the hard lesson. Nothing can be dispensed with. Nothing despised. Because the seams are hid from us, you see. The joinery. The way in which the world is made. We have no way to know what could be taken away. What omitted. We have no way to tell what might stand [...] and what might fall.”

(McCarthy: *The Crossing*, p. 143)

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WHEN IS FISHERIES MANAGEMENT NEEDED?*

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Abstract

Following a brief review of the global fisheries crisis, a medical concept - triage - is used to distinguish three, admittedly idealized, types of fisheries, i.e., those that are (a) autonomous and healthy, and thus may not require external management inputs; (b) those affected by problem resolvable by traditional fisheries management approaches; and, (c) those that are impacted by socioeconomic ills of a magnitude beyond that which can be addressed by fisheries management alone.

It is suggested that resources available for fisheries management (*sensu stricto*) should be devoted primarily to the fisheries in (b). A few ideas - some perhaps new, most recycled - are then presented on how new “governance” arrangements may lead to (the re-establishment of) sustained resource utilization in areas with fisheries such as in (c), even where there is no official capacity to formulate and/or enforce fisheries regulations.

Introduction

Given the sorry state of the world’s fisheries (Garcia and Newton 1997), and their even gloomier prospects if business continues as usual, no one will contest the need to rethink the way fisheries are managed. They are many calls for this (e.g., Christy 1993; Beddington 1995). Indeed, we might have to rethink the way we think about management including perhaps the way we define it.

The literature contains many definitions of fisheries management. In spite of their differences, however, most share enough features to be put into two subsets, *viz.*

- (i) Fisheries management *sensu stricto* (s.s.), concerned mainly with stock assessment, i.e., with the biology of the stocks, the deployment of fishing gears and their interactions (see e.g., Smith 1994); and
- (ii) Fisheries management *sensu lato* (s.l.), concerned with the performance of the fisheries sector as a whole (Gulland 1981), and implying multidisciplinary studies linking biologists, economists, sociologists, and anthropologists.

For the purpose of this paper, however, multi-sectoral coastal area development planning is not considered to be “a part” of fisheries management, even in the widest sense. Rather, fisheries management s. l. may be an element of such planning if the local importance of fisheries warrants it (see below).

My personal area of expertise is the development of quantitative methods for the research in (i). Also, I have developed some concepts pertinent to the multidisciplinary research in (ii). On the other hand, my experience is much more limited with regard to multi-sectoral coastal planning and the reader is thus asked to view the suggestions below as no more than food for thought.

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Based on a presentation at the Joint FFA/SPC Workshop on the Management of South Pacific Inshore Fisheries, June 26-July 7, 1995, Nouméa, New Caledonia. Only four references then *in press* have been updated. Also, two superfluous figures were deleted.

In this spirit, I propose to follow through on the ramifications of a medical metaphor for fisheries management, which, - who knows - may end up being more useful as a background to our research and other work than the metaphor drawn from operations research that most fisheries practitioners appear to use (see Bradbury and Reichelt 1981). The latter, articulated in various contributions edited by Haley (1981), may be viewed as comparing the components of a fishery to the various components of a machine (or an industrial production process), the job of the manager then being to adjust the various rates (here: the application of fishing effort) linking the various components of the machine or production process.

As the title of this contribution implies, we should rethink the conditions under which (i.e., when) fisheries management (either s.s. or s.l.) is needed. The operations research metaphor does not help here, as it does not allow for fisheries systems to function as self-regulated entities, and thus for management to ever become superfluous.

A medical metaphor

In 1984, at a conference on multispecies fisheries, I had noted the analogy between fisheries scientists, whose advice is often not heeded, and the staff of a hospital that would diagnose diseases, but couldn't treat them (May 1984). I now present another medical metaphor in the hope that it may help us answer the question in the title of this contribution. The new metaphor is based on the experience of battlefield surgeons who, when faced with a large number of wounded and a shortage of time and other resources, put them (reluctantly, I'm sure) into three groups:

- i. those that will survive without immediate help;
- ii. those that require immediate help for survival;
- iii. those that will not survive, even if provided immediate help.

Medical attention is then devoted to group ii.

This concept of “triage” is the metaphor I propose to apply to fisheries, following the required adaptation to our purposes of the terms “survive” and “immediate help”.

Survival of a fishery should mean here I presume:

- a) the continued existence of the biological resource upon which the fishery relies; and
- b) the continued existence of the social organization that has evolved to exploit that resource.

In contemporary terms, the former implies the maintenance of local biodiversity, while the latter implies a social organization allowing for sustainable use of a natural resource, two themes to which we shall return below. Without both of these elements, a fishery - the locus of interaction between fishers and a resource - won't survive.

However, at the risk of displaying a biologist's bias, I would like to stress that a) and b) are not equivalent or symmetrical: a resource can continue to exist (as “latent” resource) if the fishers disappear, but the converse does not hold, and hence the primacy of conservation and maintenance of biodiversity when dealing with the sustainability, i.e. with the survival of fisheries.

The concept of “immediate help” is easy to conceive when it applies to battlefield surgeons, and consists of stanching blood losses, avoiding shock, etc. Its analogy, as far as fisheries management is concerned, presumably includes those measures that must be taken to prevent short-term collapse of fisheries, through:

- i. massive and rapid build-up of fishing effort, resulting in reduction of spawning biomasses and of biodiversity;

- ii. massive and rapid destruction of habitats, usually resulting in reduction of recruitment;
- iii. resource access conflicts among groups of fishers or between fishers and other coastal resource users, leading to (i) and/or (ii).

Let us now see if our new metaphor helps us find out when and/or where management is needed.

Fisheries that do not need immediate help

What conditions may occur in a fishery that would make it unnecessary for them to be “managed” (i.e., for an external agency to try to influence the way the resource is allocated and effort is deployed)? I should like to assume that such situations exist only when:

- i. catches are small relative to the size of the resources;
- ii. some natural refuge or an area deliberately left unfished exists which protects a significant fraction of the spawning stock; and
- iii. a framework exists for local expression and enforcement of resource access and gear deployment rules.

All three of these conditions appear necessary: high catches relative to the size of the resources will invariably lead to increasing recruitment fluctuations, and an erosion of the biodiversity of the resource, and thus increasingly strain a local management system. Also, fishers’ access to the entire spawning stock supporting a fishery will usually lead to this being gradually eroded, and recruitment affected. Finally, the absence of any management system (traditional or not), and of the constraints such system implies will unavoidably lead to relatively high, and eventually unsustainable catches. An example of this may be found in the outrageous *bêche-de-mer* fishery recently opened in the Galapagos Islands, and which promises to wreck much of their ecology by the time the resource is gone.

There appear to be many fisheries in the South Pacific region for which the above three conditions still apply, and which thus may not need to be managed. The challenge may indeed be, in such cases to keep “traditional” (i.e., local) management practice uncoded, so they can continue to evolve and adjust to new challenges and opportunities (K. Ruddle, National Museum of Ethnology, Osaka, Japan, pers. comm.).

Fisheries that require immediate help

Virtually all textbooks in fisheries science and management are written in developed countries, for developed-country students, scientists, or fisheries managers. Whether explicitly or not, these books all assume developed country infrastructures, both administrative and scientific, and industrial fisheries (with sometimes considerations of sports fishing).

The constraints, in tropical developing countries, to fisheries management systems such as described in these books are rarely mentioned, and their assimilation into a global view of fisheries management are presented is still pending (Pauly 1997). For example, quotas, either as free-for-all Total Allowable Catch (TAC) or as treasured Individual Transferable Quotas (ITQ), the state-of-the-art among developed-country fishery management tools (Pauly 1996), are useless when the administrative and scientific infrastructure does not allow for (at least nearly) real-time monitoring of catches and landings, i.e., in the small-scale fisheries of tropical developing countries (Munro 1980).

“Immediate help” to fisheries cannot thus be likened to the routine work of fisheries laboratories in developed countries, which largely consists of estimating next year's TACs or ITQs.

Rather, providing “immediate help” may consist of timely interventions, e.g.,

- Evaluating newly introduced gears, or of new fishing practices in view of their regulation;
- Evaluating the prospects for expansion of a fishery;
- Resolving acute access conflicts; or
- Providing the scientific basis for new fishery legislation.

Here, the idea is that a fishery management unit should not operate “tactically”, i.e., provide fleet-management inputs, or even annually-renewed management targets, but contribute “strategically” to a fishery’s long-term orientation. Thus, a managed fishery managed “strategically” should run largely on its own once it has been launched. Timely response to the information requirements implied here requires that the Department of Fisheries or other administrative unit in charge of fisheries has a staff capable of meeting to the corresponding challenges, which brings up the concept of ‘critical mass’.

In research, the term ‘critical mass’ refer simultaneously to the size of a unit, the quality of its staff, and the resources available to it such that it can accomplish its mission. When a unit is below critical mass, it cannot do so, whatever its name and the legislation which created it.

I am not aware of any explicit study of the critical mass required for a fisheries management unit - indeed the only related study that has come to my attention is that edited by Daniels and Nestel (1993), assessing critical mass requirement for animal research in Africa and/or Latin America. Its conclusions, however, appear to apply to fisheries research as well: below 4-5 professional staff, of which 2-3 should have at least an MS degree, with adequate clerical administrative and technical support (e.g., at least a small craft in the case of fisheries research), and a small library (see e.g., suggested book list in Appendix 3 of Pauly 1984), a local fisheries unit may well be useless.

This may imply, for small countries and/or provinces of larger countries that either:

- External inputs are sought for the above-mentioned tasks (e.g., from international organizations, such as e.g., FFA, SPC or FAO, or from private consulting firms), or
- A partnership between institutions is formed, allowing pooling of resources to reach critical mass (this is further discussed in Pauly et al. 1990).

Another aspect of (fisheries) research, implied in the critical mass concept, is that it is expensive (See Box 1).

Fisheries that require more than fisheries management

Fisheries that have collapsed biologically, such as the Newfoundland cod fishery, or in which the massive ecological and social changes have occurred which I term *Malthusian overfishing* (Pauly 1994), e.g., in Bolinao, Pangasinan Province (see McManus et al. 1992) and in Maqueda Bay, Samar Province, Philippines (see Saeger 1994) do not require “fisheries management” (s.s. or s.l.). Rather, what they require are intersectoral arrangements including onshore job creations for redundant fishers. In the case of Newfoundland cod, this forced the Canadian federal government to:

- i. close the fishery, and save the few spawners left, thus hopefully allowing an eventual rebuilding of the stocks; and

- ii. provide economic support for over 40,000 out-of-work fishers and fish workers and their families, inclusive of training programs to enable young fishers and allied workers to transfer to other sectors, and for the older ones to retire.

Box 1. Scientific productivity and its costs.

Estimating the cost of research in a given country, e.g., of fisheries research is not an easy task, and it is even more difficult to assess productivity. However, if publications are considered the major output of research, then productivity can be assessed, as comparative studies do exist pertaining to the productivity of fisheries institutions or projects (Rounsefell 1961; Morgan and Hopkins 1986; Pauly 1986; Dizon and Sadorra 1995; Dizon 1995).

Jointly, these studies indicate that the formal education of scientists increases their productivity (BS < MS < Ph.D.), as does the support and recognition they get through and/or from the institutions where they work.

Also, these studies suggest, for all costs associated with generating publications (i.e., not only the “publications cost”), a mean figure of about US\$ 1,000 per page, with values below this for technical reports, and above this for papers in international refereed journals (see Morgan 1983; Mathews 1987 and Pauly 1994 for attempts to reduce costs by using length-based, or comparative approaches instead of age-based techniques for studying fish growth).

The implications of this for a small fisheries unit are obvious, and should be followed through - e.g., by relating the expected cost of studying a given fishery to the benefits (if any) that can reasonably be expected to result from improved management of that fishery.

In the Philippines and for understandable reasons, such interventions have not been forthcoming for ailing fisheries (although excellent management plans, inclusive of alternative livelihood programs have been proposed, see McManus et al. 1992). Instead, legislation has recently been passed which delegates much authority over coastal fisheries resources from the central government to local government. This has raised hopes for an increased role of “co-management” schemes, linking central and/or local governments with fisher communities in shared responsibility for the resources.

Similar schemes have been proposed

Though now much talked about in the context of tropical fisheries, this concept cannot belie its Canadian origin (Pinkerton 1989), which shows in its implicit assumptions:

- i. that the fishers are, with regard to the resources, the only stakeholders that the government needs to deal with; and
- ii. that the government in question indeed has the capacity to contribute to the partnership.

Thus, in Canada, the scientists of the Department of Fisheries and Oceans have the capacity to evaluate fisheries stocks, to estimate TAC, etc., and to propose management regimes which the government has the capacity to enforce, etc. Co-management emerged in this context as a battle-cry of marginalized groups with a tradition of fishing (such as the First Nations of Canada) who - understandably want to participate in the resource allocation process, if mainly to increase their share of the resource.

“Tropicalizing” the co-management concept thus implies an assessment of the capacity of local or central governments in tropical developing countries to serve as counterpart (or counterweight) to fisher communities, and an evaluation of whether these fisher communities should indeed be considered the sole legitimate stakeholders as far as fisheries resources are concerned. I believe this critical examination of the co-management

concept has not occurred. Moreover, I believe that a more general concept, that of “governance” as documented on the contributions in Kooiman (1991) better captures the essence of what is required to reach beyond fisheries management (even *s.l.*), and to accommodate the multi-sectoral consultations and interventions required for rehabilitating fisheries, which in cases such as mentioned above must include massive reduction of fishing effort.

Rather than for government to remain actively engaged in fisheries management, governance *sensu* Kooiman and colleagues implies the creation, through appropriate legislative action, of a “level field” through which various stakeholders are given the means to articulate their demands for access to a certain good or services), and where action must result from consensus, or a least majority agreement among groups of stakeholders.

In the fisheries context, this implies the identification of groups other than fishers with legitimate claims to the resources, e.g., NGO s promoting non-fishing livelihood programs, conservationist NGOs interested in the biological integrity of fish populations endangered by excessive fishing or, in coral reef fisheries, the owner/operators of dive resorts, who will fail to attract tourists if the fishers have blasted the reefs, etc.

This implies that such groups be given joint management authority over a resource. Fisheries management advice, in such context, would go to the joint authority (e.g., a Management Council), neither to the government nor the fishers alone, and would then have to be balanced against advice concerning non-extractive use of the resource.

Such balancing would imply that fishers would have to reduce or at least stabilize their effort level to accommodate other groups, and would have several effects:

- increased catches (and decreased catch variability) for those remaining in the fisheries;
- increase diversity within the exploited species complex;

This would also allow for some rent to be extracted (if indirectly, via taxes paid by other, taxable groups whose activity require healthy stocks, e.g., tourism operators) from fishers, i.e. a group that generally does not pay a resource rent to society at large.

This last point may seem moot to those who consider fishers the only legitimate users of fish resources, but perhaps may be appreciated by others, who can conceive of fish resources being viewed the same way we now view, e.g., wetlands or tropical forests now widely perceived as being “public” resources, which not even their formal owners have the right to wantonly destroy.

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SOUTH AFRICA'S POST-APARTHEID MARINE RESEARCH*

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Abstract

This contribution is a reproduction of a report submitted to the leadership of the South African Network for Coastal and Oceanic Research (SANCOR), in Cape Town, on September 29, 1994, after four days spent ranking 70 research proposal submitted to that body in terms of both their scientific potential and other their accounting for, and helping to overcome the pernicious legacy of Apartheid.

Introduction

The account below is a complete version of the report the three authors submitted to the leadership of the South African Network for Coastal and Oceanic Research (SANCOR; see <https://sancor.nrf.ac.za/default.aspx>), in Cape Town, on September 29, 1994, after four days spent ranking research proposals submitted to that body.

Recall South Africa's recent history, marred by a century of settlers' violence against the original inhabitants, culminating in the Apartheid that became official policy with the ascent of the 'National Party' in 1948, and revoked following the first free election in April 1994, which made Nelson Mandela the first democratically elected president of South Africa (see https://en.wikipedia.org/wiki/Apartheid#1994_election).

Apartheid distorted everything, including science, and how scientific proposals are evaluated, and the leaders of SANCOR, thus wisely asked external referees to evaluate the research proposals they received that year. The three of us were offered to do this job, although (and also because) none of us had ever been to South Africa. But we accepted, as we wanted to help the New South Africa. What follows are the observations we delivered along with the evaluation of 70 project proposals of various types. Some of these observations may still be relevant today, and in countries other than South Africa.

Our report

At the outset we would like to congratulate the initiators for devising an innovative and exciting research programme, and for attracting a large number of high-calibre proposals from people who took seriously the task of doing their research in the context provided by the New South Africa. Also, we would like to thank those who invited us to join in your effort to help overcome, in marine research, the legacy of the past and to establish a sound ecological, social and economic basis for the sustained benefits of South Africa's living marine resources.

We examined over 70 proposals in three busy days, covering three thrusts:

- A. Communities and Living Marine Resources;
- B. The Coast as a Resource;
- C. Offshore Living Resources and Society.

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Thrusts A and C concern fisheries science in the widest sense, including people and their various organizations. We perceived Thrust B as referring to the emerging field of Coastal Zone Management.

South African fisheries research has traditionally been world-class, and this is reflected in many of the proposals. However, the SANCOR programme rightly expects bold initiatives to broaden, in an interdisciplinary mode, the scope of this research to both cover the interest (expressed or not) of the country's disadvantaged majority and to include representatives of this majority at the highest possible level in the proposed research plans. This is where we saw the cold hand of the old regime still reaching out, holding back renewal. Three specific problems were evident:

- i. There are few or no potential partners for fishery scientists who would like to work with representatives from historically disadvantaged groups;
- ii. Some of these same scientists, because of their previous isolation from such groups, have problems even conceiving arrangements that would create such partners; and
- iii. Empowering women, one of SANCOR's criteria, was ignored by almost all proposers.

Point (ii) is evidenced by 'motherhood' statements, inserted at the end of many proposals, stating that "attempts will be made to involve students from historically disadvantaged universities". That not even motherhood statements were made concerning gender issues suggest that this is perceived as frivolous or arbitrary -- a view that the recent U.N. conference in Cairo should help overcome.

Reaching out to the groups in (ii) and (iii) will involve several actions. Concerning involvement and recruitment of blacks into South African fisheries sciences, we feel that a range of approaches should be covered (a few of these were incorporated into proposals), pending the gradual emergence of fully trained black scientists, notably:

- Workplace experience schemes such as "open house" for high school-aged children;
- Twinning arrangements between research institutes and high-schools or 'teknicons';
- Creation of new positions (including on-the-job training) for technicians, observers and others for which suitable work may be available.

Arrangements for drawing women (both from historically disadvantaged groups and others) into the type of activities covered by the SANCOR program may include:

- A certain percentage of funds and/or positions reserved, on a competitive basis, for female applicants;
- Explicitly addressing gender-specific issues whenever "communities" are studied (e.g. what roles or activities are seen for females if males are involved in ecotourism development);
- Checking how working conditions for female scientists or technicians may subtly discriminate against females. For example, to what extent do medical benefits include maternity leave?

There is a large body of respectable science in Europe and North America addressing these issues and South African researchers will have to acquaint themselves with it. The general lack of emphasis on these issues, despite the SANCOR guidelines, forced us as reviewers to give extra weight to those proposals that showed evidence of a concerted effort having been made to think this problem through, and to establish the relevant contacts before submission of the proposals.

However, these problems are not only due to the old racial legacy. Biologically-trained fisheries scientists over the world have problems conceiving collaborations with social scientists and community representations which does not compromise the quality of their science (although they routinely interact with industry representatives who sometimes do compromise the neutrality of their science). Fisheries scientists in South Africa, as elsewhere, will have to learn to deal with new clients and fishery stakeholders, if the discipline is perceived to be relevant, and thus funded.

We now turn to more technical aspects of the proposals. Most of them were strong scientifically, and most anticipate generating products consisting mainly of scientific publications in peer-reviewed journals. We believe that these outputs are necessary, but not sufficient to assess the aims of a project that is part of an interdisciplinary programme designed to extend social equity by outreach and training. For example, scientific papers alone would not suffice for projects supported by European or North American development agencies. The SANCOR projects are implicitly of this type.

Criteria for evaluation of projects in a research programme of this type such as proposed here may include:

- Adoption/implementation of techniques/approaches by intended clients;
- Number of persons trained;
- Levels of training achieved;
- Fraction of targeted community reached through various media;
- Social footprint of awareness of the project across the interest groups and stakeholders; and
- The evaluation of results by all interest groups including stakeholders.

In addition to formal evaluation of projects, almost no one mentioned the need for interim evaluation of progress and what criteria might be used either for self-evaluation or for a progress report. Due to the interdisciplinary nature of this SANCOR programme, we recommend that continuation of funding be made contingent upon a rigorously evaluated interim report.

An extensive literature on project evaluation has been produced by the bilateral and multi-lateral aid agencies and others. We recommend that SANCOR incorporate these in their project monitoring guidelines. Failure to do so may lead to:

- A number of SANCOR funded projects failing for lack of timely corrective measures, and
- Outside criticisms by political groups with high expectations for the program, leading to the long-term danger of curtailment of funding.

Another problem with the biologically-orientated proposals is the 'tag-on' nature of their socio-economic components, and conversely, the non-consideration of biological elements in projects proposed by economists, sociologists, or other social scientists. We believe that proposals should be jointly articulated by the biologists/oceanographers and economists/social scientists that are to work on a project, with co-leaders of high calibre representing both sides of the project, and in which both sets of disciplines illuminate different perspectives of the same object of study. Good science can be done in this mode, but this requires open-minded scientists, not those that prefer to hide behind disciplinary smokescreens.

Also, we noted that numerous proposals consisted of a 'star' principal investigator and his or her students, but very few postdoctoral or entry-level scientists. We recognize the advantages of this type of arrangement: cheap and versatile labour with no commitment to future employment. We fear that there are some hidden costs because the principal investigator may not devote enough time to the project, and that among students, the blind will lead the lame. Also, the students may lack a role model, and an obvious career path.

SANCOR provided a fixed format for proposals, but many proposers chose (apparently) to not read these instructions. Thus, many proposals were difficult to evaluate in a comparative mode because they were only one page long, lacked detail, and had grossly incomplete (or even missing) CVs. This may have resulted in unfairness. Finally, we hope that these comments will be taken in the same spirit that they are offered: as collegial advice from three scientists who feel honoured by being associated with this ambitious programme. We took our job seriously, and thus emphasized those items which we felt would most benefit from being rethought.

SIDNEY HOLT (1926 – 2019): A PERSONAL VIEW*

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Sidney Holt was a leader of various non-governmental marine conservation organizations and a former senior staff at the Food and Agriculture Organization (FAO) and other U.N. organizations, but started his career as a research scientist at the Lowestoft Laboratory of the U.K. Ministry of Fisheries and Food (MAFF).

It was at the Lowestoft Laboratory that Sidney Holt, in collaboration with Raymond Beverton, wrote the book *On the dynamics of fish populations* (Beverton and Holt 1957; Figure 1) which reshaped fisheries science by providing it with the conceptual and mathematical language that it had lacked until then. Indeed, today fisheries scientists use concepts and equations originally presented in that book without explicit reference to it.

In 1953, Sidney Holt went on to work at FAO to implement the research program outlined in “Beverton-and-Holt”, and gradually shifted his focus to the conservation of marine mammals, i.e., saving the whales, a feat for which he is better known by the public (e.g. Brown 2020).

Born in the East End of London to what he called “a poor Cockney family” (Holt 2019), Sidney’s studies, first at Haberdasher’s Aske’s Boys School and later at Reading University, were funded by scholarships. At Reading, he earned a first-class honors degree in Zoology. Lack of funds precluded further studies and in 1946, he joined the Lowestoft Laboratory of MAFF.

What ensued was a most productive scientific collaboration with Ray Beverton, recruited at the same time to Lowestoft with the explicit charge for both to develop a theory of fishing based on concepts from operations research, which had proved its utility during WWII (Hulme et al. 1947).

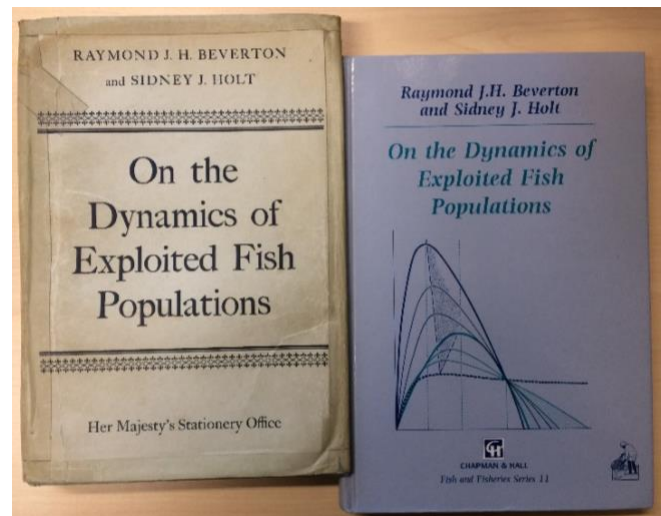


Figure 1. The authors copies of the ‘Beverton-and-Holt bible’.

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This is the ‘long version’ of a retrospective drafted for *Science*, and which was published in *Science* 367(6479): 744 doi: 10.1126/science.aba8964 .

¹ This is the reason why this book, although it has over 7,000 citations on Google Scholar, is not be the most cited work in fisheries science, contrary to various claims (see Branch and Linnell 2016). This phenomenon – that the ideas in an article of book become so widespread that citation are not needed any more - was called “obliteration through incorporation” by the inventor of citation analysis (Garfield 1977).

The result was a 533-page tome, eventually published in 1957, full of long equations whose parameters - for growth² natural and fishing mortality – enabled the computation of optimal catches of any fish species for the different mesh sizes of fishing gear and different levels of “recruitment”, i.e., the number of young fish entering the exploited part of a fish population.

Behind the forbidding mathematics there was a simple, yet ingenious idea: because the vagaries of environmental fluctuations cannot be predicted, and hence the survival of the eggs and larvae of fish cannot be predicted either, fisheries should be optimized to make the best of every young fish that happens to survive past the egg and larval stages and “recruits” into that part of the population that can be exploited by the fishery. Thus, whether one thousand or 10 million young fish are recruited, the fishery could optimize its catch or ‘yield’ by allowing the recruits to grow until loss through natural mortality would counteract further growth.

Thus, was born the concept of yield-per-recruit (Y/R), still used today³, if often in starkly modified form. Also included were equations for growth, mortality, gear mesh size, etc., that were developed to get at the estimates of Y/R.

Because these concepts and the equations behind them were all new, the Lowestoft Laboratory and later FAO, where Sidney Holt joined the senior staff in the early 1950s, organized courses in fish population dynamics in a number of countries⁴. Following various simplifications of its equations (see Beverton and Holt 1966), these courses established yield-per-recruit as one of the standard approaches of fisheries research, i.e., the ‘British School’. The other, the ‘U.S. School’, pioneered by M. B. Schaefer, was structured around the estimation of “Maximum Sustainable Yield” or MSY (Schaefer 1954, 1957), which Sidney Holt fiercely opposed throughout his scientific life, even though, it must be said, they are two facets of the same dynamic processes and can be straightforwardly reconciled.

It should also be noted that both approaches were frustratingly unable to rein in fisheries in many parts of the world, which continue to take newly recruited fish before they have a chance to grow and reproduce, and thus continue to reduce fish populations below a level that generates MSY.

² To express the growth of fish, Beverton and Holt (1957) used an equation proposed earlier by von Bertalanffy, (1938). However, while Beverton and Holt made the equation ubiquitous, they also badly misunderstood its physiological foundations, thus contributing to the controversy which needlessly surrounds von Bertalanffy’s work (Pauly 2019).

³ See for example Froese et al. (2018), Liang and Pauly (2017), or Zhai and Pauly (2019).

⁴ One of the Lowestoft courses was attended by Gotthilf Hempel, later to become my thesis advisor (see pp. 86-90, this volume). He introduced Beverton and Holt’s theory and equations to his German colleagues via his only ‘mathematical’ paper, i.e., Hempel (1961).



Figure 2. Sidney Holt and the author at Airlie House, Pethshire, UK in 1996 (?), at a workshop to work out the criteria that the then soon-to-be founded Marine Stewardship Council (MSC) was supposed to use for its assessment of sustainable fisheries. It didn’t, and Sidney later joined me and others in a paper in which we criticized the MSC for reneging on its principles (Jacquet *et al.* 2010).

My first encounter with Sidney was in 1984 in Berlin, at a ‘Dahlem Konferenz’ devoted to the ‘Exploitation of Marine Communities’ (Pauly 1986), and at which he reconnected with Ray Beverton, from whom he had been estranged for a while. We met several times afterward (Figure 2) and corresponded frequently, with him heaping praise when I had done something he liked and criticizing me mercilessly when I had written something he didn’t like; for example, that MSY was not a fraudulent concept.

Thus, when a facsimile edition of his major opus was produced (Beverton and Holt 1993; see Figure 1), Sidney agreed that I should write its foreword (Pauly 1993). To a fisheries scientist, this was equivalent to an evolutionary biologist being asked by Charles Darwin to write a foreword to the *Origin of Species*. I complied, although I was not permitted to speak about his relation with Ray Beverton, who passed away in 1995 (Pauly 1996).

Many people, however, know Sidney Holt only as the fierce conservationist who saved the whales, a reputation that is entirely deserved. His first dealings with whales were as a member of a ‘Committee of Three’⁵ who, from 1960 to 1965 and for the first time, analyzed scientifically the catch records of the International Whaling Commission (IWC). They found that under the then current ‘quotas’, i.e., killing rates, the exploited whale populations were headed straight toward extinction – a conclusion made without accounting for the huge off-the-books kills by the Soviet Union, still unknown at the time.

Sidney subsequently focused on to the conservation and protection of the great whales, lending his mathematical skill to a cause which had until then relied mainly on appeals to emotions⁶. Thus, after he left the U.N. system in 1979, Sidney Holt deepened his involvement with the IWC, including as delegate of various countries such as Chile, France and the Seychelles, while providing scientific support to various NGOs including Greenpeace, the International Fund for Animal Welfare, the Sea Shepherd Conservation Society and others in their effort to reduce the kills of great whales (Holt 2011). Gradually, he became a much-admired icon of conservation, a transformation facilitated by his informal and direct style. The movement of which he was the intellectual leader succeeded in slowing down, then turning around the machinery that had been grinding down one whale population after the other, forcing Japan and her few allies to hunt whales solely in their own Exclusive Economic Zones, and suppressing the trade of whale-derived product.

Dr. Sidney Holt has been honored with the Gold Medal of the World Wildlife Fund, the Royal Netherlands Golden Ark, UNEP’s Global 500 Awards and many more. He was both talented and pugnacious, but he also had a great heart. Talent is what enabled him, a working-class kid, to excel in school and to get the scholarship to earn his first degree. It is also talent that enabled him to formulate the bulk of the mathematics in the Beverton and Holt book (which could equally have been authored by Holt and Beverton), and later to see where the industrial exploitation of the great whales was headed.

Both his work on the dynamics of fish and on behalf of whale conservation were done against vociferous opposition. He overcame the opposition because he had a strong heart for his friends and colleagues who agreed with him, and for the whales. Many whale species are still endangered; but that they are still alive is, in large part due to the intellect, pugnacity, and heart of Sidney Holt.

⁵ Confusingly, a fourth person was later added to the Committee of Three, John A. Gulland, also an FAO staff formerly from the Lowestoft Laboratory (Pauly 1990).

⁶ However, Sidney eventually returned to fisheries issues, as exemplified by his collaboration with Rainer Froese on critiquing the EU’s Common Fisheries Policy (Holt and Froese. 2015), in which he even overcame his distaste for MSY. Sidney also collaborated with R. Froese and this author in rejecting the monstrous notion of ‘balanced harvesting’ (see Froese et al. 2015; Pauly et al. 2016).

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LEARNING FROM PEER REVIEWS

LEARNING FROM THE REVIEW OF “ESTIMATING STOCK STATUS FROM RELATIVE ABUNDANCE AND RESILIENCE”*

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Abstract

This contribution presents the detailed responses to the peer-review of Froese *et al.* (2019) “Estimating stock status from relative abundance and resilience” (ICES J. Mar. Sci. 2019) which outlined a method called “AMSY” for inferring biomass trends for stocks for which only catch-per-unit-effort and limited ancillary (‘priors’) data are available. The responses emphasize that the required priors are legitimate and straightforward to obtain, thus, making AMSY a method of choice in data-sparse situations. This is also a good example of the role of peer-review in validating and improving science.

Introduction

Transparency is the lifeblood of science (Dittert *et al.* 2001) and various approaches have been and continue to be proposed to make more of the data used in scientific research widely available, e.g., in the marine sciences (Froese *et al.* 2001; Froese and Reyes 2003; Zeller *et al.* 2005).

Moreover, we believe that more of the back-and-forth dialogs that undergird scientific articles should also be made publicly available. Here, we follow Pauly (2018) in publishing the peer-review (i.e., the editors’ and reviewers’ comments and our responses) of our contribution entitled “Estimating stock status from relative abundance and resilience” (Froese *et al.* 2019), which presented a method called “AMSY” to derive a time series of biomass from catch-per-unit-effort (or CPUE) data and priors, notably for the growth rate of the population (resilience).

* Cite as: Froese, D., H. Winker, G. Coro, N. Demirel, A.C. Tsikliras, D. Dimarchopoulou, G. Scarcella, M.L.D. Palomares, M. Dureuil and D. Pauly. 2020. Learning from the peer review of ‘Estimating stock status from relative abundance and resilience’, p. 111-124. In: Pauly, D. and V. Ruiz-Leotaud (eds.) *Marine and Freshwater Miscellanea II*. Fisheries Centre Research Reports 28(2). Institute for the Oceans and Fisheries, University of British Columbia.

Editors' comments:

E1) The large number of priors and constraints give no confidence that the method is an improvement over looking at the CPUE trend and concluding the stock status.

E1. Answer: The number of priors (2) is actually low. The number of filters, which are not priors and need no user interaction, has been reduced from 7 to 5. The influence of these filters has been documented in a new section, by running the simulations with and without filters.

E2) The text does not adequately describe how the results are sensitive to prior specifications and the chosen set of filters based on the CPUE time-series.

E2. Answer: The text has been greatly expanded (see highlighted sections) to address these issues.

E3) There are many places where more work should be done, and more considerations should be made. There are many assumptions associated with this approach, only some of which are discussed, and none that are performance tested.

E3) Answer: All assumptions are now listed and discussed. A preliminary performance testing is done against 140 real world stocks. Still, it is stressed that more sensitivity studies can be done, but that this is beyond the scope of an already substantial study that presents a new method and proof of concept.

E4) There are many assumptions being made by this model; violating these assumptions and by how much to degrade performance is the true test of how this method performs, and this needs to be done much better in the paper.

E4. Answer: The assumptions made for AMSY are the same as for a regular Bayesian implementation of a surplus-production model, the only difference being the lack of catch data. This is now made explicit in the text. Also, the effect of the filters is now demonstrated by analyzing the simulated data with and without filters.

E5) There needs to be further description and reporting on the simulations from which filters are derived in order for the reader to understand the derivation of the filters.

E5. Answer: This presumably refers to the numerical settings/thresholds used for the filters. Their derivation is now described and declared as preliminary and open to further improvements, but assumed sufficient for the purpose of this proof-of-concept study.

E6) The supplementary materials (>200 pages!), as currently presented, will be overwhelming to most readers without further clarification.

E6. Answer: The amended/expanded text and the addition of a new table and a new figure make it less necessary to consult the Supplementary Materials. But properly documenting the results of 2*24 runs against simulated data, runs against 140 real stocks, and first assessments of 38 data-poor stocks does require a lot of space. We have added a more detailed table of contents to the appendices.

Reviewer 1 comments:

R1.1: I find no technical errors in the model implemented by the authors.

R1.1 Answer: We thank R1 for the technical review of our model and note that no errors were found.

R1.2: But the large number of priors and constraints give me no confidence that the method is an improvement over looking at the CPUE trend and concluding whether the stock seems to be going up or going down or seems fairly stable. Below are some particular comments.

R1.2 Answer: The number of priors is actually not large: one prior for productivity, objectively obtained from online databases based on life history traits or previous assessments, and one prior for relative stock size in any year of the time series, obtained preferably from independent data such as length frequencies, or from expert knowledge, such as is common practice in Bayesian modelling. If Reviewer 1 refers to the applied filters, their role is now explicitly clarified and their number has been reduced from 7 to 5.

R1.3: Line 126: relative stock size Bt/k : putting a prior on the result is assuming you know the answer.

R1.3 Answer: Putting priors on parameter estimates is required in Bayesian-like analyses, such as the proposed AMSY approach. Reviewer 1 reports a common criticism of Bayesian inference, which is, however, a rigorous state-of-the-art statistical procedure. Properly applied, priors reflect the best available knowledge about a trait or parameter, and that knowledge is then updated with the available data. The point here is whether a model that only has a time series of CPUE as input can produce similar results as a model that, in addition, has a time series of catch data as input, everything else being equal. This has now been stressed in the text.

R1.4: Also, good to acknowledge the work of Alec MacCall in this regard.

R1.4 Answer: Reviewer 1 seems to refer to the DCAC method of MacCall (2009), which estimates a sustainable catch-level below MSY and requires catch, relative depletion, M and $FMSY/M$ estimates as inputs. Note the requirement for prior knowledge of relative depletion, which is the same as the B/k prior required by AMSY. DCAC needs a time series of catch data and thus is not applicable for the CPUE-only situations that AMSY is meant to deal with. Note the requirement for prior knowledge of M , which is similar to resilience: $M \sim FMSY \sim 0.5 r$. In other words, the example given by Reviewer 1 shows the common use of priors in stock assessment.

R1.5: Line 140-160: These are highly informative priors, so there is no surprise that the method works. If data-rich “full stock assessments” used such priors, they would perform exceedingly well.

R1.5 Answer: Bayesian age-structured assessments actually use the same priors, plus additional ones for natural mortality and the steepness of the left, ascending side of stock recruitment curves. While meta-analyses and largely reliable methods exist that constrain natural mortality estimates for all fish species in the world, the steepness of stock recruitment curves is not established for more than a few well-studied species. Thus, avoiding the use of this parameter is a plus.

R1.6: The CPUE data as presented in the appendix are extraordinarily clean. Normal data is much noisier.

R1.6 Answer: Reviewer 1 presumably refers to the simulated data. The CV used there for the random error for surplus production was 0.2; the CV for the random error for catches was 0.1. Given that many “full stock assessments” treat catch as free of error, we don’t think that the simulated data were “extraordinarily clean”. In any case, the simulations were only used to verify that the AMSY model works in principle; we made a point of evaluating AMSY against 140 real stocks with a wide range of life histories and environments, much more than are usually tested when a new method is presented.

R1.7: Line 155: another unjustified constraint that will improve the apparent performance of this method.

R1.7 Answer: Reviewer 1 refers here to built-in rules for the minimum and maximum range of relative carrying capacity $k \cdot q$. These specify that the lower bound of carrying capacity must be equal to or larger than the maximum observed CPUE, and that the upper bound must be larger than the lower by at least 30% and max 300%. For example, in a stock where the max CPUE was 1000 tonnes, the prior for the upper bound of carrying capacity would be not less than 1300 tonnes and not more than 3000 tonnes. This is not a small range, and the tests against simulated stocks with known ranges showed this assumption to be realistic.

R1.8: Line 165-170: Justification for including this reduced productivity at low stock size is missing and it just adds to the sense that this model is a fantasy. Then, in the discussion, the authors rationalize not using other forms of the biomass dynamics approach which might be more justified than their modification.

R1.8 Answer: This comment refers to the built-in reduction of expected recruitment at low stock sizes. That recruitment is likely to be impaired at very small stock size is well known and widely used in management. For example, ICES reduces the applicable value for FMSY linearly when $B < MSY_{Btrigger}$, which is very similar to our approach. We have added that reference.

R1.9: Line 172: productivity process error should have been identified in the earlier equations.

R1.9 Answer: We have added a statement that error terms were not shown in the previous equations for the sake of simplicity.

R1.10: Line 183-242: these filters to exclude unrealistic results create even more concern in my mind regarding the value of this approach.

R1.10 Answer: Monte Carlo methods are a well-established statistical procedure that uses the process of repeated random sampling to make numerical estimations of unknown parameters. Excluding parameter values that result in unlikely predictions, such as negative catches, is a logical addition to random sampling and is at the core of the new data-poor stock assessment methods such as CMSY. We have added a new section that explicitly looks at the influence of the filters on the results and we have reduced the number of filters from 7 to 5.

R1.11: Line 263: “This first year biomass was also used as prior for AMSY” seems like another trick to get the method to perform well.

R1.11 Answer: This refers to the time series of 50 years of simulated data, where the biomass prior was set to the ‘true’ biomass range (0.15 – 0.4 or 0.5 – 0.85) at the beginning of the time series. These are pretty wide ranges (63% - 41% of the max value). The ranges had to include the ‘true’ value for this test (otherwise they would not reflect independent correct knowledge about the stock) and they were taken 50 years before the value that would be compared with the AMSY estimate, so this is certainly no trick to make the method perform well. The text did not mention the ranges, which could have misled the reviewer. This has now been changed.

R1.12: Line 275: “...AMSY used the meanwhile available...” does not make sense.

R1.12 Answer: The reviewer has a point that the text was not clear enough. It was meant to say that during the previous BSM exercise FishBase only provided qualitative information about resilience. As part of the response to the reviewers, we have now re-run the BSM estimates and both BSM and AMSY use exactly the same prior distributions for r , based on prior knowledge available in FishBase (www.fishbase.org) or SeaLifeBase

(www.sealifebase.org). The point is to explore whether AMSY can get close to the results of BSM, using exactly the same priors for relative biomass in the first year and for r , but with the difference that BSM uses time series of catch and CPUE whereas AMSY uses only CPUE. This has now been made explicit in the chapter about how AMSY works and is also stressed in the Conclusions.

R1.13: Line 305-309: This appearance of good performance against simulated data is not surprising given the large number of constraints and priors used in the AMSY method.

R1.12 Answer: Two priors and 5 filters applying general population dynamics logic actually are not that many inputs compared with other data poor (see e.g. DCAC of MacCall above) or data rich (e.g. M and steepness) models. Note also that the resilience prior is derived ‘objectively’ from online databases and that the 5 filters operate on general rules that are built into the code, so potentially subjective user input is only required for the biomass prior. This is less than the usual priors needed for stock assessments. However, Reviewer 1 has a point in that the filter settings were fine-tuned with test runs against the simulated data; so, a comparison of results is not fair and it was removed from the text. The simulations provide only a proof of concept whereas the testing is done against 140 real world stocks. This is now made clear in the text.

R1.13: Line 311-312: If the BSM in Froese et al. (2017) uses any of the constraints and priors used for AMSY, then the similarity of their results is not surprising and might be considered simply an artifact of the methods

R1.13 Answer: The full Bayesian Schaefer model in BSM uses the same prior for resilience, but none of the filters. Instead, catch is a required additional input. The point here was to see whether AMSY can reproduce the BSM results WITHOUT knowing the catch. That is the case in the simulations even without the filters (this demonstration is new) and with most of the 140 tested real stocks.

R1.14: Table 3, Line 356: The confidence intervals are rather tight in comparison to many “full stock assessments” and there is an obvious correlation between the estimated F/F_{msy} and B/B_{msy} . Both of these observations are another indication that the method is too stiff with its many priors and constraints.

R1.14 Answer: Confidence limits of F/F_{MSY} are actually rather wide, which is the reason why F/F_{MSY} results of AMSY were explicitly NOT recommended for management in the text, in the Conclusions, and in the Abstract. In contrast, the AMSY estimates of B/B_{MSY} have confidence limits that are similar to regular stock assessments. This point has been made more explicit in the text. Also, we have picked up on the correlation between r and k , which is also stressed by Reviewer 2, and have replaced the uniform prior distribution with a multivariate one and rerun all analyses.

R1.15: I fear that use of this method will give a misleading sense of knowledge that will not necessarily result in better management.

R1.15 Answer: We agree with Reviewer 1 about the danger that insufficient or wrong knowledge may be regarded as good only because it has run through a ‘fancy’ model. But this is a danger that applies to all models and is not specific or more pronounced in AMSY. We have tried to address this problem with a long section about properties and assumptions of AMSY.

Reviewer 2 Comments:

R2.1: Overview: The authors present a new method for applying limited fisheries data to provide science-based fisheries management guidance. Specifically, the AMSY approach uses catch-per-unit effort data as a proxy for catches and applies it in a Schaefer production model in order to estimate relative stock status in

terms of biomass and fishing mortality. This method occupies a unique spot in the spectrum of data-limited methods by using CPUE to access surplus-production based reference points in order to interpret stock status. This method frees the user from having to have a catch time series, which is a common issue in many fisheries. Overall, I think the idea of this method is a very valuable one for adding to the data-limited toolkit. Regarding the presentation of this method in this paper, I found many places where more work should be done, and more considerations should be made. There are many assumptions associated with this approach, only some of which are discussed, and none that are performance tested. Below, I outline several areas I believe the paper should look to improve before publication. I hope the authors find these suggestions useful and constructive, as I think the method is a worthy contribution to the growing data-limited methods literature.

R2.1 Answer: We are pleased that Reviewer 2 shares our vision and will strive to do as many of the suggested improvements as possible in the context of this ‘proof of concept’ paper.

Major considerations:

R2.2: While the concept of AMSY is interesting, the performance testing is really only proof of concept. There are two main performance testing approaches and then application to real data. The first approach is to simulate data and parameters, apply that information to AMSY, then compare to the known simulated values. While this is a typical approach to simulation testing, all that is tested here is whether you get the right values back if the right values are given to AMSY. What is completely missing and definitely needed is robustness/sensitivity testing. There are many assumptions being made by this model (all input values being correct, CPUE not being biased or highly imprecise (lines 429-430; 445-447), q is constant, Schaefer model is appropriate for all life histories, etc.). Violating these assumptions and by how much to degrade performance are the true test of how this method performs.

R2.2 Answer: Yes, the simulations are a proof of concept but the simulation testing does more than just getting “the right values back if the right values are given to AMSY.” The simulations tested extreme situations that are rarely encountered in real world situations, such as exploring results for species with very low resilience or stocks with very light exploitation. In both cases AMSY results were found less reliable, resulting in a warning to users. This warning was checked again and made more explicit.

R2.3: Likewise, the second approach is comparing the results to a surplus production approach that uses CPUE and a catch time series. I assume all the input parameter values for each comparison are the same between both models, thus it is unsurprising they perform similarly. The differences come down to filtering treatments in AMSY and maybe slightly different priors. I did not find this performance testing convincing of the utility of AMSY beyond that it can mimic other surplus production models WHEN given the same input values and relative catch data that have a direct relationship to abundance and catch. A proper simulation test exploring these issues, or a much-expanded Discussion section talking about all of these assumptions and offering caution in applying this method until proper simulation testing is done is needed.

R2.3 Answer: Apparently we have not presented the case clearly enough, since both reviewers take issue here: The test was exactly whether AMSY, which is a “half” Schaefer model without any information about extractions (=catches) can approximately reproduce the parameter estimates of a ‘full’ Schaefer model with catch as input, everything else being equal. This statement is now made explicitly in the text. What more can one expect from a data-poor method? Reviewer 2 has a point that catch and CPUE are strongly linked in the simulations, with deviations coming only from the error terms, but this is not the case for the 140 real stocks, where variations in catch can stem from management or economics or other drivers and similarly, CPUE can be driven strongly by environment and less by catches. Still, AMSY was able to approximate most of the BSM predications. We have revisited the respective text and made it more explicit, in M&M as well as in the Discussion.

R2.4: In the description of the filters, there are several places (lines 191, 200, 211, 215, and 222) where values are “derived from simulations”. What are these simulations? It is not possible to tell how much uncertainty there is around these values, nor if these values are universally applicable. There needs to be further description and reporting on what these simulations are in order for the reader to understand the derivation of these filters.

R2.4 Answer: We have now made more explicit how the parameterization of the logical filters was done (basically, test runs against the simulated data) and that they are preliminary. However, they worked reasonably well on the wide range of 140 real world stocks and thus seem fit for preliminary use. This is now stated explicitly in the text.

R2.5: In evaluating the need for so many filters and the fact that the k_q prior is derived from Bt/K , it does not seem like the correlation structure for $r-k$ is considered. If it was, I am curious if this would decrease the number of needed filters. And given the model structure, that correlation structure is needed. Please check to see (and possibly report) the posterior relationship between r and k_q to make sure the needed correlation structure is present. If not, try to add correlation structure and see if that decreases the number of triggered filters, and therefore the possible reduction in needed filters.

R2.5 Answer: Following this recommendation of all reviewers, we have now implemented a multivariate log-normal distribution based on the posterior correlation of r and k in 140 real stocks. This is described in a new section in the text. All analyses were subsequently redone, with no major changes in results but slight improvements and the opportunity to remove two of the previous 7 filters.

R2.6: Lines 244-252: The approach of trimming the $r-k_q$ pairs further via the MSY_q distribution, then adding another 30% uncertainty (is this CV?), is strange and seemingly arbitrary (why 95% CI?). Why is this done? Why not just stick with the output distributions? And how do you know what “unrealistically narrow” CIs are?

R2.6 Answer: We have removed this trimming and now use median and quantiles of the results for most likely central value and approximate 95% confidence limits.

R2.7: Line 273: What biomass (total, spawning, other?) was used from the stock assessments? This matters as to the interpretation of what the surplus-production model is measuring, and how the underlying selectivity assumption matches the assumption of $FMSY=r/2$. This is needed to understand Table 2 results as well. Please clarify the biomass and acknowledge the selectivity assumption.

R2.7 Answer: About half of the examined stocks reported CPUE data from commercial fishers or from scientific surveys and the other half reported spawning stock biomass, which was treated as CPUE. For the purpose of this study, the type of CPUE was irrelevant because both BSM and AMSY used the same CPUE data, and the purpose of the exercise was to see whether AMSY can reproduce the results of a full Schaefer model without the catch being known. In other words, problems resulting from TSB versus SSB versus commercial CPUE versus survey CPUE would have affected both BSM and AMSY.

R2.8: On line 418, it is mentioned that selectivity is contained in the r and k parameters, which is not correct. In this case, it is contained in the CPUE.

R2.8 Answer: We agree here with Reviewer 2 and have removed the mention of selectivity in that sentence.

R2.9: Lines 361-375: The argument for using the Schaefer model is not strong. There is a good understanding, based on life history, what BMSY might be. The Pella-Tomlinson is a general formulation, thus giving a much more flexible approach, whereas using the Schaefer model may significantly overestimate overfishing. Why not allow the flexibility and have the user specify the shape parameter?

R2.9 Answer: Reviewer 2 prefers the flexibility of the Pella-Tomlinson model. However, there is no biological basis to its additional shape parameter, i.e., what values it should take as prior and thus how the deviation from the logistic S-shaped curve of population growth should be, based on the life history of the species. Given that we are dealing with a data-poor situation, it does not seem prudent to try to estimate this ill-defined parameter. We have stressed this point within the existing justification for selecting the Schaefer model.

Minor considerations:

R2.10: There are several places where values are called reference points when they are not. Line 46: $F/FMSY$ and $B/BMSY$ are not reference points. $FMSY$ and $BMSY$ are reference points.

R2.10 Answer: We agree and have fixed the text accordingly. See also R2.19.

R2.11: Line 80: Schaefer model assumes reference points (e.g., $FMSY=r/2$), it does not calculate them. Again, I think stock status is what is meant.

R2.11 Answer: While in our opinion the Schaefer model does estimate r and k , we followed the reviewer and replaced “reference points” with “stock status and exploitation”.

R2.12: Line 295: r , k_q and F are not reference points.

R2.12 Answer: F was not in the list; r , k_q and MSY_q are now referred to as “population dynamic parameters”.

R2.13: Line 168: The value of 0.25 seems arbitrary. What is it based on? Should this be stock specific?

R2.13 Answer: Half of BMSY is widely accepted as a proxy for Bpa or the border of safe biological limits below which recruitment may be impaired. In the Schaefer model $0.5 BMSY = 0.25 k$. The text has been amended to make this connection clear, with reference to the ICES advice background, i.e. their rule for reduction of F when $B < MSY$ Btrigger.

R2.14: Lines 240-241: Does this also happen in CMSY when fitting catches? It seems this may be a sign of parameter misspecification. Double check that this isn't a sign of something to address.

R2.14 Answer: This is a misunderstanding. AMSY assigns a lognormal random observation error to the input CPUE data. Thus, different runs have different observation errors for every single year in the time series, and only those parameter values and ‘observation error-corrected’ CPUE trajectories that pass all filters contribute to the results. The text has been amended to better reflect this process.

R2.15: Lines 315-316: BSM had higher k and r variance, but this could be due to the CV on the index being fix by the BSM model (same as AMSY?) and the prior on k , which is not clear if it is the same magnitude as the prior on k_q . And the fact that AMSY is more precise is not necessarily a good thing given that Bayesian models are usually better at estimating uncertainty.

R2.15 Answer: Lines 315-316 do not refer to BSM variance, so it is not clear what Reviewer 2 is referring to here. In any case, as stated, AMSY variance of F/F_{MSY} is higher than in BSM and B/B_{MSY} variance is about the same or also higher, with few exceptions. Since this may be a misunderstanding and since this is listed among minor issues, no action was taken.

R2.16: Lines 326-333: It is not obvious if comparing a relative to absolute measure (k_q vs K and MSY_q vs MSY) is a fair comparison as the absolute value is also taking into consideration the value of q . Please consider if this is appropriate.

R2.16 Answer: Reviewer 2 has a point, because the observed deviations may in part be caused by catchability q , which is not taken into consideration by AMSY. We have added a sentence that makes this potential source of divergence explicit.

R2.17: Lines 346: One of the most interesting results is that the independent LBB [Froese et al. 2018] approach and this approach may be getting similar stock status estimates. While this is not always expected as it is very common for data types to contradict each other, to be able to confirm this behavior would be good, but I do not see this comparison in the paper. Are readers expected to go and read the two references in order to make this comparison? Why not add it to Table 3?

R2.17 Answer: We agree with Reviewer 2 that the good agreement between trends in B/B_{MSY} estimates based on length frequencies and on CPUE are unexpected and very encouraging. We do not stress this more because LBB results (for a selected year) were used as priors for AMSY, so the AMSY results are not fully independent of LBB. Comparing the similarity between LBB and CPUE trends is beyond the scope of this AMSY paper, but in a way we raise a flag here for subsequent papers to explore this aspect. No action was taken.

R2.18: Lines 407-408: I do not agree one cannot use uncertainty estimates of fishing rates. By this argument there emerges some arbitrary line of what is too much uncertainty. The authors' sentiment implies that uncertainty should not be ignored, which is an important point. One therefore needs to express their risk tolerance in order to handle the uncertainty. I would remove this rejection of use and make it a strong consideration/warning on how to handle the uncertainty in this metric.

R2.18 Answer: We agree with the reviewer and have changed the text accordingly.

Edits/suggestions:

R2.19: Line 47: Biological reference points, thus those associated with MSY , are based on life history values (r , M , L_{inf} , k , maturity, etc.) and selectivity, thus they often can be estimated with limited data. It is stock status (values relative to the reference points) that is typically unknown. This sentence should probably just refer to stock status and not reference points to maintain its main message.

R2.19 Answer: The text was changed to: "...exploitation level and stock status are unknown...". This also solves R2.10.

R2.20: Line 58: Claiming that CPUE and abundance are in good agreement is loaded with assumptions, and thus should not be stated as matter of fact. Some of these issues are addressed in the Discussion section; having such a broad statement here is unnecessary. Just saying that CPUE can reflect abundance under certain conditions should be good enough.

R2.20 Answer: The text has been changed to reflect this concern.

R2.21: Line 72: “the resulting presentation” is an odd turn of phrase, and I am not totally sure what it means. Please consider revising this to be clearer.

R2.21 Answer: The text was rephrased to make this point clearer.

R2.22: Line 90: “... resulting in a factor of 1 when $B_t=0$...”. Done.

R2.23: Line 91: “ CPUE is often assumed...”. Done.

R2.24: Line 126: A prior for k_q should also be mentioned here, even though it is derived later from B_t/k .

R2.24 Answer: As the reviewer says, a prior for k_q is derived without intervention by the user by combining the relative biomass B_t/k prior with the observed CPUE in that year. Thus, it would not be correct to state that a prior for k_q is required input in addition to a prior for relative biomass. Given that the derivation of the k_q prior is explained in detail in the text elsewhere and was understood correctly by reviewer 1, we left the text here as is. See also R3.5 Answer.

R2.25: Line 134: Need more details on how r was derived from FishBase. What section? Life history tool or somewhere else?

R2.25 Answer: Done.

R2.26: Figure 1 font is very small. Just want to make sure this improves for publication.

R2.26 Answer: Figure 1 will be redone with larger fonts prior to publication.

R2.27: Line 389: “in the penultimate year were...”.

R2.27 Answer: Done.

Reviewer: 3

General comments

The authors present a novel approach for the assessment of data-limited stocks. Their method is applicable to stocks for which abundance trend information (CPUE) is available, along with estimates of stock productivity and at least one independent estimate of relative stock status (B/K). Catch data are not required. The discrete Schaefer model for biomass is recast into units of CPUE and 'relative catch' ($C[q,t]$) with associated relative reference points ($K[q]$, $MSY[q]$). The manuscript is easy to follow, but in general does not adequately describe how the results are sensitive to prior specifications and the chosen set of filters based on the CPUE time series.

Here are a few topics I'd like to see addressed in a revised manuscript:

R3.1: The method requires a prior for relative biomass ($B[t]/K$); however, the text does not clearly define how to choose a year for this prior. The LBB approach requires length-frequency data, so it seems logical that the priors developed in this manner would apply to a year during which the lengths were collected. Was that the case? Other parts of the text refer to the prior being applied to the first year in the time series (e.g. the “Simulated Data” and “Real Data” sections). When and why was the first year chosen for the prior?

R3.1 Answer: Text was added in the section ‘Priors for r , k_q and $F/FMSY$ ’ to explain the selection of the best year for the B_t/k prior.

R3.2: The results should better describe how the proposed filters affect the results. Currently, the authors state that the upper or lower end of r & k are affected, but it would be useful to include marginal density plots for key parameters as well as for derived quantities ($F/FMSY$ and $B/BMSY$) before and after the filters were applied.

R3.2 Answer: We have seriously considered this proposal; however, the effect of the filters can be very different for different simulated or real stocks, basically being a function of r and $CPUE/kq$. Exploring and showing comparative density graphs for all possible combinations of r and $CPUE/kq$ is an extensive paper in its own right, which some of the co-authors are keen to do, but it is clearly beyond the scope of this 'proof of concept' presentation of a new method and the interest of most readers. We have, however, added a section where we explain better the purpose and function of the filters and suggest that this is an area where $AMSY$ will benefit from future research. Note also that the current paper already far exceeds the testing done in other widely accepted presentations of new data-poor methods. For example, MacCall's DCAC method mentioned as good example by two of the reviewers uses two examples of fully assessed stocks to demonstrate the usefulness of the method. In comparison, this study uses 24 simulated stocks for proof of concept and 140 fully assessed stocks for evaluation.

R3.3: It's unclear whether the relative reference points ($F/Fmsy$ and $B/Bmsy$) are sensitive to changes to the assumed values of process and/or observation error. A set of values were chosen (lines 171-172), but there is no evaluation of how $F/Fmsy$ and $B/Bmsy$ are affected by these assumptions. One option is to draw from distributions of the variance parameters, examine which values are not excluded by the filters, and plot the retained values against model outputs.

R3.3 Answer: We have stressed that the chosen values are preliminary. They can be changed by the users.

R3.4: The supplementary materials (>200 pages!) as currently presented will be overwhelming to most readers without further clarification. Appendix 3, in particular, would benefit from a 'walk-through' of the method for a single stock. The 1/2 page of text at the beginning of Appendix 3 is inadequate to allow for replication of the study.

R3.4 Answer: We note that the reviewers ask for substantially more testing and details and then complain about the presentation of the testing that was already done being too long. But we followed the thrust of this comment and have revised the text in the Supplement.

R3.5: The prior for $K[q]$ is derived from the prior for $B[t]/K$ (line 150) and an observed value of $CPUE$ (at time t). How is t chosen, and doesn't that suggest that the prior for $K[q]$ is simply a transformation of the prior for $B[t]/K$? Bivariate plots showing the correlation structure of the joint prior (r , $B[t]/K$, and $K[q]$) would be useful to understand how these priors are correlated.

R3.5 Answer: The choice of the year of the prior is explained now in the text as answer to R3.1. If one has an absolute stock size Bt/k and a relative stock size $CPUEt$ for the same year, then one can calculate the range that kq can take from $kq = CPUEt/(Bt/k)$, by inserting $CPUEt$ and using first the lower and then the upper range value of the Bt/k prior. This is already stated in the text below Table 2, and in so far the prior for kq is directly derived from the Bt/k prior. In other words, the prior for Bt/k is used to preliminary put the $CPUE$ into an MSY framework. This placement is then refined by the $AMSY$ Monte Carlo filtering process. A text to this effect has been inserted in the paragraph below Table 2. See also R2.24 Answer.

R3.6: Details of the filtration process are not adequately described (see below), and the authors should include better descriptions of these filters in the text and not rely on links to the code. The fraction of MC simulations excluded by each filter should be included in the results.

R3.6 Answer: This concern has been answered under R3.2. To address it, we have added new text to better explain the purpose and effects of the filters. Also, we have removed two of the filters.

Line-specific comments

R3.7: Lines 155-156: In this case, it suggests that the prior for $B[t]/K$ is poorly specified.

R3.7 Answer: This case refers to e.g. a kq prior close to unexploited, e.g. 0.8 – 1.0. The rule for minimum kq prior range will expand this to 0.8 – 1.04. In an opposite scenario, consider a CPUEt = 100 and a Bt/k prior of 0.01 – 0.4, giving an upper kq prior range of $100/0.01 = 10000$ and a lower range of $100/0.4 = 250$. The rule of maximum kq prior range will reduce the upper range from an unrealistic 10000 to a more realistic $3 \times 250 = 750$. Yes, one could say that the lower Bt/k prior range of 0.01 is poorly defined by the user, but it is a common way to reflect uncertainty about stock size, and the built-in rules can deal with that. Since the two other reviewers had no problems here, no action was taken.

R3.8: Lines 181-190: Is ‘catch’ actually ‘relative catch’ in this paragraph? The degree of negative catch allowed (7% of K) is said to be based on simulations, but that is probably sensitive to the assumed values of process and observation error variance. A better description of the rationale used to identify the 7% is needed for users who may select different values for the error terms.

R3.8 Answer: In the context of AMSY, these are indeed relative catches and that has been corrected in the text (note that the logic of the argument presented there does not change). We revisited this number and tried different values for allowed negative relative catch in test runs against the simulated data. New values are -6% for very low and -2% for low productivity. The main purpose of the study is to present a new method with preliminary tests, not to explore optimization of all parameters. That should be the work of subsequent publications, as has been done with other assessment methods. To accommodate this criticism, we stress the need of additional sensitivity testing in the Discussion. See also R2.24 Answer and R3.5 Answer.

R3.9: Line 197: It's not clear what is meant by “empirical multipliers (based on simulations)”. Each filter should be described in detail, as this is the basis for how the model excludes parameter combinations from which the reference points are derived. Line 207: same comment -- “MSY-multiplier values derived from simulations”? Line 225: The boundaries (-3 and 5) used to identify ‘unrealistic’ values of F/F_{msy} are going to have a greater or lesser effect depending on the user's choice of process and observation error terms. How were these values chosen?

R3.9 Answer: These points are addressed in R2.24 Answer, R3.5 Answer and R3.8 Answer.

R3.10: Lines 247-248: How is this enforced? Are additional MC simulations generated from an assumed error distribution with the same mean?

R3.10 Answer: Reviewer 2 also questioned whether this additional filter was needed, and we removed it. See also R2.6 Answer.

R3.11: Lines 258-259: “...first year biomass was also used as a prior...” [see comment R31 above]

R3.11 Answer: The text was amended to explain that the first year was chosen to minimize influence of this prior on the estimated relative biomass 50 years later.

R3.12: Lines 288-303: How were the AMSY priors specified relative to 'true' values? Was AMSY given priors with the same central values at the 'true' values?

R3.12 Answer: No central or 'true' values were used as part of the priors, only uniform ranges which included the true value somewhere.

R3.13: Lines 305-307: How were the relative biomasses from AMSY converted back to unexploited biomass estimates from the BSM model? This would require knowledge of the true q value, wouldn't it?

R3.13 Answer: In the simulations, the 'true' values for kq and $MSYq$ were known (no transformation needed) and could be used for the comparison of results. Reviewer 3 has correctly noted that instead the text wrongly referred to k and MSY . We have corrected that error and thank reviewer 3 for having spotted it.

R3.14: Line 338:

R3.14: Answer: Line 338: see general comment #4. See R3.4 Answer.

R3.15: Lines 354-367: As Maunder (2003) pointed out, it is preferable to use the Pella-Tomlinson model and specify values for the shape parameter (i.e., making the assumption regarding B_{msy}/k explicit). Values of B_{msy}/k greater than 0.5 have also been proposed (Walters and Kitchell, 2001; MacCall 2002), and the P-T model would allow the user to explore these alternatives and their impacts on results.

R3.15 Answer: Maunder (2003) states: "This shape parameter can in theory be estimated from time series data, although in practice, there is generally insufficient information in individual data sets to estimate it with any precision." [...] "Such studies combine life history theory with assumptions about individual growth parameters, fishery selectivity, and other relevant age-structured effects to provide bounds on plausible values for SB MSY reference points. However, the use of such strategies to inform the shape of the surplus production relationship remain highly contested [...]" Given that AMSY is a data-poor method, and given that there are no widely accepted and easily accessible priors for the shape parameter, we followed general scientific practice and used the most parsimonious available model, i.e., the logistic curve of population growth and the resulting Schaefer model for surplus production. We have extended the text of the discussion of this topic.

R3.16: Lines 375-377: This is difficult to interpret without a better description of how AMSY was configured in the simulation study (see comment for lines 288-303) See R3.12 Answer.

R3.17: Line 461: $F_{msy} = r/2$ because of the assumed Schaefer model; variability in F_{msy} is underestimated because the model assumes $B_{msy}/k = 0.5$.

R3.17 Answer: See R3.15 for the reasoning for selection of Schaefer over Pella-Tomlinson. Note also that uncertainty in F/F_{MSY} estimates of AMSY is very high and given as a reason using these estimates with caution (if at all). The main result of AMSY, as stressed in several places in the text, is an estimate of recent stock status (B/k).

Discussion

While responding to the many points of the reviewers was tedious and changing the model and re-running about 200 analyses was a lot of work, there is no doubt among the authors that the new method was substantially improved by the review process. The authors use this opportunity to thank the Editor and the 3 reviewers for the considerable work they have invested in that process.

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FEMALE FISH GROW BIGGER – DEAL WITH IT!*

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Abstract

In the spirit of transparency, and to provide further element for a serious debate about the Gill-Oxygen Limitation Theory (GOLT), the comments of an editor and a semi-anonymous peer reviewer, and the responses that were provided are presented which preceded the publication of Pauly, D. (2018. *Trends Ecol. Evol.*, doi 10/10.1016.tree.2018.12.007). The issue was a paper by D.J. Marshall and C.R. White (2018. *Trends Ecol. Evol.* doi.org/10.1016/j.tree.2018.10.005) that reiterated a common, if mistaken, claim that high costs of reproduction limit the growth of fish. This is contradicted by the fact that, in the overwhelming majority of fish species, the females grow to be larger than the males, in spite of their higher reproductive investment.

Introduction

Following the interesting reception of the publication of my first exchange with three peer-reviewers and an editor concerning one of my articles on the Gill-Oxygen Limitation Theory (GOLT) in *Global Change Biology* (Pauly 2018), this contribution presents a similar exchange regarding a smaller paper published in *Trends in Ecology and Evolution (TREE)*.

The issue was a paper by Marshall and White (2018a), who concluded the hyperallometric growth of the gonad of some fish invalidates widely used growth models, including that of von Bertalanffy.

I took issue with this view because it built on the commonly held notion that the growth of fish is limited by the ‘energy’ they devote to their reproduction (Hubbs 1926; van Oosten 1923; Jones 1976; Lagler *et al.* 1977; Sebens 1987; Day and Taylor 1997; Charnov 2008; Quince *et al.* 2008). However, if this were correct, female fish - which have higher reproductive cost than males - would always be smaller than males. Yet, in FishBase (www.fishbase.org), over 664 (i.e., <80%) of all fish species for which sex-specific growth curves were available (n= 825), the females grew much larger than the males.

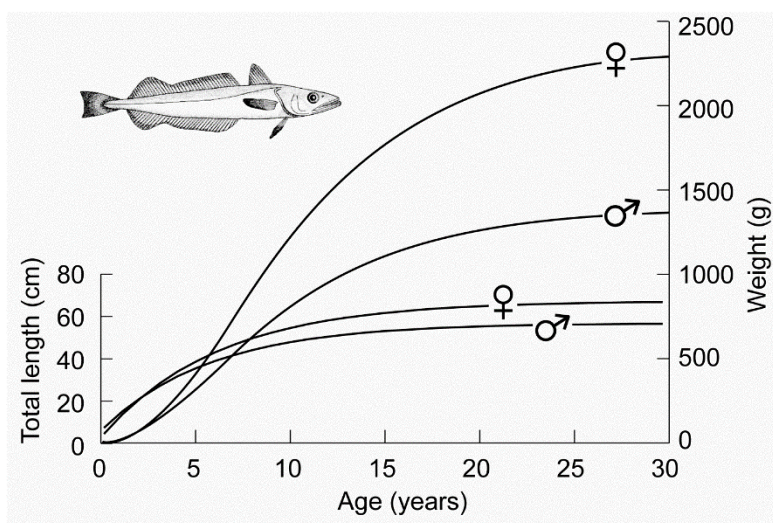


Figure 1. Female fish generally grow bigger than males, as here illustrated by hake (*Merluccius merluccius*) from the Adriatic Sea. Modified from Pauly (2019), who provides an explanation and sources for the growth curves.

* Cite as: Pauly, D. 2020. Learning from peer-reviews II: females grow bigger – deal with it! pp. 125-130. In: Pauly D. and V. Ruiz-Leotaud (eds.) *Marine and Freshwater Miscellanea II*. Fisheries Centre Research Reports 28(2) Institute for the Oceans and Fisheries, University of British Columbia.

This fact, illustrated in Figure 1, is one that I think biologists must confront, rather than conveniently ignoring it. This is why I wrote a paper on this (Pauly 2018), whose review is presented here.

Comments and Response

Dear Editor,

Many thanks for the opportunity to resubmit my contribution and for your suggestions on how to improve it, which I immensely appreciate. As you will see below, I have agreed to many of your and the reviewer's suggestions, but there are some I could not (I explain why). If this should prevent my submission from being accepted, I won't make a fuss, as I am aware of the some of my ideas being counterintuitive. Here we go:

- 1.) *While I appreciate that you've tried to make the title enticing, I'm concerned that this title, particularly the exclamation mark, could be considered antagonistic†. We want to encourage a healthy debate, not make people feel defensive. Please rethink the title and aim for something enticing yet gentle.*

I propose Female fish grow bigger – let's deal with it, which is much friendlier, but has more words than strictly allowed (but short words, not like 'hy-po-allo-me-try...).

- 2.) *The references to Pauly (1984 and 2010) form the core of your argument and they are all from your group. Do you have some references for the GOLT from different research groups? In the submission guidelines it is stated: "Letters should not be used as an opportunity to promote your own work".*

This request is one of the real problems I have: even though I have been able to marshal what I think is a large amount of evidence (including tests of some of its key aspects) for the GOLT in my 2010 book on the topic, which also contain numerous supportive quotes, papers explicitly endorsing the GOLT are still lacking. I have added two references (Thorpe 1990; Kolding *et al.* 2008) to experimental work supporting my contention that declining growth rates trigger spawning (and thus that it not spawning which reduces growth), and which explicitly cite my 1984 paper on this, with Kolding *et al.* (2008) being an explicit test. But if your criterion is that I must cite full-throated endorsement of the GOLT from others before I can defend it, then I must withdraw my submission, because I cannot meet it.

- 3.) *When I emailed with the original author about your letter he felt that the arguments presented here are very similar to those presented in your Global Change Biology paper and that the goldfish argument is also presented in your book. While I encourage you to refer to these, TREE letters should be a synthesis rather than highlighting omissions in the articles.*

The lone asexual goldfish argument is recycled here because it is a good one (almost as good as the 'universal acid' of Dennett 1995), because it undermines all hypotheses linking the shape of growth curves to reproduction (or to predation, or other ecosystem parameters). As for the *Global Change Biology* paper (I presume you are referring to Pauly and Cheung 2017), it only mentions 'reproduction' twice, very casually, to say that "concentrating on the physical constraints to which fish are exposed made it possible to explain the basic patterns of size, growth and reproduction, and their relationship with environmental change (Pauly 2010)" and that "a given species of fish will inherit a gill size that was sufficient for its ancestors' growth in the appropriate time to a size appropriate for their reproduction". Thus, it is not the case that we presented in the earlier paper the argument in my submission to *TREE*.

† The title originally proposed was 'Female fish grow bigger – deal with it!', i.e., as in this contribution.

- 4.) *The referee raises some interesting points about different growth models. I believe that some discussion of the various potential models for fish growth would be of great interest to TREE readers.*

I have no doubt that a review/discussion of growth model would be interesting to *TREE* readers (in fact, I would love to be asked, one day, to write a full review of this topic for *TREE*). Here, however, dealing with growth models in a way that would do (some) justice to the referee's ideas (see below) and to the many brilliant colleagues who have opined on the topic would be opening a giant can of worms, with a number of allowed words much too small to conjure the recapture their wriggling mass.

- 5.) *In addition, please also pay particular attention to the following points: [These points were derived from TREE's instructions to authors and do not need to be reproduced here]*

I will do all this. The figure is an original; it changed it from the first version, which was submitted in error. This does not change anything else.

Reviewer - General comments:

- 6.) *Pauly is a leader in the study of fish growth and deserves to be heard, especially in defense of his own model. However, I do not find his view and that of Marshall & White as conflicting as Pauly seems to make out. Both views focus on different aspects of the overall energy/oxygen budgets of fishes (oxygen supply via gills and oxygen/energy demand for maintenance and activity by Pauly versus energy/oxygen demand of reproduction by Marshall & White), all of which should be considered to gain a holistic understanding of growth.*

Dr. Douglas Glazier thinks that a “holistic understanding” of growth should explain the growth of bacteria, fish, hibernating bears and tomatoes (see Glazier 2015), which he recommended I read, and which I now cite. Naturally, no theory can do what he asks for, and thus he finds all of them wanting. Moreover, I don't believe that a holistic understanding of growth as defined by Dr. Glazier is possible (or that it would predict anything, if it were).

- 7.) *However, both 'constraint' views cannot explain why minnows and anchovies grow to small adult sizes, whereas carp and tunas grow to much larger adult sizes.*

But the GOLT does not claim to explain why minnow and anchovies are small while carp and tuna grow to much larger sizes. We have the theory of evolution for that. What the GOLT explain is why a minnow and a large tuna have gills which supply them, as they grow, with a declining oxygen per unit weight, and that this reduced oxygen supply reduces their growth rate until finally, they stop growing.

- 8.) *A priori, one might think that geometric constraints on oxygen-supply or allometric constraints on the energy costs of reproduction should cause fishes to reach adult sizes that vary over a narrow range, rather than the huge range that we see (>8 orders of magnitude in mass). In my opinion, what is missing from these views is the importance of biological regulation in the control of growth (e.g. see review of Glazier 2015). Growth may not be simply about oxygen/energy constraints. It may be the result of adaptive regulation molded by natural selection in response to various environmental factors.*

No ‘adaptive regulation’ exists which can enable an animal to live without an adequate oxygen supply (this applies even to crucian carp, which although can survive months without oxygen, do so by incurring an oxygen debt which must be eventually balanced). Moreover, the GOLT is not about both “oxygen/energy constraints”. It is about the fact that gills, being a 2-D surface cannot but fail to keep up with the 3-D bodies

that they have to supply with oxygen. Hence, big/old fish have less and less oxygen per unit weight; however, as I mentioned above, animals cannot live without an adequate oxygen supply, even if they have an adequate “energy” (i.e., food) supply.

- 9.)** *Specific comments: L 19-21: Higher water temperature not only increases O₂ demand, but also decreases O₂ availability, thus compounding the respiratory stress.*

Yes, but this effect is much weaker; however, it is now mentioned.

- 10.)** *L 27-29: This goldfish example is interesting, but in my opinion makes a moot point. This is because I do not think that Marshall and White are arguing that reproduction is always the cause (or only cause) of ceased growth. If this were true, all fish would be determinate growers, ceasing growth completely at first reproduction.*

Not so: the argument that is most commonly made is that increasing gonad size during the reproductive season gradually reduces the ‘energy’ available for somatic growth. The Marshall and White paper makes this point repeatedly.

- 11.)** *Obviously, this [i.e., that all fish are determinate growers] is not the case, as Marshall and White know. Are they not simply saying that given a fixed energy budget, increasing energy costs of reproduction will decrease energy available for growth, but not necessarily completely stop growth? This allocation of energy to reproduction and away from growth will be more dramatic if reproductive energy costs increase hyperallometrically with increasing female size. However, one must also consider that total food energy intake also increases with female size, thus allowing the possibility for her to grow and reproduce continuously.*

Dr. Glazier says “I do not think that Marshall and White are arguing that reproduction is always the cause (or only cause) of ceased growth.” Then he suggests that they believe “that given a fixed energy budget, increasing energy costs of reproduction will decrease energy available for growth, but not necessarily completely stop growth”. The cores of these two sentences (i.e., omitting ‘or only cause’ and ‘but not necessarily completely stop growth’) are in direct contradiction to each other.

- 12.)** *L 30-39: Why female growth usually exceeds male growth in fishes (despite greater energy expenditure by females for offspring production) is a fascinating question. The author suggests that this may be because males have greater activity costs related to mating and fighting with other competitive males that drains energy away from growth. If so, the costs of reproduction (albeit expressed differently) may be involved in the growth of both males and females, thus not contradicting the point of view of Marshall and White.*

Marshall and White suggested throughout their paper, that hyperallometry undermines most growth models, including the von Bertalanffy model as interpreted in the GOLT. As it is females that (by definition) have the biggest reproductive load, they have to be most affected by hyperallometry, and thus they should always be smaller than males – which they don’t.

- 13.)** *Furthermore, in some groups of animals (e.g. amphipods) males tend to grow bigger than females. Therefore, the author's argument is not general. In any case, I appreciate the author's point that costs of maintenance & activity should be included in energetic models of growth.*

The argument I make is that reproduction doesn't reduce the growth and ultimate size of fish, and that this is supported by the fact that females get bigger in most species of fish. A moment thought will suffice to see that this point is not refuted by males getting bigger than females in amphipods, or in a minority of fish species.

14.) L 39: Change "female" to "females"; L 41: Omit "the" before "pregnancies"; L 68: Change "male" to "males".

Done.

Discussion

Obviously, there was a response to the paper whose review was presented above (i.e., Pauly 2018) and it shows that Marshall and White (2018 a, b) are nothing if consistent: confronted with females that grew larger than males, they courageously concluded that "*Pauly's assumption that small fish have higher reproductive output than male fish is unsupported by data. There is no pattern of female investing relatively more in reproduction than male in fish (or other water-breathing ectotherms [Parker et al. 2017]). Indeed, for the species given by Pauly [Acanthopagrus butcheri], females invest relatively less in reproduction than males as a proportion of body mass (see Figure 5.5* in G.A. PhD thesis, Murdoch University, 1999)*".

Here, even hard-core supporters of the notion that fish growth is limited by reproduction will recoil: we have here biologists who are so desperate that they really suggest male fish invest more in reproduction than females, and who cite an unpublished thesis to support their claim.

I will be dealing elsewhere at length with this and related claims.

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* The figure in question was actually 5.6, but it didn't show that male *A. butcheri* have higher reproductive output; it showed only that at some point, the gonads of some males made up a larger % of their body weight than in females.

- Miscellanea Fisheries Centre Research Reports 26(2)*. Institute for the Oceans and Fisheries, University of British Columbia.
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ARE SMALLER FISH PRE-ADAPTED TO WARMER OCEANS?*

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Abstract

This contribution suggests that the well-documented genetic selection for smaller fish that is the result of decades of sustained, intensive fishing also selects for “skittish” fish with a relatively high metabolic rate. However, skittish fish are highly susceptible to the higher temperature likely to prevail in the next decades in fresh and marine waters, which should contribute to making fisheries more susceptible to the effects of global warming. We submitted a piece to this effect to a leading fisheries/marine science journal, but for reasons that are mentioned in an appendix, we did not agree to having it published along with a contrarian piece. We present here, instead, the article as originally submitted, along with an appendix with our response to the original reviewers’ comments.

Introduction

There is relatively good evidence that the larger/older fish of various species are more sensitive to higher temperatures than smaller/younger fish (Daufresne et al. 2009; Messmer et al. 2016; Pörtner & Knust 2007). It is also well documented that the intense, sustained exploitation of a given population results in the maximum size and the size at first maturity of the fish in that population to be reduced (Figure 1; Jørgensen et al. 2007; Heino et al. 2015). Combining these two lines of evidence, it could be argued that overfishing leads to fish becoming preadapted to ocean warming. In the following, we suggest that the opposite is the case, given the mechanism that actually causes fishing-induced size reduction.

To live, fish need oxygen, which they obtain through their gills. This organ, having to function as a 2-D surface held against a flow of oxygen-rich water, cannot grow as fast as the volume of the 3-D body that it supplies with oxygen. With isometric growth of head and body observed in most fish (Froese 2006), the O₂ supply per unit weight must therefore decrease as weight increases (G-line in Fig 2A).

As O₂ supply decreases, there will be a weight (W_{max}) beyond which a given fish cannot grow because it uses all the oxygen it gets from its gills for routine activities, with none left for net growth, i.e., the scope for growth has become zero.

From this, it follows that, as shown in Fig. 2B, an individual that has a smaller relative gill size, and/or is more ‘skittish’ (i.e., hyperactive), or inefficient at foraging or that has other reasons to display a high routine O₂ consumption rate, will tend to remain smaller, i.e., its scope for growth will tend to be lower than the individual in Fig. 2A (Pauly 2019).

* Cite as: Pauly, D. and R. Froese. 2020. Are smaller fish pre-adapted to warmer oceans? pp. 131-141. In: Pauly D. and V. Ruiz-Leotaud (eds.) *Marine and Freshwater Miscellanea II*. Fisheries Centre Research Reports 28(2). Institute for the Oceans and Fisheries, University of British Columbia.

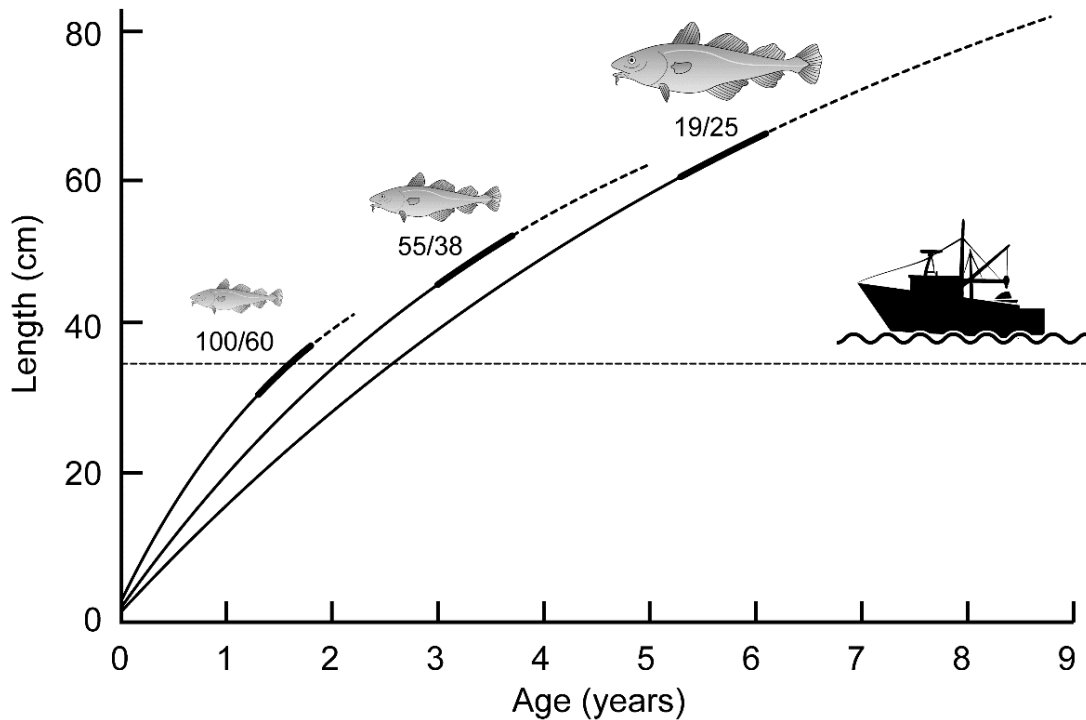


Figure 2. Impact of fishing on the reproduction of cod with small (60 cm), medium (90 cm), and large (120 cm) size growth types. The lower left part of the three growth curves indicates the juvenile phase and the subsequent parts indicate the mean duration of the reproductive phase (i.e. half of the maturing fish are still alive at the end of that phase), with (bold) and without (bold + dashed) fishing. Fish are vulnerable to fishing above 35 cm length (horizontal line), with mortality caused by fishing assumed about twice as high as natural mortality of medium sized cod. Because small cod mature before the onset of fishing, 100% reach maturity compared to no fishing, but their reproductive phase is shortened to 60% of the natural duration (bold section of curve, with indication of these percentages). In contrast, only 19% of large cod reach maturity and their reproductive phase is shortened to 25% of the natural duration. The strong reduction of the participation of large, late maturing cod in reproduction explains the fisheries-induced selection for small size and early maturity.

Fish growth and fisheries

Fish grow throughout their lives and - depending on their reproductive strategy - reach maturity between $1/3$ and $2/3$ of their maximum length (Froese and Binohlan 2000). Returning to Fig. 1, it is evident that the fish of a given population that are eliminated by intense and sustained fishing will tend to be the larger ones which mature at larger sizes, because many of them will be caught before they had a chance to reproduce. Conversely, what is left in that population are the skittish and/or inefficient runts, which managed to reproduce before they could be caught.

This, however, means that these fish do not have scope to accommodate an even higher metabolic rate. Rather, it is the larger fish that could accommodate warming because they could sacrifice some of their remaining scope for growth to accommodate a higher routine metabolism. In other words, you cannot further shrink pre-shrunk fish. This prediction is in line with historical evidence that populations that were subject to intense and prolonged overfishing were more strongly impacted by warming waters (Free et al. 2019).

A fishery that wants to avoid unnatural selection for small size and early maturity would increase the length at first capture close to the natural average length of parents (close to 80 cm in our example), where the catch for the given effort would also be highest (Holt 1958; Froese et al. 2016). Bones and otoliths of cod found in medieval middens suggest indeed a mean length in the catch and the population of about 80 cm at those times of large fish, large stock sizes, and low fishing effort (Barrett et al. 1999).

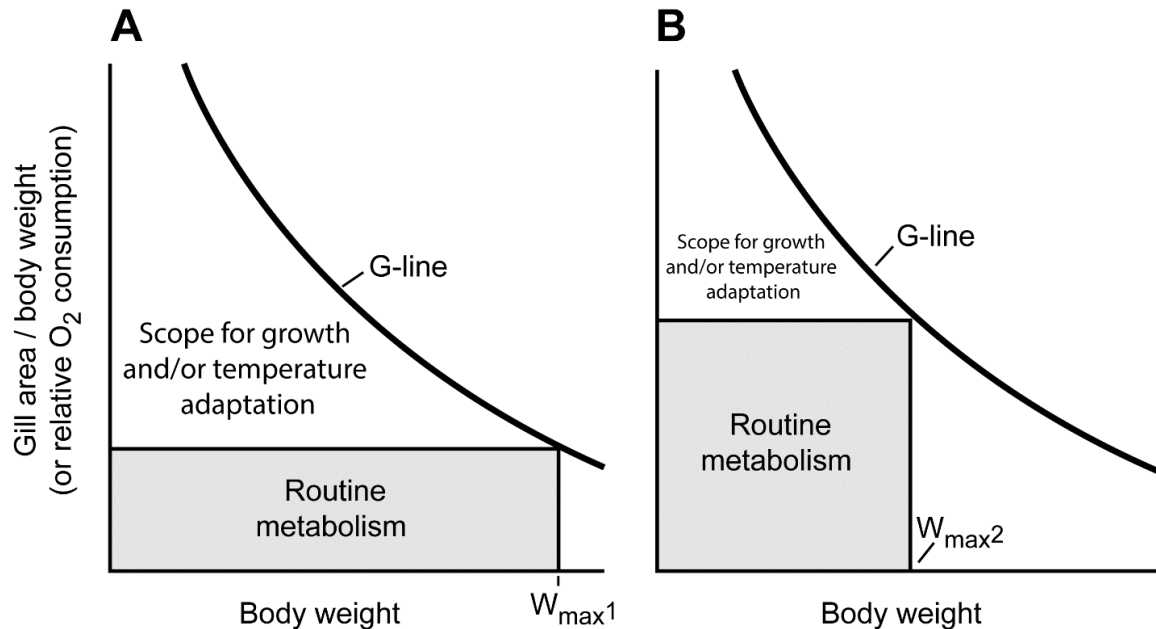


Figure 3. Schematic representation of the mechanism causing fish to remain small when their routine metabolic rate is elevated, featuring gill area per body weight (G-line) decreasing with body weight, due to gill area (a surface) not being able to keep up with body weight (proportional to volume); **A**, Relative O₂ supply (which is proportional to relative gill surface area) drops with increasing weight until a level is reached (at W_{max1}) when O₂ supply is just enough to satisfy routine metabolism. **B**, any factor causing routine metabolism to be elevated (e.g., higher temperature), or which select for fish with a high metabolic rate (size-selective fishing, as in Figure 1) reduces the maximum size that can be reached (hence $W_{max2} < W_{max1}$) and also the scope for adaptation to higher temperature.

Conclusions

In conclusion, overfishing and starting fishing at small body sizes is maladapting exploited fish populations to climate change. To reverse this trend, existing laws (UNCLOS 1982; MSA 2007; CFP 2013; HSP 2018) must finally be implemented, reducing fishing pressure below that which generates maximum sustainable yields and setting length at first capture such that large individuals can reproduce before capture. Such fishing would not only prepare commercial fish and fisheries for warming waters, rebuilding size structure, fecundity, and abundance would also stabilize catches and move exploitation closer to the sustainable maximum, thus mitigating potential future losses (Hixon et al. 2013; Froese et al. 2016; Barneche et al. 2018).

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Appendix

This appendix reproduces the editor's and reviewers' comments we received following the submission of the above contribution to a leading fisheries/marine biology journal. We provide here answers to these comments, but did not send them to the editors, because we were offered to resubmit our piece to be published as one side of a 'pro' and 'contra' pair of opinion pieces, which we didn't want to do. Thus, these responses are sharper than if we had to placate a journal editor.

The ellipses and words in square brackets are used here to mask the identity of the journal, its handling editor and one reviewer who signed his comment, and whose names would detract from the content of the discussion below.

Editor

I write you in regards to [your submission] entitled “Are smaller fish pre-adapted to warmer oceans?” which you submitted to [our journal]. In view of the criticisms of the reviewers found at the bottom of this letter, as well as my own reading of the manuscript, your manuscript has been denied publication in [our journal]. However, I have also discussed this decision with the Editor-in-Chief, and we do recognize that the argumentation behind the hypothesis you are presenting, and the reviewers' arguments against it, partly reflect discussions where the scientific community has not yet reached a consensus. In view of this, we see some merit in publishing two articles that would show both sides of the argument. Therefore, we are prepared to

consider a new submission of your manuscript that would be published back-to-back with an invited paper that presents the counterargument.

Please let us know whether this possibility appeals to you. We would then be happy to discuss how to proceed toward the new submission. Thank you for considering [our journal] for the publication of your research. I hope the outcome of this specific submission will not discourage you from the submission of future manuscripts.

Response:

We did not take the offer to present the contribution above “back-to-back with an invited paper that presents the counterargument” because this would have produced what we thought would be an unmerited stage for what arguments without merits. Rather, we are presenting the counterarguments to our submissions here, with what we think are valid counterarguments.

Comments by Reviewer 1

This article is based on the highly contested assumption that fish growth is limited by gill ability to supply oxygen. I will not dwell into multiple papers that have contested this assumption, demonstrating that oxygen supply is driven by demand and can be rapidly modified through multiple mechanisms, so as not to be limited by the gill surface area.

Response:

The vast majority of the “multiple papers” that the reviewer alludes to are contributions claiming *en passant* and without evidence that gills cannot be limiting to growth. The only authors who attempted to show that relative gill surface area can keep up with increasing body weight were Lefevre et al. (2017a, 2017b), and their argument is refuted by geometry and simple arithmetic (Pauly and Cheung 2017a, 2018). Indeed, we have developed this theme in material for a biology class aimed at teenagers (Pauly and Cheung 2017b).

Comment:

However, simply from an evolutionary point of view the idea that fish grow to a size where they become limited by oxygen supply does not make any sense.

Response:

Why not? Life is limited by all kind of factors: light, food, temperature...

Trying to hold one’s breath for a short while suggests that we don’t pay enough attention to oxygen.

Comment:

The basic premise of life-history theory is the trade-off in energy allocation between growth and reproduction (plus associated costs). Skittish individuals mature early not because they cannot get enough oxygen for growth but because they prioritize investment in reproduction versus growth.

Response:

This is demonstrably erroneous, as skittish fish display reduced growth long before they attain sexual maturity (see e.g., Vincent 1960; Bozynski and Pauly 2017). Also, this argument is illogical in that it assumes that the fish which “prioritize investment in reproduction versus growth” would also waste energy in being skittish – as if ‘skittishness’ did not have a cost, and were engaged in a whim.

Comment:

This trade-off has been demonstrated in multiple experiments, is at the core of aquaculture breeding programs (where early maturation and increased investment in reproduction is often not desired) and has been shown in many wild populations. Increased mortality selects for higher investment in reproduction at the cost of growth. There is no need to involve oxygen limitation here at all.

Response:

Breeding programs aiming at increasing meat yields always aim at getting “aggressiveness” out of the genepool (see www.welfarequality.net/media/1050/wq_decreasing_aggression_in_pigs_en.pdf). Similarly, aquaculture breeding programs, which aim for fast growing individual with delayed maturation actually selects for calm (non-skittish) fish; this is the reason with farmed Atlantic salmon (*Salmo salar*) are calm compared with wild conspecifics (Olesen et al. 2011). This also applies to Nile tilapia (*Oreochromis niloticus*), whose fast-growing GIFT strain, as a result of intensive selection for fast growth, consists of individuals that are much calmer than the controls (Bozynski and Pauly 2015).

Comment:

What does this mean for the ability of fisheries to preadapt fish to climate change? Very little is known about the effects of temperature on life-history evolution. How will increased investment in reproduction affect ability to adapt to climate change? It could be argued that earlier maturation correlates to higher metabolism, although again we don't have enough data to show this. If that is the case, then one can imagine that individuals with higher background metabolism might have little room to increase it further with climate warming. Which means that fishing is bad for climate adaptation. But there are many other alternatives. If larger individuals were more sensitive to higher temperatures, it would actually be good to mature earlier when higher temperatures don't damage you too much, so you have at least one chance to reproduce. It is all pure speculation at this stage. Moreover, we also have to consider adaption. Given large inter-individual variation in standard metabolism level there is good evidence that populations have enough additive genetic variance to adapt. A few generations might be enough to adjust metabolism to new conditions and all this fisheries-driven preadaptation becomes irrelevant.

Response:

Amidst the confusion in this paragraph, there were two points that made sense to us:

- One can imagine that individuals with higher background metabolism might have little room to increase it further with climate warming. Which means that fishing is bad for climate adaptation; and
- If larger individuals were more sensitive to higher temperatures, it would actually be good to mature earlier when higher temperatures don't damage you too much, so you have at least one chance to reproduce.

These are precisely the points that we make, and they are not “pure speculation” (see our other responses).

Comment:

I do agree with the authors that fishing is likely to hinder climate change adaptation. Not because of oxygen limitation, but simply because it is likely to be reducing genetic diversity and a basis upon which selection can work.

Response:

Well, yes. But respiratory performance and the use a fish makes of the oxygen it gets via its gills are also traits “upon which selection can work”.

Comment:

Another thing to add – populations that have been affected by fishing are indeed more vulnerable to climate change, but this can be explained by truncated age and size structure (Seccor et al. 2007 – storage effect; Hsieh et al. 2006, and others). Oxygen limitation is irrelevant here.

Response:

We agree that fisheries, by truncating the natural age and size structure, make fish populations more sensitive to environmental fluctuations, and by extension, to “climate change”. But climate change in the ocean manifests itself as increased water temperature with lower oxygen content, meaning higher metabolic requirements and lower oxygen harvest per breathing effort for the fish. How can oxygen limitation be “irrelevant” in such context?

Comments by Reviewer: 2

This manuscript [...] presents a conceptual idea based in two figures derived from previously published work but is not supported by new analyses of data or models. As such, I find this format to be within the scope of [of an opinion piece in our journal], but that the submission would have been stronger with a more rigorous analysis, and have reviewed the manuscript on this basis.

Response:

We agree that this is an opinion piece, presenting a novel way of thinking about an issue that will soon be on every fishery biologist’s mind, given the simultaneous occurrence of overfishing and ocean warming.

Comment:

The authors start from oxygen uptake as the constraining mechanism for fish metabolism, which in turn sets limits for growth and everything else. This basis is well documented and follows a long tradition in physiology. In general, I am positive to using more physiology in fisheries science and marine ecology.

Response:

We were delighted when we read this sentence, as we also think that “oxygen uptake [i]s the constraining mechanism for fish metabolism, which in turn sets limits for growth and everything else” and that “this basis is well documented and follows a long tradition in physiology”. This, however, is not known to many fishery biologists (notably Reviewer 1), who contest both points.

Comment:

The authors then take as starting point the general observation that larger fish species are most sensitive to climate warming. That is a general observation which could be made more nuanced, but the statement can be accepted for the sake of the general argument. They then combine this with the general trend of fishing to induce evolution towards smaller body sizes, which is supported by models and empirical analysis. They then ask whether fishing, as a long-term effect, would make species more resilient to climate warming. The paper develops this argument, and the details matter.

Response:

This is a fair summary of our argument.

Comment:

The authors rely on two mechanisms, of which one is the different scaling of gill area versus maintenance metabolism. This argument has been published many times before by the same authors, in papers and books, but is flawed. The same assumptions are also used by other authors and modelling tools, and go back to von Bertalanffy’s growth modelling from the 1930s. There are three main problems. First, there is now abundant

evidence that maintenance metabolism scales with weight at exponents well below 1. For life in general it is 0.71 (Brown et al. 2004).

Response:

In both von Bertalanffy's work, and its development by one of us (See Pauly 2019), maintenance metabolism is defined as the oxygen consumption of a fish such that it can generate the ATP to maintain the cellular machinery in its body, with no surplus for growth. This level of oxygen consumption can be estimated from the time-averaged metabolic rate of e.g., the heaviest fish ($W_{\max}$) of a given species in a given set of environmental conditions (especially temperature). This definition of maintenance makes the way it scales (for weight < $W_{\max}$) a moot point. In other words, the fact that oxygen consumption relative to body weight in fish scales similar to life in general does not mean that water-breathing animals are not limited by their gills. Rather, it is the intercept or height of the regression line that describes the amount of oxygen available for a given body mass, and that amount is much lower in water-breathers than in animals that breathe air.

Comment:

What matters for the argument here is the intraspecific scaling exponent, which likely is higher than between species but only in some cases as high as 1 (Killen et al. 2010). For most fish the exponent is well below 1. If gill area increases at an exponent with weight slightly higher than 2 (Palzenberger and Pohla 1992 document huge variation), then it is not at all clear that the graphical argument in figure 2 holds.

Response:

Scaling factor differences are of no relevance here. The well-documented scaling factor linking gill respiratory area (or metabolic rate) and body weight in fishes range between 0.6 and 0.9, with the higher values (e.g., in Palzenberger and Pohla 1992) usually referring to juveniles, in which this factor is indeed higher, as it is in teleost larvae (see e.g., Bochdansky and Leggett 2001); this is dealt with at length in Pauly (2010).

Comment:

Second, the authors use the intersection of the two curves as an argument for identifying the adult body size where there will be no more oxygen for growth. From a life history perspective, fish, or any other organism for that matter, don't live to grow but to reproduce. What matters is the size at which the ability to turn resources in the environment into offspring is at maximum. If one accepts that oxygen uptake would be a proxy for this, then it should be actual body mass on the x-axis, and the curves should be drawn not specific to weight but for the total body. That surplus, the difference between the two curves, most certainly peaks at a much smaller body size. Ignoring reproduction as shaping individual growth through adaptation violates the most fundamental insight from Darwin.

Response:

We do not understand this suggestion of reviewer 2, because the X-axis in Figure 2 does show "actual body mass" and the Y-axis shows relative oxygen consumption "for the total body". We do not use the intersection of two curves for anything. Rather, the two panels of Figure 2 display intersections of one curve representing oxygen supply vs body weight with two different thresholds levels, representing maintenance metabolism at $W_{\max}$ (see above for definitions), e.g., in a low and a high temperature environment.

We agree that all living organisms strive to reproduce themselves, but that doesn't mean that, e.g., a fish only has the option of putting all their eggs (so to say) either toward growth or reproduction. A good part of zoology, for example, is devoted to studying strategies and tactics that have evolved to enhance survival of offspring or of close relative.

That local condition should determine growth patterns, which then determine when size at reproduction is reached (Pauly 1984) is indeed a reversal of causal arrow (i.e., growth $\rightarrow$ reproduction) that is usually assumed to run in the opposite direction (i.e., reproduction $\rightarrow$ growth). However, most colleagues who argue for the latter have never examined its implications in depth, and the many logical and empirical problems it causes (e.g., growth in body weight peaks well after onset of reproduction in most highly fecund bony fish; see list of other problems in Pauly (2010)). All they have done is inferring causation from a correlation.

Comment:

Third, it is not only energetics that counts for expected reproduction, but also survival until one can reproduce. Natural mortality usually declines with body size, making the argument above non-linear with size in a non-trivial way. My experience with making models for this is that very few gets it right without doing the actual math. In the argument in this paper mortality is omitted altogether, and any firm conclusions about life history evolution cannot be reached.

Response:

We believe, on the contrary (with Darwin, incidentally) that evolutionary arguments that do not make logical sense, and/or rest on unverified, if widely held assumptions, do not become valid when they are put into mathematical models. For example, a single goldfish can be kept in an aquarium, and its growth, rapid at first, will cease at some point, without that fish have ever spawned or even elaborated gonad tissue. It will also not have been subjected to any mortality, natural or feline-induced. The same is true for most fish in large public aquaria, for which it cannot be argued that their growth stopped because of bad water quality or lack of space. What does this *Gedanken* experiment do? It completely disproves the causal arrow with 'growth $\rightarrow$ mortality'. (This, incidentally, is the kind of thinking that Charles Darwin used to make his points, not math).

Comment:

These three flaws have followed this graphical model and the von Bertalanffy growth curve for life history purposes for a long time. That the model has been published and used widely does not make it right, and I firmly believe it should be abandoned, the sooner the better. If this model, violating known biological observations and mechanisms, happens to make predictions that match observations it is only because there are multiple errors in it that somehow cancel, and any extrapolation or argument about causation would be without mechanistic basis.

Response:

In FishBase (www.fishbase.org), which the authors initiated, there are, as of January 2020, 11,767 sets of von Bertalanffy growth parameters, describing the growth of the Philippine goby *Mistichthys luzonensis*, with reaches 2.5 cm as well as that of the whale shark *Rhincodon typus*, which reaches 14 m. There is hardly any other model in biology that has been fit successfully to so many data sets. We find it extraordinary that the thousands of authors who generated these growth curves have been misled to the extent suggested by this reviewer. As for the sound biological basis of the von Bertalanffy growth equation see Pauly (1981, 2010/2019).

Comment:

The other mechanism the authors draw on is fishing-induced evolution, where it is correct as they state that many fisheries remove late-maturing fish before they reproduce. The consequence, as the authors also state, is that early-maturing fish succeed to reproduce, often at smaller sizes, and that their genes are therefore found in higher proportions in subsequent generations. But selection on maturation age/size does not imply selection for otherwise poor genetic makeup, as the authors describe in imprecise and unprofessional language laden with negative value (lines 50-51). The inference leading up to this statement does not follow logically from the premises stated, which takes away an important basis for their overall conclusion.

Response:

Two points made here are:

- (1) “selection on maturation age/size does not imply selection for otherwise poor genetic makeup”; and
- (2) “the authors [use] imprecise and unprofessional language laden with negative value”.

Re item (1): We agree that being small doesn’t necessarily imply being skittish. Thus, just as there are small dogs that are temperamentally skittish (terrier) and others that are calmer (dachshund, or wiener dog), there are small fishes that are small and generally calm (e.g. stonefish), while others are comparatively hyperactive (e.g. anchovies). However, this is not what is meant here. We are referring to individual fish of a given population, which are so skittish that their growth is impaired, so that they it is not caught be a gear that selects larger but calmer fish. Or as stated in our contribution above “what is left in that population are the skittish and /or inefficient runts, which managed to reproduce before they could be caught”. We have never encountered in the literature on genetic selection any arguments to the contrary and the reviewer hasn’t either. Instead, he/she complains that our language is imprecise, unprofessional and (negative) value laden.

Yet the survivors (to use a neutral term) are inefficient, at least in terms of food conversion efficiency (Gerking 1971). They are also runts. As defined in Wikipedia, “in a group of animals (usually a litter of animals born in multiple births), a runt is a member which is significantly smaller or weaker than the others.”

Thus, runt is a *precise* term for exactly what we meant, and if it has a negative connotation, it is because, often runts die prematurely. But the runts in our paper don’t die. They even reproduce and to increase their share in the population.

We do not respond to the point about “unprofessional language”.

Comment:

I realize that this review is not much of an evaluation of the submitted manuscript but maybe more of a counterargument to the methods and reasoning applied. I am generally reluctant to recommend rejection of a paper only because I disagree. I firmly believe different arguments should be published for everyone to see and judge, and that this is a fundamental strength necessary to ensure scientific progress. I therefore avoid giving a particular recommendation but leave this to the editor(s) to decide.

Response:

Fair enough. However, we decided that we would renounce the editor’s offer to present our contribution (above) back-to-back with a contribution that would elaborate on the comments presented in this appendix, which we fear, are only conventional, negative responses to novel thoughts.

Minor comments:

It is unclear how Figure 1 was constructed, why late-maturing fish also grow more slowly during the juvenile phase, and what consequences fisheries selection has for Darwinian selection on life history traits including physiology. The description in the main text is not making use of this figure or explaining it.

Response:

The three hypothetical growth curves for North Sea cod in Figure 1 have the same to but different L_{∞} values. The corresponding values for K were obtained from $\log_{10}(K) = \phi' - 2 \log_{10}(L_{\infty})$. This empirical model (Pauly 2010/2019) predicts the illustrated growth curves. In other words, it is correct that individuals with a higher K grow faster towards a smaller L_{∞} .

Comment:

“In other words, you cannot further shrink pre-shrunk fish”. This sentence is imprecise. “Shrink” is a term that may apply to an individual, but no individual has shrunk or will be shrunk with the mechanisms suggested in this paper. What the authors talk about are population distributions of body size that may change over time.

Response:

The expression “you cannot further shrink pre-shrunk fish” is an attempt to communicate to non-experts via a colloquialism.

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