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Marine and Freshwater Miscellanea III

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Contents

FOREWORD

This is the third collection of articles, authored or co-authored by Daniel Pauly, which he says were “not intended for peer-reviewed journals or pieces whose revision would have required an unreasonable amount of work.” Knowing Daniel as I do, I know he is not one to shy away from work, so I am certain that the ‘unreasonable’ amount would have to have been truly momentous. He also indicated that many of these pieces are personal in nature, and include many of his “opinions”. With as celebrated a background as Daniel has had, these personal opinions, insights, and sentiments will help you learn more about the man behind the science, and add to his legacy (though he does claims expecting to have one would be overly optimistic).

In this collection of articles, jointly edited with Elaine Chu, Daniel pays homage to a former colleague, highlights the circumstances around one of the many high-profile awards he was won, posts the transcripts of two unpublished interviews, suggests – with colleagues – a way to reorganize global action on the oceans for a post-COVID word, and presents two aspects of his Gill-Oxygen Limitation Theory (GOLT), one in form of an application to lancelets, the other in form of an expanded pre-submission version of a recent article on the GOLT in *Science Advances*.

These topics are wide-ranging, and reflect Daniel’s thoughts through several years. I invite you to review, enjoy and learn more about the man behind the science.

Regards,

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

PREFACE

This collection of 'marine and freshwater miscellanea' differs from the previous ones[1] in that it contains only contributions of which I am the author or a co-author. Thus, I expect a lot of patience from the reader.

'Marine and Freshwater Miscellanea' are pieces of various length not intended for peer-reviewed journals or pieces whose revision would have required an unreasonable amount of work. Some of the other pieces assembled here are quite personal, and besides covering various aspects of my scientific work and its dissemination through the peer-reviewed literature, these pieces include my opinions about various other media, notably 'social media' (which I loathe and do not participate in).

The reason for this possibly over-optimistic hope for the reader's patience is that 2021 is the year when I will reach 75 years of age, and I will have to consider retirement – one of these days. When that happens, I will have to clean up my desk and my computers. Publishing these miscellanea is a way to prepare for that; I would hate to find then an item at the bottom of a hard disk which I would have like to see published, if only in a report.

Another reason -- and here, over-optimism turns into grandiosity -- is that I may have something like a legacy, and that maybe, in the future, an eager graduate student may stumble over this report when writing her thesis about marine fisheries at the transition from the 20th to the 21st century, or the origins of the Gill-Oxygen Limitation Theory (GOLT), which would have been part of her curriculum in marine biology.

Daniel Pauly
February 2021

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[1] Pauly, D. and V. Ruiz-Leotaud (Editors). 2020. *Marine and Freshwater Miscellanea II.* Fisheries Centre Research Reports 28(2), 141 p.
Pauly, D. and V. Ruiz-Leotaud (Editors). 2018. *Marine and Freshwater Miscellanea.* Fisheries Centre Research Reports 26(2), 83 p.

JACK RANDALL (1924 – 2020): A FRIEND OF FISHBASE[1]

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Abstract

This account describes the work and career of the fish taxonomist John ('Jack') Randall (1924-2020), and in particular, his relationship to FishBase (www.fishbase.org) and its staff. Notably, Jack Randall supplied over 10,000 fish photos to FishBase at a time when photos were scarce. Even more importantly, his scientific credibility helped establish the credibility of FishBase.

Introduction

The public at large and scientists who are not taxonomists share a view of taxonomists as hard to connect with, and sometimes remote; this may apply to some of them, but as with everything, there are exceptions. One of these exceptions was Jack Randall.

John Ernest Randall was born in 1924 in Los Angeles, California. He studied at UCLA and then went to the University of Hawai'i, which he left in 1955 with a Ph.D. After various jobs in Florida and Puerto Rico, he became a Senior Ichthyologist at the Bishop Museum in Hawai'i (see Wikipedia), the position he held when he began his association with FishBase.

Given that he already was, at the time, the author of 10 books, over 500 scientific papers, and the person who described over 600 new species of fish, we were delighted when he accepted an invitation to an international workshop held in October 1995 in the Philippines. Jack (see photo) and other taxonomists verified the contents of FishBase and made constructive suggestions for its improvement. It is also when he decided to give FishBase access to a collection of over 10,000 underwater photographs of Caribbean and Indo-Pacific reef fishes he had spent decades assembling.

Jack's photos of fish

At the time, FishBase suffered enormously from a lack of fish pictures, most of which are copyrighted, and therefore could not directly be incorporated as is possible with other content. The situation was so bad that we resorted to scanning and showing fish stamps (which, in the process, made FishBase the largest repository of scanned fish stamps). While we are still now missing photos for many species in FishBase, Jack's gift and support of FishBase contributed crucially to its current near-universal acceptance.

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[1] Cite as: Pauly, D. 2021. Jack Randall (1924 – 2020): a friend of FishBase, p. 5-8. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1). This account was first published in marineexploration.org/jack/#comment-251

Jack Randall at an FAO/ICLARM/MSI/NORAD workshop held in early October 1995 in the Philippines, and devoted to the creation of the fishery resources guide of the Central Western Pacific (see Froese and Pauly 2000, p. 13). Photo by Rachel 'Aque' Atanacio.

Rainer Froese wrote: "What a role model; Jack is one of my heroes. I still remember how I was 'schlepping' his suitcase full of outdated photo-equipment through Manila airport, and how he gave a highly educational talk about taxonomy, showing slides of underwater photos in alphabetic sequence of the scientific names…".

Nicolas Bailly recalls: "I have seen Jack diving in strong current conditions in Durban during the 6th Indo-Pacific Fish Conference with his underwater camera of course. He was 77 then, and still continuing making underwater photos of coral reef fishes, his life-lasting pioneering and exploring activity. With Jack, a legend of coral reef fish biodiversity has passed. However, there is no doubt that his work will remain the foundation of much of ichthyology."

Note that as of early 2020, Jack has described 834 species of which 802 are considered valid. Given that further descriptions will appear posthumously (Richard Pyle, Bishop Museum, Honolulu, pers. comm.), Jack might beat the record of the Dutch taxonomist Pieter Bleeker (1819-1878), who currently has 837 valid species to his name.

In 1998, Jack was a resource person at a FishBase workshop held in Trinidad and Tobago. He went diving among the reefs of Tobago with Deng Palomares, who wrote, "I remember how elated I felt when I was given the privilege of going on a dive with Jack Randall in Tobago (I have his signature on my dive log to prove it). He was on the lookout for a fish that exhibited perfect camouflage. I remember how graceful he was underwater and how quiet he swam in spite of all the hardware he was carrying while looking for the fish he wanted to photograph. A true naturalist transformed into a fish as soon as he hit the water! That was the epitome of my diving experience as a marine biologist, which I took and will take with me on each dive."

I was on the same dive, and we observed how he patiently took many close-up photos of fish. I remained in the background, marveling at how he could make such beautiful photos without flash. But when we surfaced, he exploded “[expletive], my flash didn’t work!” -- which shows that this famous ichthyologist lived in the same world that we all do.

Other stories

This was also evident from an earlier story he told me about a South African ichthyologist trying to convince him to come work in South Africa in the 1970s, during the darkest days of apartheid. He had a good sale pitch, Jack told me, but then the guy casually mentioned that, obviously, Jack could not bring his wife Helen along because she was of Chinese ancestry….

Jack Randall was not only a fish taxonomist and an accomplished underwater photographer. From 1961 to 1965, while a professor of Zoology at the University of Puerto Rico, where he wrote his classic on Caribbean Fishes (Randall 1968), he also tagged an immense number of fish and published his entire data set (Randall 1967). This enabled their re-analysis, and the assessment that even a small summer-winter temperature difference (2 °C), affected the growth of fishes (Pauly and Ingles 1981).

He also published an extensive study of the food and feeding habits of Caribbean reef fishes (Randall 1967). Again, he made all his data available, and they were used by one of my first doctoral students, Ms. Silvia Opitz, to fill in the diet matrix for the most comprehensive ever Ecopath model of a coral reef (Opitz 1996). We also used Jack’s food and feeding habits study to guide us in designing the ‘Diet Table’ of FishBase, which now contains thousands of entries and has helped hundreds of colleagues parameterize Ecopath and other food-web models.

Ms Emily Capuli, the FishBase team member who keeps track of new species wrote, “I worked with [Jack] in Hawaii for a month and during the WCP workshop. I told him that he reminded me of Harrison Ford as the Indiana Jones character searching for new treasures and adventures, both in looks (when he was young) and career in life. [...] He gave us a lot of photos and references and was always helpful. Every time and any time (literally) I wrote him for help, he answered my emails.”

Ms. Rachel ‘Aque’ Atanacio, who is the FishBase artist, and who therefore processed the many slides he donated to us, should have the last word. She described Jack as follows in a FishBase newsletter of 2017:

“Collaborator since 1990 (www.fishbase.us/collaborators/CollaboratorSummary.php?id=50.); main contribution: more than 11,000 fish pictures for 178 families, generously made available to the public under a Creative Commons license allowing the use of the images for non-commercial purposes. Jack, as he is fondly called by friends and colleagues, has been and still is a very active collaborator of FishBase. He has visited the FishBase team [in the Philippines] twice, once in 1995 and another time in the early 2000s, thus giving us an opportunity to work with him and benefit from his expertise as a leading authority on coral reef fishes.

Now, even at his advanced age, he is still very busy describing new species, writing and editing scientific papers, and ensuring that FishBase gets a copy of his latest paper and publication. Dr Randall never disappoints and will answer whenever he is being consulted for his opinion on a fish ID. For these reasons, Dr Randall will always be considered, not only as an invaluable collaborator, but a friend of FishBase.”

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Opitz, S. 1996. *Trophic interactions in Caribbean coral reefs*. ICLARM Technical Reports 43, 341 p.

Pauly, D. and J. Ingles. 1981. Aspects of the growth and mortality of exploited coral reef fishes, p. 89-98 *In:* E. Gomez, C.E. Birkeland, R.W. Buddemeier, R.E. Johannes, J.A. Marsh and R.T. Tsuda (eds). *Proceedings of the Fourth International Coral Reef Symposium*. Manila, Philippines.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography,* 5: 665-847.

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DARWIN WAS NO BACONIAN[1]

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Abstract

In his review of three books on Charles Darwin (CD), David Quammen suggested that CD was a 'Baconian', a term generally used to characterize those who believe that the mere accumulation of facts leads, via induction, to novel scientific insights. This characterization, which is widespread, is erroneous, as CD, through his work, systematically developed the hypothetico-deductive method later formalized by Karl Popper. This brief account identifies the source of this common misperception.

Introduction

The following was sent (without the endnotes) to the editor of the New York Review of Books, to which I have a subscription. As I somehow expected, I received only their automatic reply: "Thank you for contacting *The New York Review of Books*. Since we receive thousands of letters and comments, we cannot reply directly to each one. Nor can we say in advance whether a letter will be published, although each one is carefully considered. Regards, *The New York Review of Books*

Thus, for what it is worth, I include my submission here, with endnotes to back up my claims.

The submission

To the Editors:
I much appreciated David Quammen's review of three books[1] on Charles Darwin (*NYR*, April 23, 2020). However, I must object to the characterization of Darwin as 'Baconian,' implying that he believed that simply accumulating data leads to insights.

Quammen cites Darwin saying he had "*worked on true Baconian principles, and without any theory collected facts on a wholesale scale*." This quote from Darwin's *Autobiography*[2] has a specific context: it refers explicitly to the period between the return from his five-year voyage on the *Beagle* and the day in September 1838 he read Malthus' work on population and conceived the idea of natural selection.

Darwin had been actively searching for a mechanism to explain variability in space (and, he presumed, in time as well) of the multiple species he had either observed or collected during the *Beagle* voyage. He needed material to formulate a hypothesis about the mechanisms for what we now call 'evolution.' As soon as he hit on natural selection, he returned to the hypothesis-testing method that he had initially developed, but which we now attribute to Karl Popper[3].

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[1] Cite as: Pauly, D. 2021. Darwin was no Baconian, p. 9-10. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1).

Remember: Charles Darwin formulated his theory of coral reef formation before he had studied any reef[4], and he is the person who wrote how "*odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!*[5]"

Darwin was neither Baconian nor, incidentally, a plodder.

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University Killam Professor
Author, *Darwin's Fishes,* Cambridge University Press

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[1] These three books were "Darwin's Most Wonderful Plants: A Tour of His Botanical Legacy", by Ken Thompson. University of Chicago Press, 255 p; "On the Backs of Tortoises: Darwin, the Galápagos, and the Fate of an Evolutionary Eden" by Elizabeth Hennessy, Yale University Press, 310 p. and "Evolution Before Darwin: Theories of the Transmutation of Species in Edinburgh, 1804–1834" by Bill Jenkins, Edinburgh University Press, 222 p. and their review by D. Quammen was titled "The Brilliant Plodder", another mischaracterization of Charles Darwin.

[2] Barlow, Nora (Editor). 1958. The Autobiography of Charles Darwin 1809-1882, with original omissions restored. Edited with Appendix and Notes by his grand-daughter. Harcourt, Brace and Company, New York, 253 p.

[3] See the excellent summary by Ayala, F.J. 2009. Darwin and the scientific method. PNAS, June 16, 2009, 106 (Supplement 1) 10033-10039. doi.org/10.1073/pnas.0901404106

[4] Darwin, C. 1842. *The Structure and distribution of Coral Reefs. Being the First Part of the Geology of the Voyage of the Beagle, under the Command of Capt. FitzRoy, R.N., during the years 1832 to 1836*. Smith, Elder & Co, London 214 pp. + 2 pp. with maps.

[5] From a letter sent to Henry Fawcett 18 September [1861]. See www.darwinproject.ac.uk/letter/DCP-LETT-3257.xmlIn.

FROM A BASEMENT OFFICE TO THE IMPERIAL PALACE[1]

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Abstract:

This article, which summarizes the author's positive interactions with Japanese colleagues and institutions, was written to augment the Japanese version of his book "*Vanishing Fish: Shifting Baselines and the Future of Global Fisheries*. Greystone Books, Vancouver (2019)", published in February 2021. The emphasis of this article is on the International Cosmos Prize of the Osaka Expo '90 Foundation, which the author received in 2005, and whose acceptance speech is reproduced here.

Introduction

My first reminiscence of Japan and its culture was when I was 18 years old and working as a lowly nursing assistant in a hospital in Germany. There I became friends with one of the several medical doctors from Japan[1]. I remember being involved in a contest with him to see which of us could write the same text fastest – him in Japanese, me in German: I lost, and I don't think he cheated.

I recall the next significant encounter was when I wrote to Dr. Yata Haneda, a specialist on the bioluminescence of fish and other marine animals[2]. I was then – in 1976 – working in a fisheries development project in Indonesia, but was also intrigued by fish that shone light. Later, in the acknowledgment section of a paper written on this topic[3], I thanked Dr. Haneda "for sending copies of even his oldest papers as well as comments on the manuscript." At that time, with no Internet, reprints such as those Dr. Haneda sent to me were valuable sources of information, and I was delighted that he had been so generous with his time and knowledge to a stranger.

Fast forward 30 years: I am now working on global fisheries, and some of my papers, especially those in *Nature* and *Science* on the impact of fishing, received worldwide attention, including in Japan, which is a real heavyweight in global fisheries.

The Cosmos Prize

I was visiting in Sète, in France, in the laboratory, then led by my friend and colleague Philippe Cury[4], when I was (confidentially) informed that I would be awarded the International Cosmo Prize for 2005. The only thing still needed was that I should be found to be a decent person by two staff members of the Expo '90 Foundation[5], which managed the prize.

Thus, two gentlemen came to Vancouver, and they interviewed my colleagues as to my character and assured themselves that my health was such that I could handle the visit to Japan that the prize implied[6]. They must have been satisfied, because a short while after their visit, I was officially informed that yes, I had received the prize[7]. I was now in the company of Richard Dawkins (1998), Jared Diamond (1999), and

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[1] Cite as: Pauly, D. 2021. From a Basement Office to the Imperial Palace, p. 10-15. *In*: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Reports 29(1).

Sir David Attenborough (2000)! More importantly, this was one of the first times that a major international scientific award had gone to a fisheries scientist.

Let me elaborate a little on this last point. Physics deserves its standing as queen of the sciences because of her concern with the structure of the world in which we live. And in biology, nowadays, genomics is the one reaching into the intellectual treasure trove of evolution and completing the revolution initiated by Charles Darwin[8].

However, similar to agronomy[9], fisheries research has less prestige, at least in Western countries. It was not until the late 1990s and early 2000s that people began to realize the damage that our globalized fisheries inflict on marine biodiversity. My scientific papers and articles in other media may have helped this realization. Thus, my award of the Cosmos Prize by a foundation in Japan, where fisheries - since the Jōmon Period - have always been taken seriously.

The Basement and the Imperial Palace

And so, my wife and I went to Japan to participate a series of events that began with a visit to Kyoto, which included a lecture at Doshisha University. These events had two highlights. On October 18, at Izumi Hall, the first highlight was the award ceremony in Osaka City, which was magnificent, but whose description would require a literary talent that I do not possess. It was here that I gave the speech at the end of this chapter. There was a courtesy visit to the Governor of Osaka Prefecture, who received me in his ornate office, and with whom presents were exchanged – which I mention only because of the contrast with what happened at the Ministry of Agriculture, Forestry and Fisheries, in Tokyo, another sponsor of the Cosmos Prize. There, I was received by a very low-ranking functionary who went through the motions of congratulating me in a small dingy office so dark that it could have been in the building's basement. Clearly, not everybody was happy with me having received the 2005 International Cosmos Prize.

But then came the second highlight of these events, a visit to the other sponsor of the Cosmos Prize.

My wife and I were instructed, through schematics on small paper sheets, where to put our feet during the time we would be with The Crown Prince and his wife at the Imperial Palace, and so, when we talked with the Crown Prince and his wife, we had our feet at the right place. We stayed 30 to 45 minutes, and I spoke with the Crown Prince and my wife spoke with his wife, …but no, I won't say what we talked about[10]. The Crown Prince's wife, at the time, had not been seen in public for almost three years, and when we left the room where we had been received, there was a large group of journalists who wanted to know what she had said. We said nothing.

The Acceptance Speech

What follows is my acceptance speech[11] of October 18, 2005, which states things that I still believe in.

Ladies and Gentlemen,

I would like to express in Japanese my thanks to the International Cosmos Prize committee and the Expo '90 Foundation for having me here, but I have to do so in English – a foreign language to you, but also to me.

Receiving an award such as the International Cosmos Prize invites serious reflection, and I will share with you some of the thoughts that I have had since that glorious day in early July, I was informed that I would be this year's prize recipient.

People have good reason to be worried about the fate of life in the ocean, as we now engage our whole industrial might in chasing and catching, for our food, the top predators of marine ecosystems. Increasingly, these predators are being depleted, and we now turn to their prey, smaller fishes and invertebrates, some highly valuable. This phenomenon is now known as 'fishing down marine food webs', and it explains a vast number of observations, which before remained unconnected. Fisheries have been able to move easily from larger to smaller targets, aided by high technology – such as echolocation and Global Positioning Systems – and abetted by a processing technology which can turn even the most improbable sea creatures into tasty morsels.

Life in the ocean, though, was not designed to be ground up by a transoceanic food production machine. In fact, it was not designed at all, but evolved over the eons, and its ability to produce a surplus that we can share, year for year, is an emergent property of marine ecosystems, contingent on their continued existence as complex entities. If the species we target are depleted, and the ecosystems in which they are embedded are drastically simplified, this surplus is reduced, and eventually vanishes. This is the situation we have now in many parts of the world ocean. I wish to emphasize this: global catches from marine fisheries are declining, in spite of, or rather because of, increasing fishing effort.

There are those who believe that the problems of fisheries do not justify speaking of a crisis, and that various technological fixes will suffice for solving these problems. Among these fixes are updated versions of our traditional management schemes, jazzed up to include explicit laying out of the costs and benefits of various options on fishing levels, and the presumed risk attached to each. This would enable 'managers' to make rational choices under a given set of economic and political constraints. Presently, this approach, which sees this laying out of options as all that scientists can do, and which, therefore, limits our role to that of vending machines, is very popular in fisheries sciences.

However, our inability to tackle another, much bigger problem – global warming – indicates that we are, as a species, usually unable to make rational decisions to avert long-term harm to ourselves, even if the risks can be estimated, especially if these decisions involve short-term sacrifices. The recent tsunami in South and Southeast Asia, and the even more recent flooding of New Orleans, underline this[12]. In both cases, planning for an eventual catastrophe and working with nature, not against her, would have saved thousands of lives, and avoided immense material damage. Yet, the managers had no plans, and the populations concerned, when they could vote, elected politicians who, at best, had other priorities, and, at worst, actively campaigned against such investment for the public good.

This has been similar in all the great collapses of fisheries, where after the catastrophe, in virtually all cases, the voice of prudence - usually that of scientists - was shown to have been ignored by the managers, in favor of the voices of short-term interests. Where does this put me – one single person – amidst a cacophony of voices? I understand the award of this wonderful prize to be a vindication, and an encouragement to raise the stakes. And the stakes must be raised. We scientists working on environment-related issues have been too meek when managers, lobbyists, and politicians have twisted the results of our work to fit their agenda. The main tool they have used to silence us, and to reduce us to vending machines, is the notion that an engagement for the environment would compromise our scientific objectivity. Yet this argument is never evoked in medicine. Indeed, passionate engagement for the patients, against disease-causing agents is not only the norm, but also an essential element of doctors' professional ethics.

This is not the case for environmental scientists, probably because many of us work for governments, and can be easily silenced, or even made to serve a short-term political agenda. Universities, however, are less constrained, and we should expect university researchers to make themselves heard when science is not put to use for the public good. And the public good it must be, because science is a collective venture, ultimately funded by the public, our ultimate master.

There is, presently, in a number of Western countries, an intense public debate about the compatibility of science and religion. I believe these to be incompatible, but this a minority view: most people, including many scientists, believe not only that the two can co-exist – both in one's head, and in the public discourse – but that this co-existence can be mutually enriching. If this is so, why is there so much resistance against the co-existence - in the heads of environmental scientists and in their discourse - of two eminently compatible modes of relating to nature, i.e., a 'scientific mode', which describes nature, and a 'conservation mode', which strives to maintain it?

We must learn to combine scientific integrity with taking firm positions, not only on the conservation of the plants and animals about which we have expertise, but also for the continued existence of the ecosystems of which they are parts. Humans have become the major ecological force on earth, but we can secure continued services from these plants, animals and ecosystems only if we give them the space they need, and the time they need. Most people don't know that. It is the job of scientists working on ecosystems, and on wild flora and fauna to remind politicians and the public of that, and being silent when this is not taken into account is unethical.

As the magazine *Science* sees it[13], my award of a major scientific prize by one of the most important fishing nations on Earth has put squarely in the mainstream the notion that over-fishing is, regrettably, our dominant mode of interaction with ocean life. What is not yet in the mainstream is that the simplest, and most effective approach to re-establish some semblance of abundances past is for humans to withdraw from parts of the ocean, and to let nature, there at least, heal the wounds we have inflicted. Thus, to be more specific, I will work for the establishment, throughout the world, of more marine protected areas, and similar zones of reduced human impacts. Right now, they cumulatively cover less than 1 % of the world ocean, with about only a tenth of that effectively protected. And not enough new ones are declared for the goals we have set for ourselves to be reached, e.g., protecting 10% of the world ocean by 2010[14].

I must come to an end. The best way to thank you for this unforgettable afternoon, to thank the International Cosmos Prize committee and the Expo '90 Foundation for this wonderful prize, and to thank the many people- foremost His Highness The Crown Prince – who have welcomed me and my wife in your beautiful country is to continue – with renewed vigor, the research, and public speaking for which I was awarded the International Cosmos Prize for 2005.

And so, I will. Thank you.

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[1] There is, since the days of Robert Koch and Kitasato Shibasaburō, a tradition of medical cooperation between Germany and Japan, and my friend's presence in a German's hospital was an expression of this relationship.

[2] See F.H. Johnson and Y. Haneda. 1966. *Bioluminescence in Progress*. Princeton University, New Jersey.

[3] Pauly, D. 1977. The Leiognathidae (Teleostei): A hypothesis relating their mean depth occurrence to the intensity of their counter-shading bioluminescence. *Marine Research in Indonesia,* No. 19: 137-146.

[4] The author, jointly with Yves Miserey, a French science journalist, of the book '*Une mer sans poisson*' available in Japanese translation.

[5] The full name is 'Commemorative Foundation for the International Garden and Greenery Exposition, Osaka, Japan, 1990'; see https://en.wikipedia.org/wiki/International_Cosmos_Prize.

[6] I had suffered a stroke in early 2005, and thus there was reason to the worried, as it was and it was important that I should be able to go through the events connected with the prize.

[7] This vetting of potential winners is understandable; the Cosmos Prize was then relatively new, and its prestige still depended, in part, on the reputation (and behaviour) of the prize winners. Also, the International Cosmos Award is co-sponsored by the Imperial Palace, which is a serious institution in Japan.

[8] My book on Charles Darwin, and, more precisely, the fish that Darwin worked on, was co-translated into Japanese by Muto-san, who also translated it (see Pauly, D. 2012. *Daawinfisshu: Daawin no sakanatachi A~Z* [Japanese edition of Darwin's Fishes: an encyclopedia of ichthyology, ecology and evolution. Cambridge University Press, 2004]. Translated by N. Nishida and F. Muto. Tokai University Press, Kanagawa, Japan: 444 p.), and this gives me another opportunity to thank him.

[9] Thus, when the 'Father of the Green Revolution', Norman Borlaug, was honored, he received the Nobel Prize for Peace – there is no Nobel Prize for Agronomy, even though we would all starve if it were not for the advances in agronomy in the 20th century.

[10] However, I did talk about this conversation with then Emperor Akihito of Japan, especially with Empress Michiko, when they visited UBC on July 13, 2009, and I was selected as UBC representative to have lunch with them, and then president of UBC, Dr. Stephen Toope.

[11] This acceptance speech was part of the bilingual Japanese-English commemorative booklet prepared by the Expo '90 Foundation.

[12] See Pauly, D. 2004. Rebuilding fisheries and coastal livelihood in tsunami affected areas. *Sea Around Us Project Newsletter,* November/December (26): 1-2; and Pauly, D. 2005. Rebuilding fisheries will add to Asia's problems. *Nature,* 433:457, for reflections on the tsunami of December 2004, which devastated part of South and Southeast Asia. Also note that Hurricane Katrina stuck the U.S. city of New Orleans in August 2005, less than two months before this speech was given.

[13] The news item in *Science* read as follows:
"It took decades for fisheries biologist Daniel Pauly to win broad support for his predictions that overfishing could lead to a collapse of fisheries worldwide. This week, one of the world's biggest fishing nations joined the bandwagon, with Japan's Expo '90 Foundation awarding Pauly its […] Cosmos Prize. The 59-year-old Pauly, director of the Fisheries Centre at the University of British Columbia in Vancouver, Canada, has focused on the sustainable management of marine resources (*Science*, 19 April 2002, p. 458). An outspoken critic of modern fishing practices, he once suggested that future generations might be reduced to eating jellyfish. 'I think it's very important that a major Japanese prize would go to someone who has worked fearlessly on the problem of overfishing,' says Nancy Knowlton, a marine biologist at the University of California, San Diego, and a member of the screening committee". (*Science* 22 July 2005. Vol. 309, Issue 5734, page 555. doi: 10.1126/science.309.5734.555b).

[14] These numbers and targets were current at the time (Wood, L., L. Fish, J. Laughren and D. Pauly. 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. *Oryx, the international Journal of Conservation,* 42(3): 340-351), but unfortunately, the 10 % target of effective protection by all countries was reached by only a few, notably Chile. However, the need for marine protected areas and no-take marine reserves is now better understood, and gradually, we will get there.

INVASIVE VS. VANISHING FISH[1]

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Abstract

In the summer of 2019, environmental journalist Andrew Reeves, author of *Overrun: Dispatches from the Asian Carp Crisis,* was invited by a leading Canadian daily, *The Globe & Mail,* to speak with Daniel Pauly, a fisheries biologist at the University of British Columbia, about his latest book *Vanishing Fish: Shifting Baselines and the Future of Global Fisheries*. The discussion was to take the form of an informal exchange between Reeves and Pauly, with the results being published by the newspaper. The results of their exchange, which emphasized the contrast between the state and federal responses to Asian carp in the U.S. with the subsidies awarded by numerous countries to global fisheries, was not published. The following is a record of their conversation, held via email between May 2019 and August 2019.

Introduction

In the summer of 2019, the first author, an environmental journalist and the author of *Overrun: Dispatches from the Asian Carp Crisis*, was invited by the leading Canadian daily, *The Globe & Mail*, to exchange ideas with the second author, a Professor of Fisheries and Principal Investigator of the *Sea Around Us* initiative at the University of British Columbia (see www.seaaroundus.org) and the author of *Vanishing Fish: Shifting Baselines and the Future of Global Fisheries*. The discussion was to take the form of an informal exchange between Reeves and Pauly, with the results being published by the newspaper. The results of their exchange, which, among other things, contrasted the U.S. state and federal responses to Asian carp with the subsidies awarded to by numerous countries to their marine fisheries, were never published. The following is a record of their conversation, held via email between May 2019 and August 2019.

The 'Asian carp' of which we speak below are mainly silver carp (*Hypophthalmichthys molitrix*), but sometimes include bighead (*Hypophthalmichthys nobilis*) and grass carp (*Ctenopharyngodon idella*); all three are invasive species in the U.S. (see also FishBase; www.fishbase.org). What follows is a slightly edited version of our exchanges.

Andrew Reeves (AR): There are so many ways to start this conversation, but I wanted to begin with something that has stuck with me in the weeks since reading your book. It is the idea that for a host of reasons (the catastrophic damage caused by deep-ocean trawlers, the decline of small-scale fishers, robbing subsistence fishing communities of their much-needed hauls) that the time has perhaps come for us to stop eating fish until we can staunch the bleeding of our oceans, as it were.

You've got a great line – "Eating a tuna roll at a sushi restaurant should be considered no more environmentally benign than driving a Hummer or harpooning a manatee." Since I read this line, my

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[1] Reeves, A. and D. Pauly. 2021. Invasive vs. Vanishing Fish, p. 16-21. *In*: D. Pauly and Elaine Chu (eds). *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Reports. 29(1).

personal fish consumption has tanked; I have not been able to do it. And I contrast this with Asian carp, which, while a scourge in North America, has become an endangered species in China, in their native range, largely through overfishing.

In short, our fisheries (both ocean and inland, it would seem) are a mess. How do we steer ourselves out of the morass we have put ourselves in?

Daniel Pauly (DP): Perhaps surprisingly given the apparent success of consumer-led concerns with eating “sustainable” fish, I would not write anymore the phrase you cited, and indeed, I now think that it pointed in the wrong direction. Obviously, we should not stuff our faces with endangered species; but is this enough? And is the “display of virtue” that comes with not eating certain fish when we go out with our friends appropriate behaviour in confronting the biodiversity crisis we face? I think not. In fact, we should conceive of ourselves less as consumers – influencing things with our stomachs – and more as citizens influencing things with our brain, and our hearts.

In other words, when I do a public lecture and the inevitable question arises, “What fish should eat?” I answer now that people should, “Eat a sandwich, join an environmental NGO, and raise hell.”

Now to your Asian carp, and since we are talking about hell: Why not fish the hell out of it? The United States has a good record of overfishing things, see e.g., New England cod, and it should be capable of emulating China in this regard. (Though the U.S. is doing much better these days, and is in fact leading the international struggle against overfishing).

Seriously: What prevents Asian carp from being fished to oblivion?

AR: I like that advice! On my book tour I’ve been asked what people can do to stop Asian carp – and while it’s always felt a bit cheap, the suggestion that people educate themselves and call their Congressperson demanding action still stands as one of the best ways I can think of to effect change. Raising hell wouldn’t hurt, either.

To your question: What prevents Asian carp from being fished to oblivion? Many things, sadly, but nothing that cannot be overcome if we want to. The fish has a bad reputation, and so while many people polled say they would eat Asian carp, few do when and where they have the chance. They are also incredibly bony – and while this poses less of a problem in many non-Western countries where eating bone-in, whole-fish is common, in North America, the culinary tradition is for processed and/or prepared fish. But many people I spoke with say that in order for restaurants to make serving Asian carp worth their while, they would need to charge $60 or more per plate. No one would pay that for bigheaded carp!

We also do not pay fishers enough money to make catching Asian carp worth their while. The economics of catching bigheads and silver carp for $0.10 or $0.25 per pound simply do not make sense. And so, the fish remain in our rivers. I could go on, but suffice it to say we have had the better part of three decades since their gradual introduction and dispersal from the early 1960s to the late 1970s to determine how market forces could be brought to bear on fishing these invasive species down, yet we have failed to make it work. That’s not to say it cannot work, but we would need to make these fish available for sale in more restaurants, hospitals, casinos and the like to make this viable, or help fishers and processors by subsidizing the cost of catching them or making them into a product people actually want to buy.

I understand that subsidies in the world of marine fisheries is a bit of a dirty word.

DP: I am just re-emerging from nearly two months of incessant travels in May and June, and then celebrating on June 28th the 20-year anniversary of the *Sea Around Us*, the research project I lead here at UBC. This allowed me to reconnect with Peter Sorensen, whom I know since he started about two or three years ago to stop in at UBC on the way to his summer hut somewhere on the Gulf Island.

Peter is a character in your book, and I asked him about it. He mentioned that a lot has happened since the book appeared, but he did not give me any example of anything big having changed your descriptions since you wrote your last chapter. In that last chapter, you mention that some individual Asian carps have been recorded in the Great Lakes. Peter suggested that these few fish will not reproduce, which I thought was odd. Why wouldn't they?

Peter also mentioned that subsidized fisheries for these carp in the Mississippi River basin is a very good thing, not only because it reduces populations of problematic fish, but also because of the income it provides. I find myself agreeing: in fact, this is one of the first times that I can see where fisheries subsidies make sense.

AR: What a small world. Peter was a great help in writing the book, and an excellent source of information for what has been happening with Asian carp in North American, and around the world. I learned from him on the book tour that Asian carp are effectively an endangered species in their native range in China, having been fished almost to the point of extirpation. This might go some way toward explaining why so many people are keen to discuss shipping the caught fish back to China, where interest in eating them is significantly higher.

Peter is also contemplating some work on marine protected areas, I understand, and whether the principle could be applied to inland, freshwater environments to strengthen the level of protection afforded to them in an effort to keep out Asian carp. It's early days from what I understand, but I would be curious to know more about the idea if it materializes.

And yes, Peter is right that Asian carps have been found in the Great Lakes – grass carp mostly, and most often in tributary rivers of Lake Erie and, to a lesser extent, Lake Ontario. Despite their presence, these fish have largely been understood as worrying one-offs, rather than the tip of the spear of a larger, perhaps unseen, invading population. Many (but not all) of those fish found in the Great Lakes have also been triploid (sterile), likely raised sterile in-hatchery, and intended for use cleaning aquatic weeds in an irrigation ditch or a golf course pond somewhere within the basin.

That's not to say that Asian carp couldn't reproduce in the Great Lakes, however. Some of the earliest Asian carp research to come out of Canada, especially the federal Department of Fisheries and Oceans, looked at whether the fish would be able to find tributary rivers to the Great Lakes that were long enough to allow their eggs to hatch. The more attuned the research got, the shorter the length of rivers we discovered that they needed to spawn successfully. Some scientists have predicted that as few as 10 females and 10 males are needed to establish a breeding population in the Great Lakes, though that number is slightly contested.

You mention that Asian carp could be the first instance you recall where a subsidy could make sense. Can you elaborate on the ways that subsidies have failed or, as I'm sure is the case, made things worse in other parts of the world?

DP: Here is some prose that I wrote about an earlier round of subsidy negotiation in Geneva, at the World Trade Organization:

The current round of negotiations at the WTO emphasize the reduction and possible elimination of government subsidies to fisheries. Such subsidies have been widely recognized as detrimental to the sustainability of the fisheries resource, and thus to the long-term viability of fisheries. In the short term they do, however, help mitigate a political problem with the fisheries sector and continue therefore to be dispensed in alarming amounts. This is particularly true in developing countries where the livelihood of coastal populations is heavily dependent on fisheries, both in the short and the long term, and where the fisheries sector may contribute more to the overall economy than in developed countries, where the fisheries sector is often miniscule compared to the overall GDP. Thus, in the course of the present negotiation developing countries' delegations at the WTO are tempted to request exemptions such that their country can continue to subsidize fisheries development, even if developed countries are asked to reduce such subsidies.

The inherent perception that is behind such demands is that without such subsidies the fisheries will not develop and that they will not serve as a motor for contributing to the overall economy. The key point about subsidies, however, is that they can have a positive effect toward the development of fisheries only if untapped fisheries resources exist along the coast of the country in question, which can be accessed only with subsidized vessels. After a few years, so the assumption goes, the fisheries become profitable, subsidies are not needed, and sectors have been strengthened. However, this logic applies only if the stocks along the coasts of developed countries are unexploited. As they become exploited, they should generate benefits or profits which can be used to augment capacity and fish the resource at the appropriate level without the need for subsidies. Such 'first' fisheries tend to be very profitable and quickly grow on their own accord – one example is the trawl fisheries of Southeast Asia, particularly Thailand, which were initially subsidized both in the form of a technical assistance project, and through capital funds from the Asian Development Bank, but which quickly acquired a dynamic of its own within a few years. In fact, this dynamic became so strong that the problem then became one of handling the resulting overcapacity.

The problem with subsidization of fisheries in developing countries in the 21st century, however, is that unfished or lightly-fished stocks do not occur along many coasts. There is currently no country in the world which has not a substantial fishery along its coast that has reduced the abundance of its fish below that considered to generate maximum sustainable yields. This level is 40-50% of the pristine or unexploited biomass and it is, generally, within a few years of the initiation of a fishery on a new resource that such reduction happens. Thereafter, stocks decline less because the remaining stocks are more distant and less amenable to profitable exploitation.

This means that most fisheries of the coasts of developing countries produce less than they could if effort was reduced, or, put differently, in most developing countries nowadays fisheries capacity-enhancing subsidies have the effect of reducing rather than increasing catches. This reduction effect can be partly masked when a developing country has foreign fishing vessels in its EEZ. In such cases, the subsidies can contribute to a larger share of a shrinking pie being accessible by the coastal country, but in this case, it would be more profitable for the two partners, the coastal country and the distant water fleet, to agree on sharing the resource rather than competing for it. This logic also implies that with regard to subsidy the only role of fisheries science is to assess whether a stock is unfished or underfished, or is under severe pressure. Such evaluation doesn't require sophisticated models and can be determined based on data which most developing countries' departments of fisheries already have.

Moreover, as already stated, the fisheries resources in most countries are already heavily-exploited and thus the default assumption for any place in the world should actually be that the fishery has already reduced the biomass of coastal and shelf fishes below the level which would generate MSY and therefore subsidies cannot increase benefit from fisheries. The fishery departments in such cases have the job of identifying the exceptions to this general rule, thus reducing the assessment problem to a simple problem of assessing the gross impact of fisheries, not of performing detailed stock assessments.

This was a rather long answer to your query about subsidies, but it is also a topic about which I feel very strongly, and about which I have worked a lot.

AR: I wanted to pick up our conversation with a question. Is there any example you can provide of subsidies *working* as they were intended? Where a country provided a subsidy and, once the market became profitable without being exploitative, the subsidy was removed and the market remained stable? I ask in relation to Asian carp, because I know many fisheries biologists and state agencies are worried about creating a market for an invasive fish. Others worry about a constant drain on the public purse. But has it been done before that a subsidy has been removed once the market is up and running? That could help cajole state governments into seeing such a financial support as temporary, which could make it more palatable.

DP: I have consulted with my friend and colleague, Rashid Sumaila, who has led most of our work on fisheries subsidies. He confirmed that capacity-enhancing subsidies always have a negative effect on the resource base (the fish), and eventually on the fishery itself. This is certainly true at the "tactical" level. However, at the "strategic" level, regarding the long-term structure of the maritime economy of a country, this assessment would be more difficult.

Thus, for a country like France, fisheries subsidies have had a negative effect on the structure of the fishery (overexploited stocks, permanently unhappy, old small-scale fishers, a few well-connected fat cats, lies, and one scandal after the other). Where it gets difficult to decide is the case of Thailand, which was transformed from a backwater into a major player in the international fisheries and seafood world by massive subsidies to its nascent trawling industry from the Manila-based Asian Development Bank. This fishery is extremely destructive, and it was largely illegally run in various countries. Yet neoliberal economists would see this as a successful case of economic development.

The United States economy, overall, will remain unaffected by anything that is done to the fishery for Asian carp, and the pros and cons of subsidization can be evaluated without reference to the overall economy. I continue to believe that subsidizing a fishery for invasive carp (including subsidies for developing edible dishes) is cheaper than attempting to limit their expansion by mechanical means.

AR: The subsequent challenge would be convincing people to actually eat Asian carp, however they were caught. Their boniness and the stigma of eating Asian carp, often thought of as a "trash" fish, has kept them from catching on in North America, though willing consumers exist on the other side of the world. Perhaps the subsidy here should be less about paying fishers to catch them, but subsidizing the entire structure of catching, processing, and shipping the fish to parts of the world where people want to eat them, or where animal protein is difficult or too expensive to come by.

I was fascinated in your book by the way you detail how we are simply moving through an unseen roster of available fish to eat in search of the next "best" fish that exists in numbers large enough to meet our demand, leading many to eat fish that, not that long ago, would have been not worth the time to catch. Do you see that trend continuing?

DP: Perhaps your second paragraph is the answer to the dilemma in the first paragraph – we are now eating fish that we would not have touched before, because we have little alternative. And I am confident that folks capable of making artificial meat that can fool hamburger-loving people could find a way to process Asian carp such that they become acceptable to more consumers.

To answer your question about "trash" fish use – yes, I see this trend continuing, mainly because of aquaculture. Thus, you can have out-of-control trawl fisheries, using illegally small meshes (such as the Chinese coastal fishery and the Thai fishery), having no incentive to improve their act because they can sell the slop that they catch, which consists of tiny fish, the juveniles of bigger fish, and zooplankton, to fish farmers, who turn this slop into fish feed. This is then used to feed larger fish, *et voila* – the public thinks there is no problem because, they think, aquaculture reduces the pressure on fisheries. Actually, it enhances it.

Further readings

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Pauly, D. and U.R. Sumaila. 2018. Subsidizing Disaster: a Conversation/Ask Dr. Pauly. *Oceana Magazine*, Spring 2018, p. 26-27.

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SHARING SCIENCE: AN INTERVIEW OF DANIEL PAULY BY ISTO HUVILA[1]

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Abstract

This account on 'Sharing Science' is based on a two-part interview conducted as part of one of Isto Huvila's research projects on July 17, 2020 (Part 1) and July 21, 2020 (Part 2). This contribution presents a transcript of these two parts, slightly edited to increase intelligibility. The topics covered include doing science, publishing ones' results in peer-reviewed journals and all the supporting data, improving the peer-review system, publishing books and book chapters, maintaining positive interactions with journalists, and avoiding the social media swamp.

PART 1

DP: I agree with being recorded, and I agree with all the stuff you told me.

IH: Ok, thank you very much. All right, could we start with you telling me a bit about your research discipline and your areas of research? I've done a little bit of, kind of, background work, but I would like to hear you to tell about it.

DP: I'm a fishery scientist, and I studied in Germany; I was prepared to investigate the fisheries in the North Sea or in the North Atlantic, one species at a time. However, I got my first exposure [to tropical biodiversity] after I got my master's in working in Indonesia, where there were lots of fish species in the catch, and there was no way that you could study each of them with the same intensity that we focus on cod or other species in the North Atlantic. And I saw the need to develop generalized rules that would apply to the vast number of species - because the fishery would always be multi-specific. And this insight, or epiphany, occurred at the same time as computers - personal computers - became available, for example the Apple II. So, I was able to combine the understanding that we needed rules with the availability of personal computers, and I transposed lots of the software that existed to investigate these multispecies into personal computers and programmable calculators.

And I became specialized in understanding tropical fisheries. Tropical fisheries have few datapoints and the scientists who study them have very little institutional support. They had no access to international journals; it was before the Internet, right? They didn't travel the way researchers traveled in Europe. So, we had a communication problem in addition to a problem with too many species to study. I tackled each of these issues with my computer-based methods, studying them different ways. And I started very early to do what we now know as "meta-analysis". That is, putting big data sets together and inferring things. Some of my papers got lots of citations because they were useful meta-analyses. And I also began in the late 1980s to understand the need to have a database on fish that not only gave references to literature -

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[1] Cite as: Pauly, D. and I. Huvila 2021. Sharing Science: an interview of Daniel Pauly by Isto Huvila, p. 22-34. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1).
This two-part interview was conducted as part of one of Isto Huvila's research projects on July 17, 2020 (Part 1) and July 21, 2020 (Part 2).

like bibliographies - that was relevant to our work, but that it should give the data themselves. What was needed was not a tag indicating where you can get information - because you still couldn't get it - but the information itself. And that became FishBase, a huge database of fish that is extremely successful. It gets about 50 million hits a month from half a million to a million users a month. Unique users. And this was extremely successful, and it's used very widely. This got me a certain degree of notoriety.

I moved to Canada in the mid-1990s, but I continued to have this emphasis on the Tropics - or, rather, my interests in fisheries became global. And the one thing that my style differs from that of my colleagues: I don't do much fieldwork anymore. I did fieldwork in Ghana for my master's, and fieldwork inspired my PhD, but since, I've basically become an analyst of data that exists, of secondary data. I have been able to convince major philanthropic foundations to give me lots of money for a long time, and I have created a project called the "*Sea Around Us*", which celebrated recently 20 years of activities, and we have tackled a number of issues. One of them was creating a worldwide database of fisheries' catches that is more detailed than the official database that the Food and Agriculture Organization of the UN produces. And the *Sea Around Us* and I get lots of credit for that.

I express myself through my writing a lot, through formal papers, and also newsletter articles and lots of informal papers. And in the late 1990s and the early 2000s, I began working closely with journalists and environmental NGOs, because I realized that government scientists are hampered in their ability to communicate and even to pick up issues that are relevant to the sustainability of fisheries. These colleagues are not supposed to work on that because government agencies really are captured by the fishing industry. And so, I realized when I was working in the developing world that the ministers of fisheries and the fisheries decision-makers didn't care about the science. And when I moved to Canada and became more involved with what happens in North America, and Europe as well, I discovered that essentially, the decision-makers choose to allow fishing whatever the state of the stocks is. And the only social force that can be marshaled against that is really the environmental community, the NGO community. And so, I allied myself to the NGO community and am on the board of a big one called Oceana, but I'm explicit about it. I never say I'm not. My sources of funding are mainly philanthropic organizations, foundations that also fund environment NGOs, and this has brought me into conflicts with the representative of fisheries science as it is currently constituted, i.e., as a supporting system for the fishing industry. And so, the arguments go back and forth. But I think we are winning - but for the wrong reason - we are winning because the fish are losing. We are winning because the fishing industry is actually doing a lousy job of maintaining, or sustaining the resources that depends relies on. And so, the argument that you have to be more prudent, you have to conserve more, is becoming more credible.

So, there I am, I'm quite productive. My papers are mainly conceptual and involve lots of work. I don't have the kind of focus that allows me to go into the guts of equations, but I compensate that by working hard, and having a team that assembles data from various sources and puts them together. And I very much believe in making the data behind a paper or claim widely available. And so, in addition to FishBase, we have created SeaLifeBase, as a database for marine animals other than fish. Also, the *Sea Around Us* has a huge database and website that allows you to download all the data that we produce. So that's where I am.

IH: That's very good, thank you. You already told a lot about how you disseminate your research, but, do you, kind of, is there something specific about, kind of, dissemination that you didn't mention already? How you- yeah.

DP: The analyses that I did in the past always included the data they are based on. So, the result can be reproduced. I made data available through FishBase and *Sea Around Us* website. All these data are free, so people can work with these data. And I talk a lot with journalists, and since about 2000, I interact with journalists on a regular basis.

IH: Yeah.

DP: I even employ a journalist who writes our press releases and other outreach materials. So, everything we do is disseminated at the scientific level and at the public level. I even work with teachers on high school lessons. So that people get the stuff at different levels.

IH: Right, that's very good. If we, kind of, think the other way around, how did you get to know about the research others are doing?

DP: I read a lot. I read *Science* and *Nature* every week. Also, I have a service that my wife actually created, which sends me references to all the papers that cite my own work. I don't do that because I'm pleased to see myself cited, but because the people who cite my own work are the people who work on the same problems I do. So, basically by looking at what people who cites me write, I can keep track of the literature. Also, I'm an avid reader of science books, so I can contextualize my field in the general field of natural sciences. So, at the big picture level, I can situate fisheries in the context of marine biology, which is a part oceanography, which is one of the Earth sciences, which can be seen in the context of Exobiology and Cosmology. I can see this very straightforwardly and I can move between these levels. I also read science fiction, so [laughs] the things that I don't know, I can make them up.

IH: [laughs]

DP: I recently read about, a book about "Alien Ocean", about a possible ocean on "Europa", a moon of Jupiter and other moons of the solar system. Anyway, so there are 4 or 5 moons in our solar system that likely have huge ocean, and they had these oceans for hundreds of millions of years. Thus, it is possible that they contain life, and then you can imagine all kind of scenarios for that, right? All under water.

IH: OK.

DP: And, so, I get my information by reading, reading regularly these two weekly journals and reading the literature that connects to my work via citations. I also read *Scientific American* and its French version.

IH: That sounds very good. Now I would like to ask you about, about a few specific genres of scholarly communication or, kind of, types of media. And for each of those I would, kind of, like you to, kind of, think aloud a little bit, how you, kind of, think about those as means for you of disseminating your own research, and then, on the other hand, about, kind of, getting to know about others' research? And why these different genres or formats could be good or, kind of, positive or negative size they have. The first one is about videos, and then video presentations. That could be anything from, kind of, from TED Talks to visualizations to reconstructions…

DP: I was very much into TED Talks for a while, and I have done one. But I gradually realized that TED Talks have a bias toward individualized solutions. TED Talks always have one hero that finds something. They never emphasize public or collective solutions. And so, I don't look at TED Talks much anymore. And neither do I look at videos much because they have to make concession to the public; they have to be jazzy, and they are all jazzy the same way. There is always a dashing hero sailing into the sunset, or diving into reefs, but after a while, this is boring. Also, in books, it always starts with someone waking up, it's a beautiful morning, and they go diving, or they go jumping, or they do something, and then gradually, they introduce the field that they are interested in, and basically, I'm not interested anymore. It's like lettuce. Not nourishing. So, videos, they don't tell you much, at the end of the day. Though, yesterday I saw a video that was really emotional about fisheries observers. This was a story about onboard observers of fishing vessels that were being killed. And one of them was being thrown overboard, and that will hit you in the gut and makes you want to cry. If you want your emotions stirred up, obviously that's videos. But if you want to explain something, it usually doesn't work. OK. Next?

IH: Mmhmm. Yeah. About audio, kind of, either podcasts, or radio documentaries, or….

DP: I have no patience whatsoever for social media.

IH: Yeah, precisely. How about social media? Do you follow it, or…?

DP: I avoid them like the pest that they are. And the more I read about it, the more I find out about it, the more disgusted I am. I have tried a few times to read the threads under papers, and you can almost mathematically predict that on the fourth exchange, people will accuse each other of being idiots. And on the next one, they will trade obscenities. I don't believe in non-curated exchanges. I really don't. Because people cannot resist "letting the pig out". This is a German expression. To let your inner pig out. And if there is a place where the pigs run freely, that's social media. It's like people running in pajamas on the street. There is absolutely no restraint, and I think it's absolutely disgusting. We should have another internet where people have to identify themselves. If people have to identify themselves, they could not hide behind anonymity, and this problem would not occur. I think it's completely disgusting that people can pretend to be whatever, and spew poison or venom or stupidity at the world, [scoffs]. Social media, I think, it is a pit.

IH: Mmhmm. Good. And then you already told quite a lot about research data and, kind of, the importance of sharing not only, kind of, the results but also, also the data to, kind of, be able to redo the studies that you've been doing.

DP: Yeah.

IH: Can you elaborate a little bit more on your views about that kind of research data dissemination?

DP: Actually, I thought, I invented a concept in the 1980s, where the place where I worked produced good books, and I included huge data tables into the book which allowed the reader to reproduce everything. I called this "data rich books". Now, many journals require you to make the data available as supplementary material or put them in a database, and it's excellent. Because data are expensive to get, you can get cost-effective research by analyzing the data that others have produced. And I think we should do more of this because if you want to construct a pyramid that reaches high, you to have a broad base. If you try to reach high on a narrow base, the thing will fall down. So, we need lots of data to infer new things. For example, genomic databases now allow a huge number of inquiries about the ancestry of people, about migration and stuff. But if somebody was to only work with the data that he or she can collect, they would never get anywhere. So, data sharing is a very important thing. Yeah.

IH: Mmhmm. Good. Thank you. What about illustrations? Kind of, infographics, visualizations? Maybe even interactive ones?

DP: I believe in very good graphs. And I'm a pain in the neck as a co-author because I always think about the graphs, what they have to say. Basically, you have lots of scientific papers that include graphs that must be explained. Which is actually the contrary to what they are supposed to do. Graphs are supposed to explain things, they're not supposed to require explanation. And, in fact, I have a booklet halfway done about how to make graphs. I'm a fan of [Edward] Tufte, who wrote a lot of books about how to present data through graphs. And in the papers that I am the first author, I give lots of emphasis to the graphs. Again: graphs must be explaining things and not require explanation. And that is very difficult for some people. On the other hand, I don't really like cartoons and animated graphs; that is for kids. It's not for grown-ups. So, here I am.

IH: Good. Is there, kind of, when it comes to the visual forms, is there something specific about that, kind of, good at conveying something, or…?

DP: Yeah! The eye can absorb a lot of information, and if a graph is well-constructed, it can tell you a lot. That's the saying that a graph is worth a thousand words. If it's conceived well, it can actually convey lots of information. But most graphs, in most papers, are stupid.

IH: [laughs]

DP: They are not necessary, or they don't convey any information, or they use only one of the axes, and the other, they don't. And this is also a waste of color, colors are used all over the place. You can tell that people don't think about graphs, and I give a lecture once a year to my students here about "bad graphs". I say that bad graphs really are necessary if you want to contribute bad papers. I turn it around. And I show examples of bad graphs and explain why they are bad.

IH: That's very good. Do you, kind of, yourself, read or watch or look at graphs or is that, kind of, that you look at them, if there would be a process, at what stage do they come? Kind of, do you go first for the diagram, or…?

DP: I kind of look at the graph and ask myself, "How can I best present the data?" And I play with the data, and when I have a design that seems to be OK, I have a person who draws for me, and we go back and forth until it is perfect.

IH: That's very good.

DP: Yeah.

IH: Mmhmm. Yeah. OK, well, now I guess we have, at about half an hour, so if you would like to ask…

DP: You can ask one more question, and then I go.

IH: All right, OK. What about, kind of, research posters? It's, as a genre, do you…?

DP: Well, posters…

IH: What do you like about them?

DP: Well, posters can be very nice. But lots of people misunderstand, totally, what posters are. And they try to keep the form of a paper in a poster, which is completely ridiculous.

IH: [laughs] Yes.

DP: I've seen posters with abstracts - as if the poster itself was not an abstract! You can look at guidelines "How to Make Posters" that are completely wrong. Posters are shown at conferences and people walk along the posters at about one-meter distance. One-meter distance. So, the poster must be attracting people that are one meter away. And, so it cannot include little things. But the authors of posters don't know that. They think they are doing a paper on a poster. Posters can be very good, can be very useful, can be very powerful when they are conceived as posters. And what you can do is in the corner of your poster is a bag with real papers that can be distributed once you have attracted people. But the guidelines for posters that most research agencies provide are completely stupid, because they conceive the posters as mini-papers, which they are not.

IH: Precisely. OK, good. Excellent. Thank you very much.

PART 2

IH: Last time, we closed with discussing about different genres of scholarly communication and, kind of, we talked about videos, and social media, and illustrations, and the final one we talked about was posters as a, kind of, way of disseminating research and getting informed of others' research. And, there's, kind of, one more thing on my list, on the different genres. And it's about books of different kinds.

DP: So, books-

IH: Do you write or read books?

DP: [laughs] My house is bursting with books. And I pay nearly $400 a month for storage of my other books and my reprint collections. I have a big problem, a book problem. I have books all over the place. But I have written about, edited, and written about 30 books. And all of them are fairly technical and had minuscule sales. A few, 2 or 3 of them, had a little bit more; especially the last one, called 'Vanishing Fish'. I have written a book, titled 'Darwin's Fishes' that was translated in Japanese, it's very successful. So, I do books. I like doing books, and I like expressing myself that way. But I don't like the fact that the many book chapters I wrote hardly get cited. I don't know why I continue to do that. I must have done a hundred or two hundred book chapters over the years; I don't know why I do that because they get cited - and thus used - much less than papers. And books don't get cited much except, obviously, the textbook that documents FishBase, and which is cited enormously. But that is in connection with the database. So, books… I use books for self-expression, really. Because they are not reviewed the same way as journal articles, and you can write personal opinions. So, I have done lots of books, both edited and authored. There was a time I went every year to an event that UBC organizes, called, "UBC Authors and Their Books." And I was happy that for several years, I was having a new book to contribute. And then I met a gentleman from the English Department who was publishing a book every year, books about some US army guy, like Clancy, you know, who writes books that read like weapon catalogues?

IH: Oh, yeah.

DP: And he was selling every year a hundred thousand or more of this trash, every year. So, I decided not to go anymore to this event, because I was conceited enough to believe that by publishing a book every year, which I did for a time, I would be doing something. But then "Darwin's Fishes" was quite successful; it's been translated in Japanese, as is my latest book "Vanishing Fish". So, self-expression is working.

IH: Do you, yourself, read books? To get informed of research? Obviously, if you have a lot of books, you do… but professionally?

DP: I read about 50% fiction and 50% nonfiction. When I go on a trip, which I don't do now because of COVID, I get two airport books: one fiction, one non-fiction. It's always the same. And I alternate between genres in fiction; I read lots of science fiction, actually. But also, all kind of intermediate genres. For example, I just read a book called, "Fish Don't Exist", a very personal account of the life of David Starr Jordan, a fish taxonomist and politician and first president of Stanford University. And he is a very shady character because he's the founder of the eugenics movement in the States. Yeah, I read lots of books about science in general and philosophy of science, and I teach it. I have a course every winter about philosophy of science. So, books are very much my thing. But those I write are not written - and this is true - with a reader in mind. I write to express myself.

IH: That's good. All right, that's great. Then, last time you mentioned that you work a lot with science journalists, and NGOs, and so on. Then, you probably have noticed that at least during the last few years there has been a certain kind of an upsurge of different kinds of science communication consultants offering their services. Have you, kind of, experienced that? And how have you reacted?

DP: Well, at the beginning of my involvement with science communication, I became a friend of a person who became a teacher, a mentor to many scientists. She is a former journalist called Nancy Baron. She is Canadian, but lives in the US, and she has taught science communication to many, many scientists. In fact, she was running the Leopold Leadership Program – named after the conservationist Arnold Leopold, in which people are taught how to speak to the press. I didn't do this program, but Nancy used interviews that I gave as teaching material because I tend to use metaphors and simple imagery in what I say, and give take-home message. And so, she used me for a while for her teaching. Now I'm used to that, and I know lots of journalists. I have even hired one, from the School of Journalism here at UBC, who does our press work. And I respect journalists. Because contrary to what many scientists believe, journalists don't want to sell newspapers - that's the editor's job. What journalists want is to see their articles in the first page, above the fold. And journalists also care about what is under their byline. And, contrary to many scientists' belief, journalists do mind being wrong. I know many journalists and, for example, in Canada, I'm probably the only Francophone fisheries scientist on the west coast and so I get called a lot by Quebec-based journalists at Radio Canada, and asked to comment on things. And, so, I'm aware of the danger of speaking about things that I don't know. When people ask me about salmon, for example, I don't tell them

I have no expertise about those. There is some temptation to talk about everything, right? But I don't talk about things that I don't know anything about. Still, because we employ a journalist who does press releases, I got lots of callbacks. "What is it that you have done?" I talk about what we have done; and I do podcasts.

IH: That sounds great, thank you. Then, we have to talk about, kind of, communication and dissemination of science using different kinds of media, if you like. But if we, kind of, think about a research project or research endeavor, so, I'm, kind of, thinking about how important you think that it's… share? And to get information about different aspects of research that, kind of, sharing now that you're doing, but then also knowing about the research others are doing.

DP: Sure, because if you want to collaborate with someone and you want to get them on board with what you're doing, you have to offer them something in return that will interest them. And, therefore, you have to know what they're doing. Thus, our 'catch reconstruction' project was done in collaboration with about 300 people in different countries. And they had to be motivated to work with us for free because we didn't have money pay anybody. So, what I offered to each of them is to write about the fisheries in their country, in a certain format. If they wrote in this format, then they could compare what they documented for their country with what was happening in other countries as well. If they wrote in another form, they could not. And so, they all participated for free - this is a project that the World Bank could not have done because it would have had to pay lots of people, lots of money. And they all did the work over more than 10 years, and each of them produced a chapter, which we then put online. Now, half of these papers are published in the primary literature. So, for many colleagues in developing countries, we provided an opportunity to publish. And mentorship. And structure. Most of them I knew from previous interactions because I've been teaching courses in different countries in the world. And people write me, and so, I have these contacts in almost all countries of the world, I have somebody I either know or somebody who knows somebody. So, yeah, you have to know what happens in your field if you want to collaborate, especially if you cannot offer financial support.

IH: Of course, yeah. When you're reading a journal article, so, is it important to know who wrote it and from what kind of a…?

DP: No; well-known authors and little-known authors are equally capable of writing stupid stuff. And so, it is not important who wrote an article. For new ideas, I read *Nature* and *Science*. For additional papers, that fill holes in what I do, I look mainly at papers that cite my own work, because they will generally be about stuff that interest me. Also, for FishBase, we need growth parameters and certain parameters for certain fish. When I read papers and I find growth parameters, I send them to the Philippines, where they'll be encoded. This is the more routine thing. The other thing, I mentioned before, is reading about original ideas, well-known authors are not likely to be coming up with a new thing; it is new people who have new ideas, usually.

IH: Precisely, yeah.

DP: And then I read the papers of my close friends, obviously. But I often comment on my friends' papers before they get published, so they are not surprising.

IH: Precisely, yeah. How is it - when there is a, let's say, a paper published, or whatever kind of result is coming out, how important is it to know about - for you - to know about, let's say, a little bit bigger context of all the study - the design of the research study as a whole, within which this research has been conducted?

DP: I don't understand the question - you're asking whether I look at the design of how the study was done?

IH: Yeah, precisely.

DP: OK, I have to confess something, I'm not very good at math. And so, I will not look at the power of the test, for example. Or things like that. Or whether a Bayesian analysis would have been more appropriate than a frequentist analysis, or whether the criteria for using an Anova were all met. In fact, I'm likely not to detect if an error was made. But what I'm looking at whether the results are interesting. Do, they connect with something else I know? Do they connect with previously unconnected things? Because I'm interested in what E.O. Wilson called "Consilience," things have to fit. And if they don't fit, something, perhaps they are broken and need to be rebuilt. Things have to fit. And, so, if somebody proposes something completely, shatteringly new, it is either wrong or all the other stuff around it is wrong. And that is what makes it interesting.

I must say that I'm not interested so much in precision, I'm interested in accuracy. Lots of colleagues spend a huge amount of time on defining their uncertainty of what they say, its precision. But what is interesting is "Can it be an accurate representation of reality"? What are the implications? And they are things that are done with high precision, with sophisticated software, that are bullshit. For example, my work on growth of fish and oxygen suggests very strongly - no, actually, shows - that when the water temperature is elevated, fish get smaller. And there are good reasons for that, which you can verify completely, and the physiological mechanisms for this are well established. And recently there was a paper published in Australia, based on underwater visual census of fish, that suggested that with temperature increasing, the fish either get smaller or get bigger. How can they get bigger? This paper has measures of uncertainty all over the place, but it is fundamentally rotten. And, with a few friends, I looked at this paper, it is so badly documented that it is not reproducible - we cannot trace back what they have done. I have asked some Australian friends if they can help me find out where the tumor is. The point is - and that's something, I'm trying to find a philosopher who confirms this – that some things cannot be the cause of a certain thing and of its very opposite. In other words, if a temperature increase is the cause of fish getting smaller, it cannot be, at the same time, the cause for them getting bigger. But the paper was published with all kind of precision metrics, right? But at the level of accuracy, is it even reasonable? It's not. So, I find that there is a huge drift toward crap that has confidence intervals. You know, crap with confidence intervals remains crap. And that is distressing, especially as statistics get more and more complex, but at the core of it is crap. In this case, you have to know some fisheries biology. For example, many of the fish that got bigger are fish that have been managed well, and so the fishery on it has declined. And that, I guess, is the reason why they got bigger - fishing made the fish smaller, and when fishing was reduced, the fish got bigger, and overcompensated the warming of the water. And I think that's the explanation, because they don't deal with the effect of fishing at all. However, demonstrating this is going to be lots of work, and life is short. Especially for a 74-year-old. That's me. Anyway, so that is my relationship to this... to the literature.

IH: When you said, kind of, in the study that you mentioned, the data wasn't documented-

DP: Very badly.

IH: It was documented very badly, what is good documentation of data?

DP: A good documentation should allow you to redo the analysis. And lots of people are reluctant to do that because they feel that their word - their analysis that they present - should be enough. So, the documentation they present is not sufficient to redo the analysis. And we talked about, the first time we met, about making data available to people in journals, but specifically, people should be able to redo the analysis. I know that the replication problem is more complicated than that; journal articles can be replicated only when you master the method that people have used. Because there are lots of those things that cannot be stated that must be known. But the data that, the key data must be available. Clear.

IH: How much do you have to know about how the data was collected or compiled? And, kind of…?

DP: As much as possible.

IH: Yeah.

DP: As much as possible because if you don't know crucial things, the results are going to be nonsense.

IH: Precisely, yeah. What would be crucial? [laughs] That's an impossible question, sorry.

DP: No- do you remember the kerfuffle with the Hite Report?

IH: Yeah…?

DP: It was a researcher who was investigating the sexual behavior of women, supposedly. And she – Shere Hite was her name - she sent to women, probably ten thousand or so, a questionnaire, and she had a very low response rate - about 10 or 15%. And these responses were saying, "I don't like sex with men, I prefer to satisfy myself because men are horrible persons." So, this became the main finding of the Hite Report. And she was heavily criticized because, [laughs] because she had no way of dealing with responder bias. But she said that she knew how to - there was a "woman's way of knowing" so that was how she could deal with it. She was hounded out of research. She left the U.S. and went to Germany.

I had a Brazilian PhD student who was working on sport fishing in Brazil. She did a questionnaire and she also had a very low response rate, and she was afraid of this problem, of this responder bias. And so, my advice to her was – because I view myself as a feminist – to write to Shere Hite and ask her how she dealt with it. [laughs] Because I believed at the time that she had found how to deal with responder bias. And, so, this student of mine wrote a very friendly, respectful letter to Shere Hite asking "How did you deal with responder bias? I have a big problem with responder bias, and could you tell me how you dealt with it?" And she got a hateful, hateful response. It was like the computer jumping at you. My student was part of a conspiracy to get her down - it was horrible. The student still, 20 years later, she's now a professor in Brazil, she still is under shock from the response from Shere Hite. [laughs] So, there we are. That's the story with Shere Hite. Incidentally, I have another student now who is doing a questionnaire, and I am still so shocked by Hite's response that I pushed her to send a questionnaire that would consist of one question, and the questionnaire is sent as a private email, separately, so it is not a bulk thing. And she has a response rate of 70% because it's personalized and asks only one question. The 70% response rate is because I became aware that there is a problem that Shere Hite didn't know how to deal with. So, in general, I'm not interested in the power of tests. I would not be a very trusted medical researcher. Because I'm interested in the accuracy of the result, not their precision. And I have authored a textbook of fish population dynamics where I showed how to obtain various parameter estimates, but for most of the things that I proposed solutions for, I don't even show how to compute the confidence intervals.

IH: Yeah, [laughs].

DP: Yeah, but this is a long time ago now, I wouldn't be able to write a textbook like this anymore.

IH: Precisely, yeah, then, I guess I just have one more question to go, and it would be, kind of, an imagination exercise. Let your fantasy guide you. And, kind of, if you could describe an ideal scientific communication system, kind of, how you would be able to disseminate and inform about your research, and how would you get to know about what others are doing, if there weren't going to be any kind of restrictions or problems with the resources or any problems with reality? How would it look like?

DP: I think what we need is to get rid of for-profit science publishing. What we would need is to get back, if it's possible, to publishing by scientific societies that are not out for profit. I think that the profit motive, when injected into science, is as bad as when it is injected into education or health care. These are three sectors where the profit motive must be absent. Health care, we can see in the U.S., cannot be run with the profit motive. We can also see what it does with education. I think if we could get rid of the profit motive in science publishing, we would all benefit. We have solved many problems that affected science before, the fact that it was only a selected group of people who could participate. Now, women can participate, people of color can participate, everybody can participate. It's the publication cost that is the remaining problem. The peer-review system, I think, should be maintained, but it should be connected with some sort of rewards. Not monetary, but, for example, a free subscription to the journal in question if you do a certain number of reviews, or accelerated review of your own papers. An idea I have is that if you submit a paper to a journal, you must promise, within a year, to review 2 or 3 articles by others. This would guarantee that the journal that published your work, gets reviews done by people who are competent in this area because that's your area of specialization. A scheme like that would work because my motivation for reviewing is largely guilt. I cannot justify to myself turning down a request to review by a journal that has accepted my papers. So why not turn guilt into a contract? We would publish your stuff, but you agree to review 2-3 papers. Incidentally, I have become, the first of July, a member of the Advisory Committee of *Science* and I have reviewed the first 3 papers - not really reviews, only pre-reviews, assessments of whether they should be reviewed or not.

So that's my only good idea. That's my only idea about this reform. That the journals should require of all authors that they have published papers, that 2 or 3 are reviewed. And that would, I think, resolve the big problem of reviewing that we have, that reviewers are so hard to get. I'm an editor of a special research topic in one of the *Frontier of Science* journals, and finding reviewers is very difficult; you might have to ask 20 people before you get somebody, who then doesn't deliver. It's awful. People expect their papers to be published in peer-reviewed journals but do not want to review. That is out of whack. But I think that the science journalists do a good job, and that scientists are now increasingly aware that they have to communicate with science journalists. When, when I was a young scientist in the 1980s, there still were colleagues who thought that, "oh, we are too good to be interacting with science, this will pollute the science." Nowadays, science denialism is so strong that scientists must intervene. They must participate in societal debates. And the best way to do it is to work with a science journalist because the scientists themselves mostly don't know how to present the science they do.

IH: That's a good point. All right, then, I don't have any more questions, but I'm wondering if you have anything you would like to ask me, or if you would like to comment or say something more…?

DP: I don't know what you do. So, tell me what you do, just for information. What will do you with this?

IH: What will I do with this? Yeah, we're doing a bunch of interviews, about 20, at least to start with, and what we're trying to figure out is how scientists and scholars - in the sciences and social sciences - how people are disseminating their research to others, mainly for research, but also to other stakeholders. And then to see what kind of preferences scientists and scholars have about getting informed about others' research. And to try to figure out how the, how people are knowing, are getting informed about things nowadays because it's very much not what it was before, that people are reading a bunch of journals and reading, new books. So, it's more like people are using many diverse strategies nowadays, but there is this kind of a hunch that these things might not really match at the present.

DP: Are you finding any well-established scientists who spend any time on social media? Or social…?

IH: Well, so far, we haven't, extremely a lot of interviews yet, but yeah, we do. But it's really, kind of… not everyone. I would- I can't really quantify, it's impossible on the basis of this. But there are, kind of, there are those who think that social media is very useful, and then there are those who use social media only in their free time to communicate with their friends and family and so on and absolutely don't do anything professional on social media. So, it's- it's really an interesting question that, kind of, why, and if there is something that explains why certain people find it useful and others don't.

DP: It's not that I find it useless, it is that I hate it.

IH: [laughs]

DP: OK, what I'm left is for having to apologize again…

IH: No worries…

DP: OK, so, in 2 years, when your study is finished, send me a PDF of it.

IH: I will, absolutely. After this interview- so thank you once more for your time and for your great insights into this whole thing. We'll be sending you a transcription of the interview, you can comment, edit, add whatever you'd like to it if you'd like. You don't have to do that. And then you will also get a gift card to the UBC bookstore. And that will be happening kind of…

DP: I'll be waiting for that!

IH: So, you can get more books.

DP: OK, thank you very much.

IH: Thank you, thank you yourself.

THE OCEANS' SHIFTING BASELINES: COMMENTS ON A TED TALK[1]

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Abstract

On April 7, 2010, the author, on board a cruise ship in the Galapagos, gave, a TED Talk titled 'The Oceans' Shifting Baselines' to an audience of NGO representatives and 'celebrities' with an interest in ocean conservation. This talk presented the idea behind the author's 1995 contribution ("Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10(10): 430), put in the context of current Galapagos marine biodiversity. What is presented here are the comments to this TED Talk, which, along with those of other TED talks, are being taken down from the website where there were initially posted.

Introduction

The comments on my TED Talk of April 7, 2010, titled The Oceans' Shifting Baselines' are reproduced below without editing (except for typos). However, in some cases, a note was attached (see Endnotes). Several of these comments, dated from the time my TED Talk was posted (about 6 months later), can be understood only after one has seen that talk – I am just saying!...

Greg Keydel
Posted 2 months ago
Another example of shifting baselines[i] is the standard of life we think is acceptable for animals vs. the standard of life as evolution intended. This is true for both our 'pets' and for the animals stuck in our food system. The difference between the two, is we try to act out of love for our 'pets' but we usually act out of greed with other animals[ii].

חגית מזרחי
Posted 7 months ago
I am troubled by your claim that marine protected areas present the past situation. At best the present the state of events at the time they were created. And they also deteriorate over time. With real restoration actions, things will go only one way – down[iii].

Mary Vannoy
Posted 9 months ago
Amazing post.

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[1] Cite as: Pauly, D. 2021. The Oceans' Shifting Baselines: Comments on a TED Talk, p. 35-40. *In:* D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1).

Cheng-En Chuang

Posted 8 years ago

Every time I watch such video about the environment impact issue, I always get little frustrated, because of the too little thing I can do. I really hope that our people can really made up our mind to just has enough on our need[iv].

Bastiaan Vermonden

Posted 9 years ago

If you are a diver please fill out a survey for my website diveselector.com http://www.diveselector.com/survey/standard. With this data I hope to accurately compare diving destinations so that divers can consistently choose to visit destinations with abundant marine wildlife. This will provide economic rewards to countries that ensure effective protection for their big fish, turtles, rays, sharks and seahorses. I hope that this will help motivate people, businesses and organizations to use their creativity, ingenuity and competitive spirit to find ways to return the ocean to health and ensure it remains a place of wonderful exploration.

Punit Jamba

Posted 9 years ago

Reminds me of how my grandfather used to reminisce of his childhood. Of how things have become 'expensive' from being 'in plenty' earlier. The planet seems overburdened with humans. But nature is fighting back by evolving.

Dean Jacobson

Posted 9 years ago

Living on a coral atoll in the Marshall Islands with a heavy human population, I wonder how its reefs have changed...I have worked hard to document how various diseases are related, I think, to human waste, and in less than 10 years have photographed many hundreds of corals, as individuals, being killed (sometimes this takes 6 years, as an infection slowly spreads over a watermelon-sized brain coral). It is slow, gradual, and now with digital cameras people can document the baseline very convincingly (I take over 4000 images each years of coral alone). On the surrounding low-population atolls (and I have been diving on 12 of them), *all* the coral are healthy, beautiful, but not on over-populated Majuro! The conclusion: people living a western life-style and growing above an ecologically tenable density are incompatible with living coral; the remaining coral are all dead, but they just don't "know" it yet. Conclusion 2 (which very view people have the ethical, moral and intellectual strength and courage to admit): non-aboriginal humans are an invasive species gone amuck. There, I said it. What do we do about it? Continue to take pictures while so much of the natural world dies, is overfished, poisoned, over-heated? How about confronting our corrupt political systems! (Also, it was my choice not to reproduce, and not to own a car, but I still eat beef, I've got to stop that...)

james dracos

Posted 9 years ago

We don’t need to over complicate this with massive no fish sanctuaries - we need diversely located sanctuaries that allow for recreational fishing = CATCH AND RELEASE ONLY AREAS. We also need bans on BAIT taking which is used for protein for animals - IF we have Bait and areas no take but fishing allowed = PEOPLE WILL SEE THE CHANGE. Now for an old fishing story - when I was 14 - 50 years ago I would fish on the Pensacola Beach pier - and there were many fish - but most of all there was plenty of bait. we would see schools of bait surrounded by predator fish. One time I remember a massive school of ladyfish (small predator) go by the pier for several days - it went around the end of the pier about 50 feet wide at about 2 miles per hour. If you put anything in the water, they would attack it. KEY is BAIT and Areas where any Catch is prohibited - in AREAS.

dave tribbett
Posted 9 years ago
This is old news, unfortunately. We are on the 4th type of fish to make "fish sticks" because we overfished the other species. Humans are inconsiderate and really don't deserve to have this wonderful planet - unless we change radically. The Earth/Universe will do what they do, purge and restart at some point. With capitalism driving the planet, looks like we'll drive ourselves to extinction by just doing what we do.

Dean Jacobson
Posted 9 years ago
Too true… ideologies trump reason until it’s too late, like on Easter Island!

Martie Anderson
Posted 9 years ago
In reply to: This is old news, unfortunately.... by dave tribbett
I hear what you are saying about the coral reefs. I think this talk helps me understand it in a different perspective. I didn't know that trash in unfished areas was covering the sea floor. I didn't know that the sizes of fish are declining. I'm a vegetarian and don't eat fish or other animals so maybe I'm not as in touch with the issues he is discussion.

I do feel your frustrations though and it comes through loud and clear.

Chris Edgell
Posted 9 years ago
(I, too, miss thumbs up AND thumbs down) ... also wish you'd do like Yahoo and notify how many thumbs up and replies... What I came to do is to ask a question...if the whales are protected species and a whale eats 1 or 2 tons of seafood a day, is this not humans causing depletion of fish? I call it unnatural imbalance.

Jamie Godfrey
Posted 9 years ago
It depends what species of whale you are talking about. The majority of species that people think of when they think of whales actually eat planktonic organisms such as krill.

Thomas Costick
Posted 9 years ago
It's always struck me as ungrateful and arrogant, the way commercial fishing reaps resources from the seas, as if the supply is endless.

The damage done to the environment in reduced fish numbers, out-of-balance ecology and a physically wrecked sea floor may once have been attributed to ignorance on the part of the fishing crews. This can no longer be presented as an excuse.

Vincent Brandon

Posted 9 years ago

Reading and listening to involved speakers like this leads me to information I never knew I wanted to know. Is that the power of education? Is that the broadening of mind? I wonder if the less exposed don't care and don't want to care. Can they care, having not been introduced to the evidence of a debate?

I wonder how far the "shifting baseline" goes. We are an incredibly adaptive species - within a generation we can easily forget the primes of our own past, nonetheless the greatness of previous civilizations and natural order. If something like this could be studied by psychologists, the information could empower a generation of change. As I see it, believing in the concept of our 'shifting baselines (we are designed to get bored, even of the beautiful), the elders are the only ones capable of understanding the brevity of the situation; the only ones with the experience to demand sustainability. I just wonder if there isn't an inherent fallacy within humankind that could lend itself to catastrophe.

By the time we could even record the 'state' of our oceans with any precision, poor practices had decimated millions of hectares. But, not just that. Before we could record and document CPI and median incomes, we had no idea what the division of wealth even looked like across a society, and today cannot fathom the division between species. There's no question that all life contributes to the biosphere. The ultimate test may very well be accounting for our own predatory fallacies before we destabilize not only society, but billions of years of evolution.

Fred van Zwieten

Posted 9 years ago

Mr. Pauly will get what he asked for. Here is a quote from Cameron: "Avatar 2 narrows the spotlight instead of just nature in general or the rainforest. It focuses it a little more on ocean issues, because we have a planet that's a blue planet. From a distance, you look at it, the Earth is a lot more blue than it really is, you know brown, the land mass. We're making the oceans un-survivable for a lot of the species right now. For a lot or reasons. It's just a way to focus a little energy in that direction."

Arno Hayes

Posted 9 years ago

I find it so interesting that the Tilapia are maturing when they are smaller[v]. Darwin would probably find it interesting too. Could it be that smaller fish have a better chance of surviving? What would that mean from a "bigger is better" perspective?

Thomas Costick

Posted 9 years ago

In the case of the fishery mentioned in this example, my guess is that smaller fish tend not to be caught by the nets, so they go on to breed again. In this artificial environment, smaller *is* better.

Dan F

Posted 9 years ago

Biologist like myself like to compare current data with what we perceive as a relevant measure to the more distant past and more "natural" conditions. Despite the fact that the data of the past may be less qualitative and/or quantitative. That view seems logical and justified when one thinks in terms of biology and historical time lines. The speaker is asking us to appreciate this perspective and many of us agree with him. It is important because our impact and legacy as a species on earth does not necessarily revolve around what we chose to selectively believe or justify.

It seems we are more inclined to measure things closer to home and of our own life span and experience - perhaps relying more on education about the past seems too abstract and fuzzy. People tend to dismiss such concerns and contend environmentalist are the ones that need to adjust their thinking to the extent human activities and influence on the environment is the relevant new natural, and furthermore we should be more thankful about that fact. Sort of an all or none attitude.

Excellent topic and an appropriate tap on the shoulder.

Tom Comerford
Posted 9 years ago
There's nothing like an ocean to make people feel small. Whether from a beach, a cruise ship, or in flight, an ocean seems almost infinite. It's difficult to comprehend that marine ecosystems can be so easily impacted. Yet so much of the world's population is dependent on the fisheries' harvest, and when that ecosystem is at risk, so is that population.

More people need to see this presentation.

W T
Posted 9 years ago
These are excerpts from a 1995 article:
"'Plenty more fish in the sea,' runs the saying. But it is wrong," notes *The Economist*

"The sea's abundance has been stretched beyond its limit." Since its peak in 1989, the world's marine fish catch has been declining.

The reason is simple: "Too few fish have been left in the sea to maintain spawning stocks. Fishermen are living off capital, consuming the resource that should yield their catch."

According to the United Nations Food and Agriculture Organization, 13 of the world's 17 major ocean fisheries are in trouble—4 of which are classified as commercially depleted.

Sophisticated technology—such as sonar and satellite communications—has made it possible for fishermen to locate the fish even in remote areas and to return to precise prime fishing spots.

Huge factory trawlers the size of football fields, with even larger nets, haul in excessive quantities of fish.

Very sad indeed.

Richard Krooman
Posted 9 years ago
Avatar 2 under water hmmmm.... what about Avatar 0.2 called The Abyss?

John Smith
Posted 9 years ago
"We transform the world, but we don't remember it" - We are so weak in the face of the shifting baseline due to our limited memory and lacking experience of past scenarios. What can humans do to face the shifting baseline? Can we do more than sustain it where it is? Can we shift it positively?

Elon University Philosopher Anthony Weston wrote about this when he described his philosophy of "possibilism". He advocates for pushing for the opposite possibility for our relationships with the environment and other species - what he calls the "more than human world". Following his ideas, if we work instead to uplift other beings to new, healthier, stronger, natural possibilities, and if we believe in a positive shifting baseline, we will see the opposite stories - increased life and increased resilience of the system. How can we shift the baseline positively?

jesse jones
Posted 9 years ago
Makes sense: Raise the standards, raise expectations, don't settle for terrible.

No one would be ok with a bad relationship if they knew what a good one was like. No one would settle for a rundown home if they had the experience of living in a nice home. Who would expect a bad government if they were used to a good one? Who would enjoy a grizzly steak if all their life they had well-prepared filet mignon?

Treat someone or something around you better and maybe you'll teach them to expect/rise to a higher standard of existence.

Endnotes (added in January 2021)

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[i] See Pauly, D. 1995. "Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10(10): 430.

[ii] There is, however, a trend toward animal welfare which also includes fish and other marine animals; see Pauly, D. and D. Zeller. 2019. Agreeing with FAO: Comments on SOFIA 2018. Marine Policy, 100: 332-333. doi.org/10.1016/j.marpol.2018.12.009 and Jacquet, J., Franks, B., Godfrey-Smith, P. and Sánchez-Suárez, W., 2019. The case against octopus farming. Issues in Science and Technology, 35(2): 37-44.

[iii] Actually, marine biodiversity can be re-established in areas where it was degraded, and can be made to resemble the status quo ante; see for example Palumbi, S.R. and Sotka, C., 2011. The death and life of Monterey Bay: A story of revival. Island Press, Washington D.C.

[iv] Yes. Gandhi is supposed to have said that "Nature could accommodate our needs, but not our greed".

[v] Actually, I will publish later in 2021 a paper showing that tilapia, including the blackchin tilapia (*Sarotherodon melanotheron*) mentioned in the TED Talk and the often-farmed Nile tilapia (*Oreochromis niloticus*) do not mature when they 'smaller' than other fish. They spawn at the same fraction of the maximal size they can reach as other fish; however, they are hardier that most other fish groups, and they can tolerate stressful conditions better than other fish. The stressful conditions reduce the maximum size of tilapia, and thus also their size at first maturity (see Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances* 7: eabc6050.

THE OCEANS AND COVID-19: A TEN-POINT AGENDA FOR ACTION[1]

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Abstract

The article presents 10 points with brief elaborations, which would, if implemented, re-energize our economies and avert the biodiversity and climate change crises of which the present COVID-19 crisis represents a portend. These 10 points, which reflect the authors' professional interest in marine biology, are: (1) promote carbon neutral economies to mitigate global warming; (2) support local food provisioning and sustainable land-use practices; (3) strive for social and economic dignity; (4) promote sustainable fishing; (5) create large no-take marine reserves; (6) promote sustainable aquaculture practices; (7) place a levy on fossil-fuel-based manufacturing and products; (8) reduce maritime traffic; (9) apply the One-Health principle to ocean conservation and management; and, (10) promote conservation of coastal land and seascapes.

Introduction

Worldwide threats -- such as SARS-CoV-2 -- are becoming more pervasive with global change. Solutions to environmental issues challenging nature and humanity are well-identified, but our modern societies have, so far, failed to implement them (Ripple et al. 2018). Yet, as the SARS-CoV-2 crisis demonstrated in a spectacular manner, the functioning of entire nations can be transformed within days if needed. Because of the current pandemic, humanity will adjust and more people than ever are ready to transform the world we live in. This is a historical opportunity to reboot our socio-economic systems and revise the values that underpin them, to achieve sustainability and equity. It is essential for environmental scientists to stand up now, to provide guidance before our societies are pushed back into business-as-usual.

The oceans are the cradle of life on earth, a critical part of global biogeochemical cycles, and harbor essential natural resources. Marine life has suffered from the tragedy of the commons, with extremely unequitable share of ocean services captured by wealthier nations. As humanity is challenged by the

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[1] Cite as: Grémillet, D., B.D. Hardesty, H.K. Lotze, D. Obura, D. Pauly, Y-J. Shin and U.R. Sumaila. 2021. The oceans and COVID-19: A ten-point agenda for action, p. 41-44. *In*: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1)

current crisis, we need well-functioning oceans more than ever to ensure our own resilience and survival. We are, therefore, calling for immediate and rapid global action on ten key commitments to ocean conservation, with the overarching objective of a collective, legacy mindset to decision making, to ensure the health and well-being of both current and future generations.

The ten points

The following ten commitments encompass major anthropogenic drivers that impact ocean ecosystems and marine life, as well as dependent human well-being:

1. Promote carbon neutral economies to mitigate global warming (Gençsü et al. 2020) and climate-change effects on ocean ecosystems, as well as associated goods and services (Lotze et al. 2019; Boyce et al. 2020). Ending jet fuel subsidies will be an essential step that will challenge our current mobility and mass tourism, which have large impacts on coastal ecosystems worldwide. In rich countries, the SARS-CoV-2 crisis has shown that much personal mobility is actually superfluous, proving that this target is achievable.
2. Support local food provisioning and sustainable land-use practices, including agroecological practices, sustainable forestry and land-conversion, moving away from the massive use of fertilizers, pesticides and other chemicals (Dainese et al. 2019). This will have the triple benefit of shortening supply-chains, reducing pollution of coastal zones, and providing livelihoods for inland populations which otherwise overcrowd and severely alter coastal ecosystems. Such changes are on the top of the environmental agenda because agriculture, notably as it is operated in wealthy nations, is currently the main driver of environmental degradation (Pe'er et al. 2020).
3. Strive for social and economic dignity (Sperling 2020). This includes creating a universal minimum income while ending harmful subsidies to all sectors, notably those leading to fishing and agricultural overcapacity, and ensuring fair labor practices to avoid modern slavery (Tickler et al. 2018). Nearly thirty countries around the world are seriously considering implementing a universal minimum income, and most attempts thus far report success.
4. Promote sustainable fishing by moving towards less destructive and more selective fishing practices, by regulating fisheries' access to the high seas (Sala et al. 2018), and protecting areas within national exclusive economic zones (Pauly 2018). This will also be achieved by preserving local food production capacities, local markets, and local communities (Harper et al. 2020). At the moment the COVID-19 crisis has been detrimental for small-scale fisheries, but there are also positive effects in terms of globally-reduced fishing pressure and the revival of local seafood supply chains (Bennett et al. 2020).
5. Create large no-take marine reserves along a fraction of all coastlines and very large offshore reserves to ensure that fish and other animals exploited and/or impacted by fisheries can rebuild and maintain viable populations, ensure that fisheries in adjacent grounds can thrive, and mitigate the impact of climate change on exploited marine animals (Roberts et a. 2017).
6. Promote sustainable aquaculture practices. This will include farming lower-trophic level species, preferably not salmon and other carnivores (Rosa et al. 2020), to move away from the use of fishmeal and oil, and reduce pollution, destruction and other harmful effects in coastal zones. This is achievable, notably, through the use of novel feeds (Cottrell et al. 2020) and low-contaminant integrated multi-trophic aquaculture systems.
7. Place a levy on fossil-fuel-based manufacturing and products (Forrest et al. 2019). Tax plastics at the top of the supply chain – and throughout – to ensure consistent pricing that supports circular economic principles and promotes recyclability and economic benefits for waste pickers – all of which will reduce plastic leakage to the ocean (Worm et al. 2017). This point seems particularly important as

the SARS-CoV-2 crisis is in the process of generating large volumes of additional non-biodegradable waste.

8. Reduce maritime traffic. This will be achieved by preserving and rebuilding local industries and supply chains, moving away from imports of luxury products, and reducing trade globalization and global tourism (Kellerman 2020). This will also have the added benefits of reduced ocean pollution (noise, light, discharges), reduced ship strikes of vulnerable species (e.g., whales), and reduced transport of invasive species. Such changes are now being strongly supported by incentives to revive national industrial activities, reducing global trade (Ozili & Arun 2020)
9. Apply the One-Health principle to ocean conservation and management (Destoumieux-Garzón et al. 2018). Our societies must recognize that marine biodiversity and human health are intricately linked. More diverse, productive and resilient marine ecosystems are needed to support a humanity otherwise riddled with socio-economic stress and chronic disease (Blanchard et al. 2017; Boyce et al. 2020). Shaken by the current crisis, humanity is ready to rethink its relationship with wild nature (Martin et al. 2018).
10. Promote conservation of coastal land and seascapes, including the protection of key habitats such as wetlands, mangroves, saltmarshes, kelp forests, seagrass beds, oyster and coral reefs. Those biodiversity hotspots serve as essential nursery, foraging, breeding, and spawning grounds for a multitude of species. They also capture carbon, stabilize sediments and protect from storm surges. A recent synthesis demonstrates that rebuilding marine life is indeed achievable by 2050 (Duarte et al. 2020).

Conclusion

Some will argue that nature conservation has become optional under COVID-19, because humanity has more urgent matters to deal with. We strongly disagree with this short-sightedness and think that we will face many similar crises if environmental issues are not being dealt with via a transformation of our societies. Taken together, the emergency measures we propose in favor of ocean health challenge the notion of unmitigated blue growth (Otero et al. 2020), but raise hopes for alternative socio-economic trajectories enabling a future for humanity under the sea wind.

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THE MARINE BIODIVERSITY OF FRENCH POLYNESIA[1]

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Abstract

The marine biodiversity of French Polynesia (Marquesas, Tuamotu, Society, Gambier, and Austral Islands) was studied with emphasis on pelagic fishes, based on FishBase (www.fishbase.org), SeaLifeBase (www.sealifebase.org), and other sources which complemented these two information systems. Mapping the distribution of pelagic fishes led to the identification of a well-defined area in the southeast of French Polynesia (i.e., in the Gambier and Austral Islands) with a very high biodiversity of pelagic fishes and which appears very suitable for setting up a marine reserve.

Introduction

The French Polynesian archipelago (Marquesas, Tuamotu, Society, Gambier, Austral Islands; see Figure 1) has an EEZ covering 4.8 million km^2, a shelf area of 6,713 km^2, for a total land area of 3,520 km^2 (ISPF 2014)[2]. One of the most remote group of islands in the Pacific, French Polynesia has 20% of the world's 425 atolls (most of which are found in the Tuamotu Archipelago; see Salvat et al. 2003). These conditions suggest a high diversity of habitats, and thus of species. Meyer and Salvat (2009) reports 1,024 marine fish species, 1,500 mollusks, 978 crustaceans (51% of which are crabs), and 176 corals. Many more species are still to be described during the course of scientific surveys (see, e.g., Pierce et al. 2003)[3]. Compared to other archipelagoes in the region, however, the endemic marine fauna is less speciose in French Polynesia, but is consistent with trends in regional diversity (Meyer and Salvat 2009; Caley and Schulter 1997), i.e., distance from an area with a high biodiversity, for instance the Coral Triangle (Carpenter et al. 2010), which limits the number of species that can colonize an area (see, e.g., Glynn et al. 2007; Scheltema 1986).

This study investigates species diversity in French Polynesian waters by establishing some preliminary trends in 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 for other marine vertebrates and invertebrates (www.sealifebase.org). It also investigates the time series trends in habitat preferences of commercially exploited species using catch data from the *Sea Around Us* database (www.seaaroundus.org). Special attention is given to pelagic species.

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[2] See also the French Polynesian EEZ data by the *Sea Around Us* at www.seaaroundus.org/eez/258.aspx .

[3] See also the web site of Pacific Discovery: A voyage to French Polynesia at www.thekermadecs.org/pacific-discovery-a-voyage-to-french-polynesia .

Material and Methods

Scientific literature (including online checklists and resources) that explicitly mention the occurrence of species in French Polynesia and its islands were obtained, and data on the distribution (geographically referenced occurrence of marine species) and ecology (habitats and depth ranges) from these sources were encoded in two global species information systems: FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). The resulting number of species by taxon encoded in FishBase and SeaLifeBase were compared with those in Meyer and Salvat (2009), as well as to other islands in the same broad biogeographic region (Pitcairn and Easter Islands).

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 ($SI=1/\Sigma p_i^2$), i.e., the weighted mean of the proportional abundances of species occurring in a given cell (see Peet 1974). Here, we refer to this as the Habitat Preference Index ($HPI=1-SI$), 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 French Polynesian EEZ. HPI values approaching 1 represent cells with a low number of species 'preferring' those habitats, while HPI values approaching 0 represent cells with a high 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 Close et al. (2006) and Palomares et al. (2016), were obtained from species ecology data in FishBase and SeaLifeBase. Species habitat preferences (HPI_{spp}=number of habitat where species is present/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 Bale et al. (2009). The average annual $HPI_{catch}=(HPI_{spp}*Catch_{spp})$/Total Annual Catch was then plotted over the 1950-2010 period of reconstructed marine fisheries catches.

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 French Polynesian waters.

Phylum	Class	Order	Family	Subfamily	Genus	Species	Author	Habitat
Chordata	Mammalia	Cetacea	Balaenopteridae		*Balaenoptera*	*acutorostrata*	Lacépède, 1804	Pelagic
					Balaenoptera	*borealis*	Lesson, 1828	Pelagic
					Balaenoptera	*musculus*	(Linnaeus, 1758)	Pelagic
					Balaenoptera	*physalus*	(Linnaeus, 1758)	Pelagic
					Megaptera	*novaeangliae*	(Borowski, 1781)	Pelagic
			Delphinidae		*Delphinus*	*delphis*	Linnaeus, 1758	Pelagic
					Feresa	*attenuata*	Gray, 1874	Pelagic
					Globicephala	*macrorhynchus*	Gray, 1846	Pelagic
					Grampus	*griseus*	(Cuvier, 1812)	Pelagic
					Lagenodelphis	*hosei*	Fraser, 1956	Pelagic
					Orcinus	*orca*	(Linnaeus, 1758)	Pelagic
					Peponocephala	*electra*	(Gray, 1846)	Pelagic
					Pseudorca	*crassidens*	(Owen, 1846)	Pelagic
					Stenella	*attenuata*	(Gray, 1846)	Pelagic
					Stenella	*coeruleoalba*	(Meyen, 1833)	Pelagic
					Stenella	*longirostris*	(Gray, 1828)	Pelagic
					Steno	*bredanensis*	(Cuvier, 1828)	Pelagic
			Kogiidae		*Kogia*	*sima*	(Owen, 1866)	Pelagic
			Physeteridae		*Physeter*	*macrocephalus*	Linnaeus, 1758	Pelagic
			Ziphiidae		*Mesoplodon*	*densirostris*	(Blainville, 1817)	Pelagic
					Ziphius	*cavirostris*	Cuvier, 1823	Pelagic
Chordata	Reptilia	Testudines	Dermochelyidae		*Dermochelys*	*coriacea*	(Vandelli, 1761)	Benthopelagic
Chordata	Actinopterygii	Anguilliformes	Synaphobranchidae	Ilyophinae	*Meadia*	*abyssalis*	(Kamohara, 1938)	Benthopelagic
		Beloniformes	Exocoetidae		*Cheilopogon*	*pitcairnensis*	(Nichols & Breder, 1935)	pelagic-neritic
		Beryciformes	Holocentridae	Myripristinae	*Ostichthys*	*archiepiscopus*	(Valenciennes, 1862)	Benthopelagic
		Clupeiformes	Engraulidae	Engraulinae	*Stolephorus*	*indicus*	(van Hasselt, 1823)	pelagic-neritic
				Coiliinae	*Thryssa*	*setirostris*	(Broussonet, 1782)	pelagic-neritic
		Elopiformes	Elopidae		*Elops*	*hawaiensis*	Regan, 1909	pelagic-neritic
			Megalopidae		*Megalops*	*cyprinoides*	(Broussonet, 1782)	Benthopelagic
		Gonorynchiformes	Chanidae		*Chanos*	*chanos*	(Forsskål, 1775)	Benthopelagic
		Mugiliformes	Mugilidae		*Liza*	*alata*	(Steindachner, 1892)	Benthopelagic
					Mugil	*cephalus*	Linnaeus, 1758	Benthopelagic
		Perciformes	Blenniidae	Salariinae	*Praealticus*	*caesius*	(Seale, 1906)	pelagic-neritic
			Carangidae	Caranginae	*Caranx*	*lugubris*	Poey, 1860	Benthopelagic
					Decapterus	*macarellus*	(Cuvier, 1833)	pelagic-oceanic
			Coryphaenidae		*Coryphaena*	*hippurus*	Linnaeus, 1758	pelagic-neritic
			Emmelichthyidae		*Erythrocles*	*scintillans*	(Jordan & Thompson, 1912)	Benthopelagic
			Gempylidae		*Diplospinus*	*multistriatus*	Maul, 1948	Benthopelagic
					Nealotus	*tripes*	Johnson, 1865	Bathypelagic

Phylum	Class	Order	Family	Subfamily	Genus	Species	Author	Habitat
			Istiophoridae		*Istiophorus*	*platypterus*	(Shaw, 1792)	pelagic-oceanic
					Tetrapturus	*angustirostris*	Tanaka, 1915	pelagic-oceanic
			Kuhliidae		*Kuhlia*	*sandvicensis*	(Steindachner, 1876)	Benthopelagic
			Lutjanidae	Etelinae	*Etelis*	*carbunculus*	Cuvier, 1828	Benthopelagic
			Scombridae	Scombrinae	*Acanthocybium*	*solandri*	(Cuvier, 1832)	pelagic-oceanic
					Euthynnus	*affinis*	(Cantor, 1849)	pelagic-neritic
					Katsuwonus	*pelamis*	(Linnaeus, 1758)	pelagic-oceanic
					Thunnus	*alalunga*	(Bonnaterre, 1788)	pelagic-oceanic
					Thunnus	*albacares*	(Bonnaterre, 1788)	pelagic-oceanic
					Thunnus	*obesus*	(Lowe, 1839)	pelagic-oceanic
			Symphysanodontidae		*Symphysanodon*	*maunaloae*	Anderson, 1970	Benthopelagic
			Xiphiidae		*Xiphias*	*gladius*	Linnaeus, 1758	pelagic-oceanic
		Stomiiformes	Stomiidae	Melanostomiinae	*Eustomias*	*bulbornatus*	Gibbs, 1960	Bathypelagic
Chordata	Elasmobranchii	Carcharhiniformes	Carcharhinidae		*Carcharhinus*	*longimanus*	(Poey, 1861)	pelagic-oceanic
					Galeocerdo	*cuvier*	(Péron & Lesueur, 1822)	Benthopelagic
					Prionace	*glauca*	(Linnaeus, 1758)	pelagic-oceanic
			Sphyrnidae		*Sphyrna*	*lewini*	(Griffith & Smith, 1834)	pelagic-oceanic
					Sphyrna	*mokarran*	(Rüppell, 1837)	pelagic-oceanic
		Lamniformes	Alopiidae		*Alopias*	*pelagicus*	Nakamura, 1935	pelagic-oceanic
Chordata	Elasmobranchii	Lamniformes	Alopiidae		*Alopias*	*vulpinus*	(Bonnaterre, 1788)	pelagic-oceanic
			Lamnidae		*Isurus*	*oxyrinchus*	Rafinesque, 1810	pelagic-oceanic
		Squaliformes	Dalatiidae		*Isistius*	*brasiliensis*	(Quoy & Gaimard, 1824)	Bathypelagic
Arthropoda	Malacostraca	Decapoda	Aristeidae		*Aristaeomorpha*	*foliacea*	(Risso, 1827)	Benthopelagic
			Benthesicymidae		*Benthesicymus*	*investigatoris*	Alcock & Anderson, 1899	Bathypelagic
			Nematocarcinidae		*Nematocarcinus*	*gracilis*	Bate, 1888	Benthopelagic
			Oplophoridae		*Acanthephyra*	*curtirostris*	Wood-Mason, 1891	Pelagic
					Acanthephyra	*eximia*	Smith, 1884	Pelagic
					Oplophorus	*gracilirostris*	Milne-Edwards, 1881	Bathypelagic
					Oplophorus	*spinosus*	(Brullé, 1839)	Pelagic
					Systellaspis	*debilis*	(Milne-Edwards, 1881)	Pelagic
			Penaeidae		*Funchalia*	*taaningi*	Burkenroad, 1940	Pelagic
					Funchalia	*villosa*	(Bouvier, 1905)	Pelagic
Mollusca	Cephalopoda	Octopoda	Argonautidae		*Argonauta*	*argo*	Linnaeus, 1758	Pelagic
		Teuthida	Onychoteuthidae		*Onychoteuthis*	*banksii*	(Leach, 1817)	Pelagic
			Ommastrephidae	Ommastrephinae	*Sthenoteuthis*	*oualaniensis*	(Lesson, 1830)	Pelagic
			Thysanoteuthidae		*Thysanoteuthis*	*rhombus*	Troschel, 1857	Pelagic

Results and Discussion

Data from more than 1,600 references for fishes and almost 1,100 references for marine vertebrates and invertebrates were used to gather distribution, biological and ecological data for about 3,500 marine species, i.e., 31% Arthropoda (mostly Decapoda), 27% Mollusca, 25% Pisces, 5% Cnidaria (mostly corals), and 5% Chordata (mostly Ascidiacea and Aves). The remainder of the marine species were other groups, especially echinoderms and algae, most of which are found in neritic waters, or at depths of 0-100 m (Table 2; Figures 1A-1B). Of these, 25 species were identified as endemic (48% Pisces, 24% each of Arthropoda and Mollusca), and more than 600 of these are classified as endangered (300 fishes, 21 marine mammals, 49 seabirds, 3 reptiles, and 292 invertebrates; see Figure 1C).

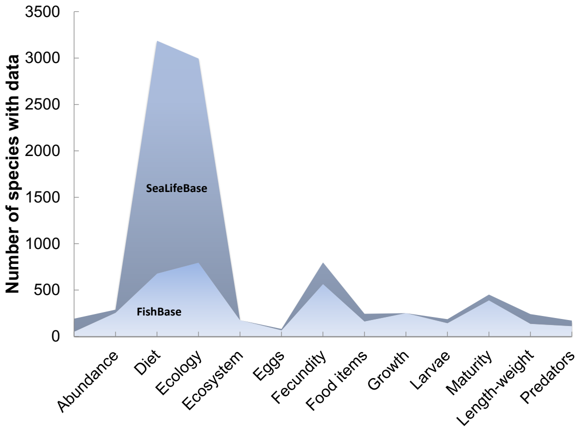

Figure 1A. Data currently in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) for over 3,000 marine species occurring in French Polynesia based on about 2,700 published sources.

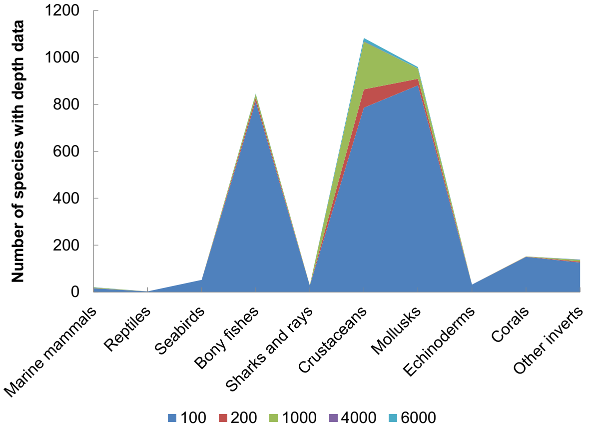

Figure 1B. Number of species by taxa, by depth for over 3,300 species with depth data in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org).

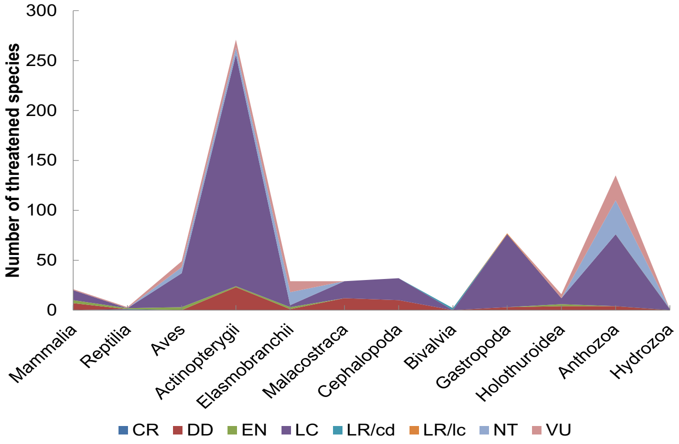

Figure 1C. Threatened species (according to the IUCN version of 2015) occurring in French Polynesia make up more almost 20% of the over 3,400 species gathered for this study in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). Fishes, sharks and rays make up half of this, and the other half is dominated by corals, decapods, cephalopods, gastropods, seabirds and marine mammals.

Table 2. Number of marine species reportedly occurring in French Polynesian waters by higher taxa, by archipelago and geometric mean depth (m) available in FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). There are over 3,000 species reported for French Polynesia, i.e., 31% crustaceans (mostly decapods), 27% mollusks, 25% finfishes, 5% cnidarians (mostly corals), 5% chordates, and the rest being other groups, especially 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 6,000 published sources used to assign species to the five French Polynesian archipelagoes can be obtained from the FishBase and SeaLifeBase online search pages.

Archipelago	**Geometric mean depth (m)**	**Marine mammals**	**Seabirds**	**Seasnakes**	**Bony fishes**	**Sharks and rays**	**Crustaceans**	**Mollusks**	**Echinoderms**	**Corals**	**Other inverts**
Austral Archipelago	100		13		317	13	66	91		8	
	200				2		31	3			1
	1000				1	1	85	20			2
	4000						1				
	6000						6	4			
Subtotal			13		320	14	189	118		8	3
Gambier Archipelago	100		19		254	13	84	69	2	6	
	200						1				
	1000					1	22	8			1
	6000							2			
Subtotal			19		254	14	107	79	2	6	1
Marquesas Archipelago	100	5	11		403	19	195	130	12	2	20
	200	1			3		31	5			1
	1000	1			5	1	76	11		1	
	4000										1
	6000	1			2		3	3			
Subtotal		8	11		413	20	305	149	12	3	22
Society Archipelago	100	5	6	1	645	22	475	170	8	51	54
	200	1			5		18	1			1
	1000	1			12	1	64	9			2
	6000	1			1		2	2			
Subtotal		8	6	1	663	23	559	182	8	51	57
Tuamotu Archipelago	100	5	11	1	481	22	314	155	7	37	20
	200	1			5		25	2			2
	1000	1			6	1	83	10			2
	4000						2				
	6000				1		3	2			
Subtotal		7	11	1	493	23	427	169	7	37	24

A comparison of species numbers obtained for other islands in the region (Pitcairn, Kermadec, and Easter Islands) shows that French Polynesia has a low number of endemic species compared to the Kermadec Islands, which is nearer to the Great Barrier Reef (see Table 3). The Pitcairn Islands have even fewer endemic species, as it is even farther east from the Great Barrier Reef. Our results echo the conclusions made by Meyer and Salvat (2009) and Glynn et al. (2007).

Habitat preference indices were estimated for 78 pelagic species with AquaMaps data (Table 1), made up of 41% bony fishes, 20% dolphins, 13% decapod crustaceans, 12% sharks, 6% whales, 5% mollusks, and 1 species each of sea turtle and sea snake. Resulting HPI values ranged between 0.65-0.97 for fish species and 0.50-0.95 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 southeast corner of French Polynesia, i.e., Gambier and Austral Islands, an area dominated by a large percentage of oceanic habitats as opposed to the considerably larger land masses and many small islands forming the Marquesas and Tuamotu archipelagoes (see Meyer and Salvat 2009), hosting more reef-associated and demersal species. The HPI ranges also suggest that for any one half-degree cell in the archipelago, an average of over 30 pelagic fish species may occur, and within the area of high diversity, i.e., Gambier Islands, that average may go as high as 50 species.

The time series trend of habitat preference indices of exploited species in French Polynesia, obtained from the *Sea Around Us* database of marine catches, indicates a change from dominantly demersal to dominantly pelagic species in the last decade (Figure 3). We calculated habitat preference indices for 33 fish species, 1 invertebrate species and 16 higher taxonomic, i.e., less disaggregated groups (HPI range of 0.20-0.22 for pelagic preference and 0.15-0.26 for demersal preference), exploited in French Polynesia based on catch data extracted from the *Sea Around Us* database (www.seaaroundus.org). The trend in average habitat preference indices weighted by the catch (range of 0.28-0.35; Figure 3, upper panel) shows an increase in the proportion of species preferring pelagic habitats. This is mostly driven by the increase in the proportion of tuna species (notably of albacore, *Thunnus alalunga*, and yellowfin tuna, *T. albacares*), from just over 15% to just about 50% in the last decade (see Figure 3, lower panel), presumably resulting from the fishing subsidies introduced in the 1990s under the programme 'Le Pacte de Progrès' (see Bale et al. 2009 and Walker and Robinson 2009). Note the dramatic decrease in the proportion of the bigeye scad, *Selar crumenopthalmus*, a reef-associated species that dominated the marine catches until the late 1990s.

Table 3. Number of species by taxa and island groups available from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). French Polynesian species counts 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, with French Polynesia as the third, which follows the conclusions of Meyer and Salvat (2009).

	Easter Is		**Pitcairn Is**		**Kermadec Is**		**French Polynesia**		**Baseline comparisons**
	Native	**Endemic**	**Native**	**Endemic**	**Native**	**Endemic**	**Native**	**Endemic**	
Chordata	51		58		63		165		19 [NETBIOME (2014)]
Ascidiacea					3		84		-
Aves	31		35		47		56		16 - Gambier [Waugh et al (2013)]
Mammalia	15		21		9		22		16 [NETBIOME (2014)]
Sea turtles	4		2		3		3		3 [NETBIOME (2014)]
Sea snakes	1				1				
Pisces from FishBase	193	12	346	2	242	6	892	12	800 [Salvat et al (2000)]
Arthropoda	225	4	50	2	277	29	1126	6	800 [Decapods, NETBIOME (2014)], 205 shrimps & 26 Stomatopoda [Poupin (1998)]
Rotifera	19								
Mollusca	221	16	294		452	50	964	6	1160 [NETBIOME (2014)], 1500 [Salvat, et al (2000)]
Echinodermata	28	1	56		91	26	32		30 [Salvat et al (2000)]
Brachiopoda			1		1		9		-
Cnidaria	60	1	89		56	1	182	1	176 [Corals, netbiome (2014)], 170 [Corals, Salvat et al (2000)], 22 [hydroids, Vervoort and Vasseur (1977)].
Bryozoa	2				200	2	1		-
Chaetognatha							4		-
Porifera	19		8		27		17		-
Gastrotricha							1		-
Gnathostomulida							9		-
Sipuncula					5		7		-
Nemertea	1								
Annelida	43				27		5		-
Foraminifera	30		8		10	2	1		-
Algae									425 [NETBIOME (2014)], 346 [Salvat et al (2000)]
Dinophyta							4		-
Ochrophyta	24	3	2		12		4		-
Chlorophyta	31		1		13		17		-
Rhodophyta	61	6			19		12		-
Cyanobacteria	1								-

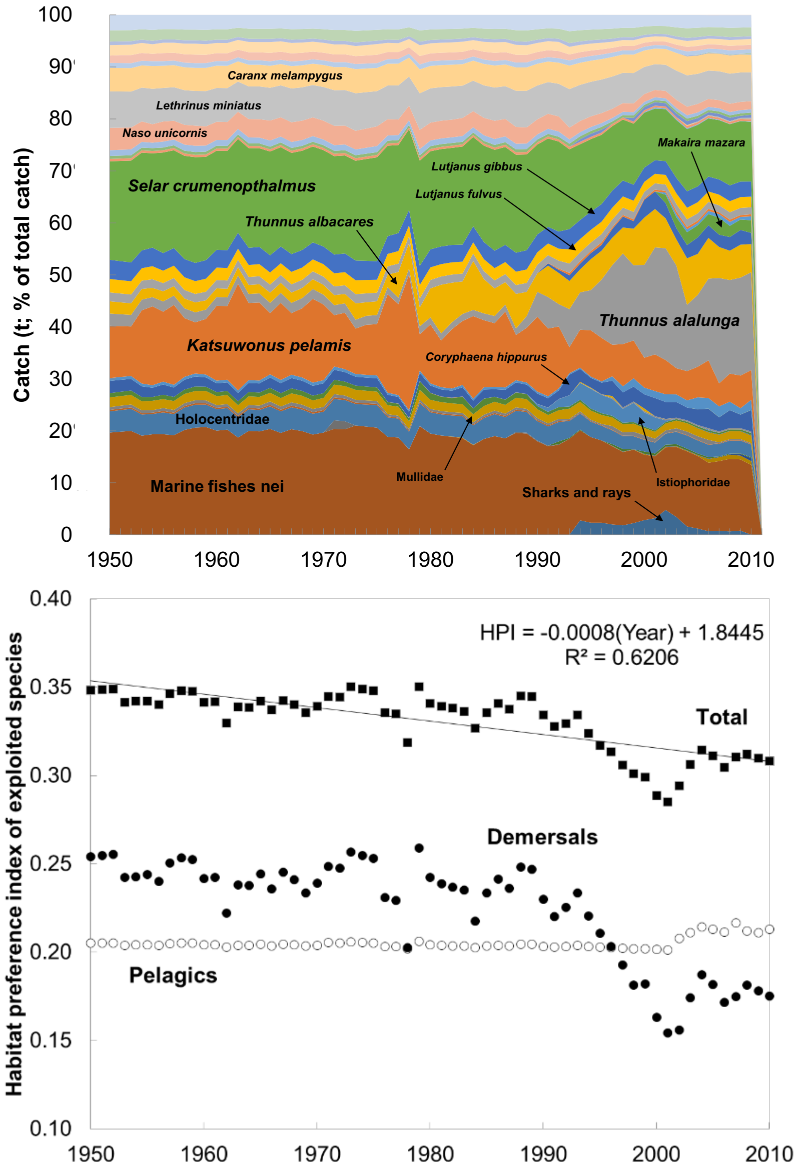

Figure 3. Time series trends of exploited marine species (33 fish species and 16 higher hierarchy taxa) in French Polynesia based on catch data extracted from the *Sea Around Us* database (upper panel; www.seaaroundus.org). The trend in average habitat preference indices weighted by the catch (lower panel) shows an increase in the proportion of species preferring pelagic habitats. This is mostly driven by the increase in the proportion of tuna species (notably of *Thunnus alalunga* and *Thunnus albacares*; lower panel), presumably resulting from the fishing subsidies introduced in the 1990s under the 'Pacte de Progrès' programme (see Bale et al. 2009 and Walker and Robinson 2009).

In conclusion, the maps in Figures 2A and 2B show a clear pattern of high pelagic species diversity in the southeast of French Polynesia, notably in the Gambier Islands. This robust pattern suggest that this area should be a prime candidate for setting up a marine reserve, especially since it is not a prime fishing area for tuna, whose fishing grounds are mainly further north around the Marquesas Islands (see Bale et al. 2009).

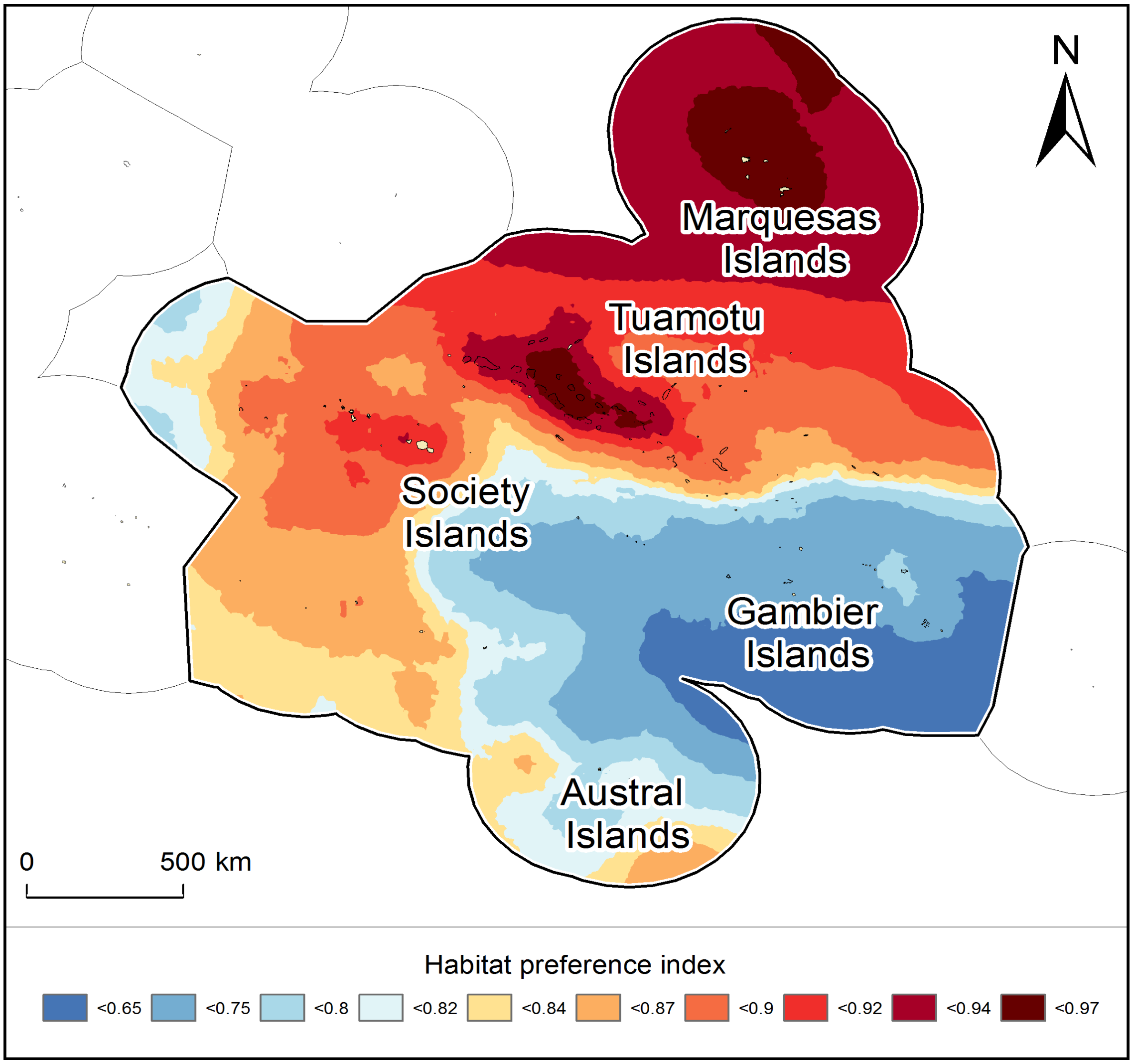

Figure 2A. Distribution of habitat preference index (HPI) of 51 pelagic fish species occurring in French Polynesia (see Table 3). HPI here is analogous to Gini's index of evenness, i.e., a cell with HPI=0 indicates that the cell is preferred by all 51 fish species (blue), while a cell with HPI=1 indicates that it is preferred by only one species. HPI values for the species considered in this study range from 0.65-0.97, which indicate that most of French Polynesian waters will contain more than half of those 51 species. However, most pelagic species are concentrated in southeast French Polynesia, i.e., Society, Gambier, and Austral Islands.

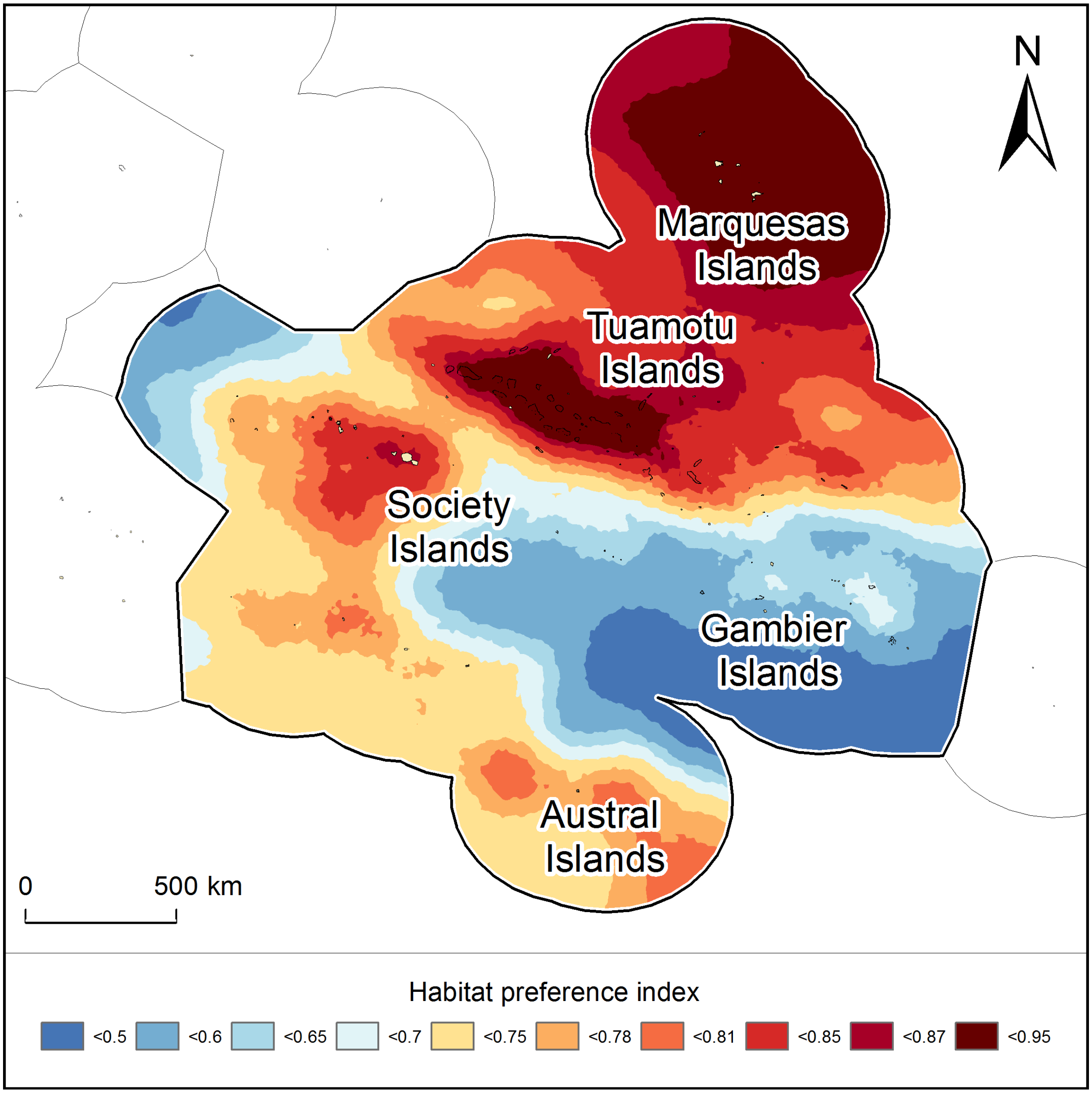

Figure 2B. Distribution of habitat preference index (HPI) of 17 species of whales and dolphins, 10 decapod crustaceans and 4 cephalopod species occurring in French Polynesia (see Table 1), ranging from 0.50-0.95.

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KEY TRAITS OF AMPHIOXUS SPECIES (CEPHALOCHORDATA) AND THE GOLT[1]

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Abstract

Major biological traits of amphioxus species (Cephalochordata) are presented with emphasis on the size reached by their 32 valid species in the genera *Asymmetron* (2 spp.), *Branchiostoma* (25 spp.), and *Epigonichthys* (5 spp.) and on related features, i.e., growth parameters and size at first maturity. Overall, these traits combined with features of their respiration, suggest that the cephalochordates conform to the Gill Oxygen Limitation Theory (GOLT), which relates the growth performance of water-breathing ectotherms to the surface area of their respiratory organ(s).

Introduction

The small fish-like animals know as 'lancelet' or 'amphioxius' belong the subphylum Cephalochordata, which is either a sister group, or related to the ancestor of the vertebrate animals (see Garcia-Fernàndez and Benito-Gutierrez 2008). The cephalochordates consist of 3 families (the Asymmetronidae, Epigonichthyidae and Branchiostomidae), with one genus each*, Asymmetron* (2 spp.), *Branchiostoma* (24 spp.) and *Epigonichthys* (6 spp.), as detailed in Table 1 and SeaLifeBase (www.sealifebase.org). This contribution is to assemble some of the basic biological traits of lancelets (Figure 1), notably the maximum size each of their 34 species can reach, which is easily their most important attribute, though it is often ignored (Haldane 1926).

Finally, reported lengths at first maturity of cephalochordates were related to the corresponding, population-specific maximum length, to test whether these animals mature as predicted by the Gill-Oxygen Limitation Theory (GOLT; see Pauly 2021a, 2021b).

Also assembled here are the few length-weight relationships (LWR) and two proximate analyses, which should allow conversion of lengths into wet and dry weights. For a few species, estimates of the parameters of the von Bertalanffy growth function (VBGF; for both seasonal and non-seasonal growth) are presented that were newly computed, or corrected from publications in which the VBGF was misapplied.

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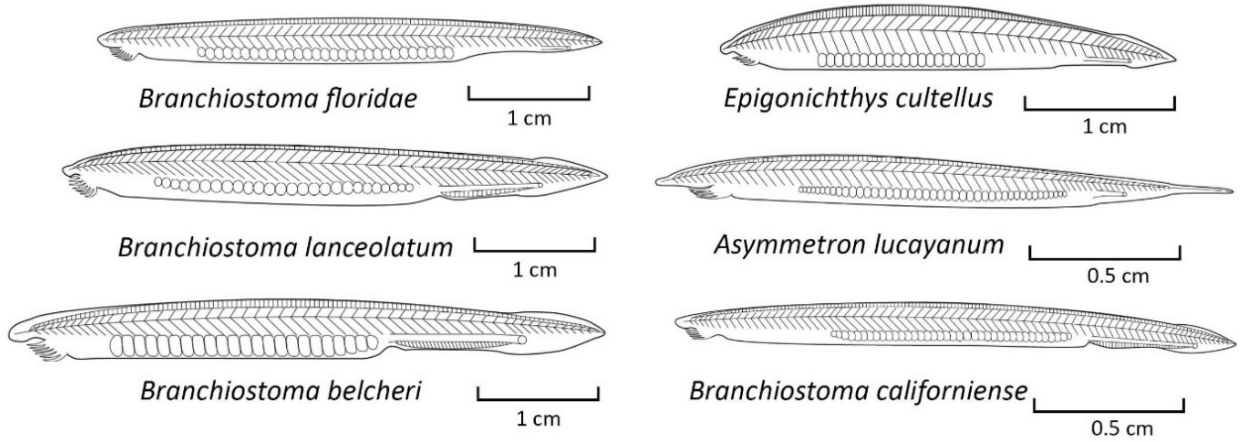

Figure 1. Simplified drawing of 6 species in 3 genera of lancelets. Redrawn by Elaine Chu from a variety of sources. Note uniformity of basic shape.

Material and Method

The species names of cephalochordates in SeaLifeBase were downloaded, and for each, a reported maximal length was identified in the pertinent literature, and input into both Table 1 and into the relevant field of SeaLifeBase. Many of these lengths originated from Hubbs (1922), but some refer to the holotype or a few paratypes, and may thus may underestimate maximum lengths. The literature was scanned for published LWR of cephalochordates of the form $W = a \cdot L^b$, which were converted such that they referred to weight (W) in g, and total length in cm. Note that when b = 3, growth is isometric, i.e., the body remains self-similar as it grows (Froese 2006).

Organic growth (dw/dt) can be defined as resulting from two opposite processes (Pütter 1920; Bertalanffy 1938) i.e.,

$$dw/dt = Hw^d - kw \qquad \text{...1.)}$$

with Hw^d expressing the rate of synthesis of body tissues, and kw expressing the rate at which the proteins and other molecules making up the tissues are denatured, and thus need to be re-synthesized (Pauly 2021a, 2021b). Synthesis requires energy in the form of ATP, the synthesis of which requires oxygen (O_2). The exponent d links the respiratory surface i.e., the O_2 supply of water-breathing ectotherms (WBE) to their body weight (i.e., $O_2 \propto W^d$), and ranges between 0.5 and 0.9 in fishes and other WBE with gills (De Jager and Dekkers1974; Pauly 2021a, 2021b). In cephalochordates, which lack gills, various external and internal body surfaces are used for respiration (Schmitz et al. 2000). Thus, to the extent that that post-metamorphosis cephalochordates maintain their basic shape as they grow (which they do, as attested by their LWR having exponents near 3, see below), their respiratory surface(s) should grow in in proportion to 2/3 of their weight, i.e., $d \sim 0.67$.

Assuming that $d = 2/3$, Equation (1) can be integrated into the VBGF, which, for growth in length, has the form:

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

where L_t is the mean length at age t of the WBE, L_∞ their asymptotic length, (i.e., the mean length attained by the surviving WBE after an infinitely long time), K a growth coefficient (here in year^{-1}) and t_o is a parameter with adjusts for the feature that the VBGF generally fails to properly describe the growth of the earliest (larval and post-larval) stages of WBE. Therefore, t_o, by expressing the age WBE would have at the size of zero if they had always grown as predicted by the VBGF, allows it to correctly represent length-at-age in larval and post-larval stages (Pauly 1998).

Growth in weight can be described by

$$W_t = W_\infty \cdot (1-e^{-K\cdot(t-t_o)})^b \qquad \ldots 2b)$$

where W_∞ is the weight corresponding to L_∞, b is the exponent of an LWR as defined above, and the other parameters are defined as for Equation 2a.

When the growth of WBE is seasonal (and it almost always is, even in the tropics; Pauly and Ingles 1981, Pauly 1998), the VBGF can be modified to account for seasonal growth oscillations, i.e.,

$$L_t = L_\infty\{1-exp-[K(t- t_o)+S(t)-S(t_o)]\} \qquad \ldots 3)$$

where $S(t) = (CK/2\pi)\cdot sin(2\pi(t - t_s))$, $S(t_o) = (CK/2\pi)\cdot sin(2\pi(t_o - t_s)$, and L_∞, K and t_o are defined as above.

Equation (3) involves two parameters more than the VBGF: C and t_s. Of these, the former is easiest to visualize, as it expresses the amplitude of the growth oscillations. When $C = 0$, Equation (3) reverts to Equation (2). When $C = 0.5$, the seasonal growth oscillations are such that growth rate increases by 50% at the peak of the 'growth season' (i.e., in 'summer'), and, briefly, declines by 50% in 'winter'. When $C = 1$, growth increases by 100%, doubling during 'summer', and becoming zero in the depth of 'winter'.

The other new parameter, t_s expresses the time elapsed between $t = 0$ and the start of a sinusoid growth oscillation. However, visualization is facilitated if we define $t_s + 0.5 = WP$ ('Winter Point'), which expresses, as a fraction of the year, the period when growth is slowest. WP is often close to 0.1 (i.e., early February) in the Northern Hemisphere and 0.6 (early August) in the Southern Hemisphere.

The growth performance of animals having the same basic shape can be compared using

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

while the growth performance of animal of different shape can be compared using the parameters of their weight growth curve growth.

Finally, we tested whether cephalochordates reach maturity and spawn at a fraction of their maximum length (L_{max}) that is similar to that of fishes. In fish, mean length at first maturity (L_m, i.e., when 50 % of the individual have become mature) occurs when $L_{max}^D / L_m^D \approx 1.35$, with $D = 3(1\text{-}d)$ (Pauly 1984, 2021a, 2021b; Meyer and Schill 2020). With few exceptions (e.g., figure 3 in Holland 2011), the cephalochordates literature reports only the minimum length at which individual mature (which we shall identify as L_{min}), rather than the length at which 50 % mature (see, e.g., Stokes and Holland 1996). Also, in many cases, articles reporting L_{min} fail to report the corresponding L_{max} value. Nevertheless, a number of L_{min} & L_{max} data pairs could be assembled, and a mean L_{max}^D / L_m^D ratio estimated for cephalochordates. Here, it was hypothesized that this ratio would be slightly above 1.35, given that, by definition, $L_{min} < L_m$.

Results

Table 1 lists the currently recognized species of cephalochordates and the maximus length (in mm) reported for each. Note that some of these values (notably that for *Branchiostoma africae*) are likely to be underestimates, as they were based on holotypes, or the largest of a few paratypes.

Table 1: The 32 species of cephalochordate in SeaLifeBase (www.sealifebase.org) and WoRMS (www.worms.org) and the maximum length (in mm) reported for each; the latter will be underestimates when their sources are the original descriptions, as they will be based on holotypes, or a few paratypes.

No	Scientific name	Author	Max. length[a)]	Source
1	*Branchiostoma africae*	Hubbs, 1927	(20)	Webb (1955)
2	*Branchiostoma arabiae*	Webb, 1957	41	Webb (1957a); Dawson (1964)
3	*Branchiostoma bazarutense*	Gilchrist, 1923	42	Gilchrist, 1923
4	*Branchiostoma belcheri*	Gray, 1847	65	Feng et al. (2008)
5	*Branchiotoma bennetti*	B&G 1966	34	Boschung & Gunter (1966)
6	*Branchiostoma bermudae*	Hubbs, 1922	54	Hubbs (1922)
7	*Branchiostoma californiense*	Andrews, 1893	84	Hubbs (1922)
8	*Branchiostoma capense*	Gilchrist, 1902	69	Hubbs (1922)
9	*Branchiostoma caribaeum*	Sundevall, 1853	51	Hubbs (1922)
10	*Branchiostoma elongatum*	Sundevall, 1852	64	Webb (1957b)
11	*Branchiostoma floridae*	Hubbs, 1922	61	Hubbs (1922)
12	*Branchiostoma gambiense*	Webb, 1958	33	Webb (1958a)
13	*Branchiostoma indicum*	(Willey, 1901)	(27)	Prashad (1934)
14	*Branchiostoma lanceolatum*	(Pallas, 1774)	58	Hubbs (1922)
15	*Branchiostoma leonense*	Webb, 1956	(28)	Webb (1956a; 1956b, 1958a)
16	*Branchiostoma longirostrum*	Boschung, 1983	47	Boschung (1983)
17	*Branchiostoma malayanum*	Webb, 1956	45	Webb (1956c)
18	*Branchiostoma minucauda*	Whitley, 1932	55	Richardson & McKenzie (1994)
19	*Branchiostoma moretonense*	Kelly, 1966	42	Kelly (1966)
20	*Branchiostoma nigeriense*	Webb, 1955	(35)	Webb (1958b)
21	*Branchiostoma platae*	Hubbs, 1922	56	Hubbs (1922)
22	*Branchiostoma senegalense*	Webb, 1955	59	Gosselck and Spittler (1985)
23	*Branchiostoma tattersalli*	Hubbs, 1922	75	Tattersall (1903)
24	*Branchiostoma virginiae*	Hubbs, 1922	53	Hubbs (1922)
25	*Asymmetron inferum*	Nishikawa, 2004	(15)	Nishikawa (2004)
26	*Asymmetron lucayanum*	Andrews, 1893	(28)	Richardson & McKenzie (1994)
27	*Epigonichthys australis*	(Raff, 1912)	(25)	Richardson & McKenzie (1994)
28	*Epigonichthys bassanus*	(Günther, 1884)	44	Richardson & McKenzie (1994)
29	*Epigonichthys cingalensis*	(Kirkaldy, 1895)	30	Kirkaldy (1895)
30	*Epigonichthys cultellus*	Peters, 1877	34	Richardson & McKenzie (1994)
31	*Epigonichthys hectori*	(Benham, 1901)	63	Paulin (1977)
32	*Epigonichthys maldivensis*	(Cooper, 1903)	30	Nishikawa (1980)

a) Lengths in brackets may also refer to annual species (see text)

Table 2 presents LWR for 5 species of *Branchiostoma*, which allow for converting their total length to their wet weight. Also, the table provides the average water content of two species, i.e. 77% in *B. floridae* and 88% in *B. senegalense*.

Table 2 Length-weight relationships of 4 *Branchiostoma* species

Species	**Location**	**a**	**b**	**N**	**Source**
B. belcheri	Hong Kong	0.003	2.853	30	Chen et al. (2008)
B. belcheri	Naozhou Isl. China	0.0014	3.290	530	Feng et al. 2008
B. californiense	B.C. Mexico	0.00522	3.01	60	Campos-Dávila et al. (2019)
B. floridae	Tampa Bay, Fla.	0.00236	2.895	44	Stokes (1996)$^{a)}$
B. malayanum	Hong Kong	0.003	2.922	30	Chen et al. (2008)
B. senegalense	N.W. Africa	0.0069	2.71	--	Gosselck & Spittler (1979)$^{b)}$
a) Mean water content = 77%; b) mean water content 88%					

Table 3 provides 6 estimates of growth parameters for 4 species; 2 sets of growth parameters account for seasonal growth oscillations (see also Figure 2). All pertain to the VBGF and are either new estimates, or correct for inconsistencies in their original presentations.

Table 3. Growth parameters of *Branchiostoma* species ; L_∞ = cm; K = year^{-1}; Ø'= log(K) +2·log(L_∞)

Species	**Location**	L_∞	K	**Ø'**	**Remark / Source**
B. belcheri	Xiamen, China	7.2	0.44	1.36	See Figure 3
B. elongatum	Chile	6.5	0.45	1.28	Vergara et al. (2012)$^{a)}$
B. senegalense	N.W. Africa	6.4	0.47	1.28	Gosselck and Spittler (1979)
B. lanceolatum	Helgoland, Germany	6.3	0.50	1.30	from Sager & Gosselck. (1985)
B. belcheri	Hong Kong	4.5	0.89	1.26	Recomputed from Chen et al. (2008)$^{a)}$
B. malayanum	Hong Kong	3.6	1.72	1.35	
a) The parameters were recomputed because the authors used a variant of the VBGF, which later misled Vergara et al. (2012) into performing inappropriate comparisons.					

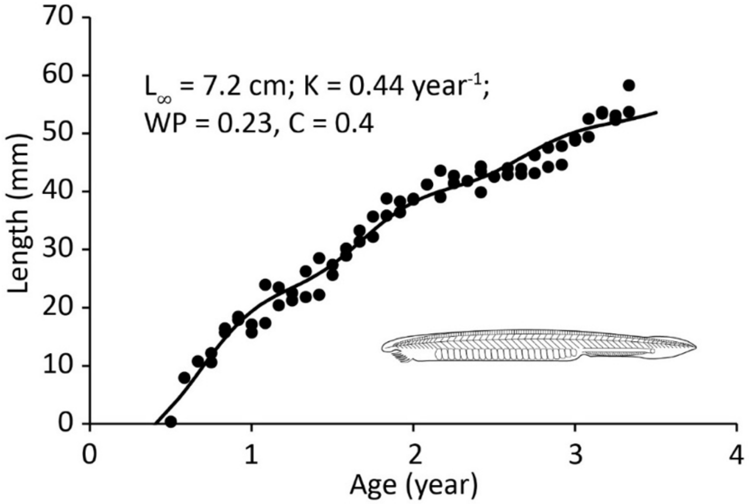

Figure 2. Seasonally oscillating growth of *Branchiostoma belcheri* in the harbor of Xiamen, China (based on length-frequency data in Chin 1941 [figure 14] fitted with Equation 3).

The oxygen consumption of *Branchiostoma lanceolatum* was studied by Schmitz et al. (2000), and some of their results are presented in Figure 3.

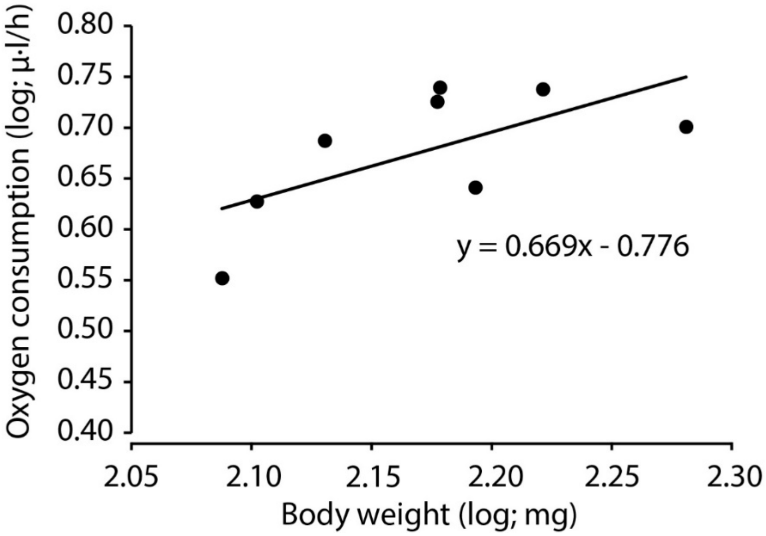

Figure 3. Oxygen consumption as a function of body weight in *Branchiostoma lanceolatum* at 11 °C ($r^2 = 0.46$, $p < 0.05$; redrawn and recomputed from Schmitz et al. 2000). Note that the slope of this relationship is about 2/3.

Table 4 presents 9 L_{min} & L_{max} data pairs in 5 species and 2 genera of cephalochordates. The *b*-values, in the LWR of Table 2 are reasonably close to 3; thus, with $d \sim 0.67$ (see text above and Figure 3) and $D = 3 \cdot (1-d)$, D can be assumed equal to unity, and the mean L_{max}^D / L_{min}^D ratio can be estimated from the mean L_{max} / L_{min} ratio (Figure 4). This ratio was found to be 2.07, with a 95% confidence interval of ±0.105. As hypothesized, this is higher than the estimate of 1.36 ± 0.15 for fishes.

Table 4. Length at first maturity (**L_m**) and maximum length (**L_{max}**) in lancelet (mm)

Species	Location	L_m	L_{max}	Source
Asymmetron lucayanum	Bimini, Bahamas	10	25	Holland (2011)
Branchiostoma belcheri	Amakusa, Japan	25.5	54	Nagakawa (1897)
Branchiostoma belcheri	Xiamen, China	29	57	Chin (1941)
Branchiostoma belcheri ♀	Hong Kong	25	51	Chen et al. (2008)
Branchiostoma belcheri ♂	Hong Kong	23	49	Chen et al. (2008)
Branchiostoma floridae	Tampa Bay, Fla.	23	50	Stokes & Holland (1996)
Branchiostoma lanceolatum	Naples, Italy	15.5	28	Langerhans (1876)
Branchiostoma malayanum ♀	Hong Kong	18	35	Chen et al. (2008)
Branchiostoma malayanum ♂	Hong Kong	15	34	Chen et al. (2008)

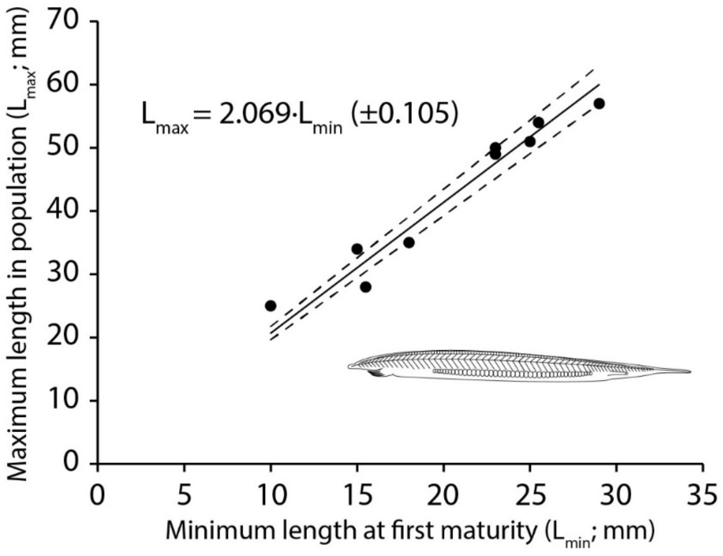

Figure 4. Estimating the mean L_{max}^D vs. L_m^D ratio and its 95 % confidence interval in 5 species of lancelets, based on the data in Table 4. The insert shows *Asymmetron lucayanum*.

Discussion

The lancelets or amphioxus, i.e., the cephalochordates, have intrigued biologists since Darwin established the descent of vertebrates – including us – from "lower" fish-like animals that may have resembled lancelets. Ernst Haeckel and other German evolutionists celebrated those animals in an almost cult-like fashion, believing them to be, the ancestors which would yield the mysteries of our existence (Hopwood 2015). Similar enthusiasm for amphioxus studies emerged a few decades later in China, which connected studies on the vertebrates' ancestry with the renewal of Chinese science (Luk 2020). Also note that China was the only country from which a targeted amphioxus fishery was reported (Light 1923; Chin 1941).

Nowadays, genomic studies of cephalochordates appear to have established that their ancestors were not direct ancestors of vertebrates, but shared with our putative ancestors several important genes and traits, notably gill slits. However, there are no gills behind their slits – lancelets respire through their integument (Schmitz et al. 2000) and use their gill slits only for feeding.

The lack of specialized gills implies that lancelets have a lower oxygen supply than fish of similar size, which, given the GOLT, implies that they should grow more slowly than fish of similar size (Pauly 2021a, 2021b). Here, we created a profile of lancelets that differed from most extant accounts to test this inference because they are discussed primarily in the context of taxonomy (Hubbs 1922) and evolution.

This account emphasizes the (maximum) adult size, assembled for nearly all species (Table 1), and their length-weight relationship (Table 2), and growth parameters (Table 3), which allowed comparing their growth with that of fish and chaetognaths (Table 4), the latter being another gill-less group. This led to the conclusion that growth of lancelets, as predicted by the GOLT, is less rapid than that of fishes.

Table 5. Comparison between the growth performance of 3 species of fish and a species of cephalochordates (Ø = logK+ 2/3logW∞).

Species[a]	**W_∞ (g)**	**K (year^{-1})**	**Ø**
Thunnus albacares	198,940	0.250	2.93
Mugil cephalus	13,890	0.110	1.80
Cottus bubalis	102	0.230	0.70
B. senegalense	~1	0.480	-0.32

a) The 3 species of fish are documented in Pauly (1981). *B. senegalense* is taken as representative of cephalochordates in general (see Table 5).

The GOLT's prediction, that length at first maturity of lancelets is reached at the same fraction of their maximum length could not be tested; researchers specialized in cephalochordates tend not to define length at first maturity as other biologists do. However, the results obtained with a substitute measure had the expected bias, given its definition. This still allows for the L_{max}/L_m ratio of cephalochordates to be similar to that of fishes.

Overall, the asymptotic growth and other features of lancelets suggest that their biology is compatible with the predictions of the GOLT.

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PRE-SUBMISSION DRAFT OF 'THE GOLT AND ITS CRITICS'[2]

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Abstract

This contribution consists of the pre-submission version of a now-published article by the author, titled "The Gill-Oxygen Limitation Theory (GOLT) and its critics" (*Science Advances*, 2021:7: eabc6050), of two anonymous reviewers' comments, and the author's responses to these comments. The format of the citations -- 'author(s), date' -- was maintained, such as to allow the reader to quickly evaluate the references that were used. Also maintained were photos, which a reviewer wanted deleted, of pond aeration devices in Chinese fish farms. Overall, a comparison of the formally published version with that presented here allows one more case study of how peer-review improves submissions, or not.

Table of Contents

ABSTRACT

The Gill-Oxygen Limitation Theory (GOLT) is presented to provide mechanisms for key aspects of the biology (food conversion efficiency, growth and its response to temperature, the timing of maturation, migrations, and others) in water-breathing ectotherms (WBE, i.e., fish and aquatic invertebrates). The

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[2] Cite as: Pauly, D. 2021. Pre-submission draft of 'The GOLT and its critics', p. 67-115. In: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III.* Fisheries Centre Research Reports 29(1).

GOLT's basic tenet is that the surface area of the gills or other respiratory surfaces of WBE cannot, as 2-dimensional structures, supply fish with sufficient oxygen to keep up with the growth of their 3-dimensional bodies. Notably, the reduced oxygen supply per body weight induces sexual maturation, and later a slowing and cessation of growth, all accompanied by an increase of physiological processes relying on glycolytic enzymes and a declining role of oxidative enzymes. Because the 'dimensional tension' underlying this argument is widely misunderstood, emphasis is given to a detailed, point-by-point presentation of the published objections to the GOLT and their refutation. Aside from having a wide theoretical scope, the GOLT has potential practical applications, e.g., in optimizing the way fish farmers aerate their ponds and in predicting how WBE populations will react to the warming and deoxygenation of the waters they inhabit[3]. The GOLT still needs to be refined and put on a solid quantitative basis, but this can only occur after the misconceptions surrounding it are put to rest.

LIST OF FIGURES AND TABLES[4]

LIST OF ACRONYMS AND SYMBOLS[5]

°C: degree Celsius (or centigrade); a measure of temperature;
A: ratio of gill surface area (or metabolic rate) at W_∞ over the gill surface area (or metabolic rate) at W_∞;
ATP: Adenosine triphosphate, the major supplier of 'energy' in living bodies;
b: exponent of a length-weight relationship (LWR) of the form $W = a \cdot L^b$; $b \approx 3$ is very common;
C.I.: confidence interval (here: 95%);
D: a convenience parameter, i.e., $D = b \cdot (1-d)$;
d: exponent of the relationship linking the rate of anabolism (H) and body weight (W);
d_G: exponent of the relationship linking the gill surface area of WBE and their body weight (W); d_G causes d_{O_2} and d;
d_{O_2}: exponent of the relationship linking the oxygen supply to the body ('metabolic rate') to its weight (W); d_{O_2} is caused by d_G and causes d;
dP: difference between the oxygen partial pressure on either side of a membrane;
dw/dt: rate of growth in weight;

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[3] This highlighted section was removed from the published version to shorten its abstract.
[4] Not included in submitted and published versions.
[5] Not included in the submitted version.

G: gill surface area; respiratory surface area in WBE lacking gills;
g: gram, a measure of weight;
GOLT: Gill-Oxygen Limitation Theory;
H: coefficient of anabolism (as defined by the GOLT);
k: coefficient of catabolism (as defined by the GOLT);
K: growth coefficient (of dimension time^{-1}) of the VBGF, expressing how fast the asymptotic length or weight is approached; note that $K = k/3$;
K_1: food conversion efficiency, i.e., individual growth during a time interval/food consumed during that interval;
L_∞: asymptotic length, or mean length attained after an infinitely long time by a WBE of a given population whose growth is described by the VBGF;
L_m/L_∞: 'reproductive load';
L_m: mean length at first maturity;
L_{max}: the maximum observed length of a fish or other WBE in a given population;
L_t: mean length at age t (e.g., as predicted by the VBGF);
LWR: length-weight relationship of the form $W = a \cdot L^b$;
O_2: Oxygen;
OCLTT: O_2 and capacity limitation of thermal tolerance; a hypothesis developed by the physiologist H.-O. Pörtner, and which shares some features with the GOLT.
Q: oxygen uptake by (or oxygen *supply* to) a WBE; this conceptually different from its *demand* (see text);
t: time, or age of a WBE;
t_0: the (mostly negative) age WBE would have had at $L = 0$ or $W = 0$ if they had always grown according to the VBGF;
U: Krogh's diffusion constant (see Equation 2);
VBGF: von Bertalanffy Growth Function;
W: weight, here taken as equivalent to mass;
W_∞: asymptotic weight, or mean weight attained after an infinitely long time by a WBE whose growth is describe by the VBGF;
WBD: Water-Blood Distance, i.e., the thickness of the tissue between the outside water and the blood;
WBE: Water-breathing Ectotherm, of water-breathing fish and invertebrates;
W_i: weight at the inflexion point, i.e., where the growth rate (dw/dt) is highest;
W_m: mean weight at first maturity;
W_t: mean weight at age t (e.g., as predicted by the VBGF).

INTRODUCTION

The need for a theory

While there is clear evidence that the generation of scientific data has been increasing exponentially since 1600, and that the rate of growth accelerated after WWII (Bornmann and Mutz 2015), it is not as clear that our knowledge about the natural world has also increased this fast. This may be because[6] to make sense of scientific data and their patterns, robust theories are required which can either provide an interpretative context for new findings or which cannot, in which case the new findings are either problematic or very interesting (Popper 2005).

However, a situation can emerge in which the practitioners of a given scientific discipline have forgotten how, "*odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service*! (Darwin 1861). They not only publish articles that test nothing, but in the process appear to have become utterly theory-adverse and argue that the organisms or processes they study are so unique that only their *ad hoc* hypotheses can explain the data they generate.

This attitude is very problematic at a time when we, as a scientific community, are challenged to devise novel ways to protect marine and freshwater biodiversity threatened by overfishing, pollution, habitat modification (Boonstra et al. 2015; Reid et al. 2019), by global changes with its attendant ills, ocean, and freshwater warming (Pinsky 2013; Cheung et al. 2013a, 2013b; Liang et al. 2018; Schindler 1997), acidification, and deoxygenation (Bednaršek et al. 2016; Breitburg et al. 2018; Prince and Goodyear 2006).

This is why the Gill-Oxygen Limitation Theory (GOLT) is being introduced, and why the case is made for the GOLT to be seriously examined. Despite it being counterintuitive to the air-breathing mammals that we are, the GOLT is coherent in its content and the range of the phenomena that it claims to explain. A critical examination should replace dismissals based on untenable arguments, which have created the strange situation wherein the GOLT has become controversial, e.g., in internal deliberations of the Intergovernmental Panel for Climate Change (W.W.L. Cheung, IOF/UBC, pers. comm.)[7] even before it has become widely known.

To counter the tendency to knock down[8] proposed hypotheses (rather than *test* them), in this paper, after a brief presentation of the key tenets of the GOLT, a detailed presentation of the objections to the theory will be provided. Many of these objections do not pass simple tests of scholarship (e.g., they cite things that were not stated), strong evidence, or logic. Thus, the intention of the paper is primarily to clear the field of frivolous arguments, such that a serious debate can begin.

This contribution is also an attempt to change the minds of aquatic biologists about notions most think are obvious but which are incompatible with the fact that, for water-breathing ectotherms (WBE, i.e., most fish and aquatic invertebrates), life is shaped more by the distribution and concentration of dissolved oxygen and the temperature of the water surrounding them than by the availability of food, which is more important for endotherms (birds and mammals). The tendency to project our mammalian

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[6] This highlighted section was removed from the published version (Pauly, D. 2021. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7: eabc605) at the request of a reviewer (see the last section of this piece, i.e., RESPONSE TO REVIEWERS. In the following pages, highlighting refers mainly to formulations that were softened.

[7] Deleted from *Science Advances* version, as this journal does not allow for personal communications.

[8] Softened to 'discredit.'

biases onto WBE has resulted in a misunderstanding of many features and life histories of fish and marine invertebrates.

These are strong claims, especially since the framework of an alternative vision of the lives of WBE, i.e., the GOLT (Pauly 1981, 2010) has, to date, not found many adherents. Recent extensive (Pauly 2019c) and shorter elaborations (Pauly and Cheung 2017a; Pauly 2019a) of the GOLT exist. Each explains parsimoniously a number of biological features, behaviors and experimental results on WBE that mostly have no other (simple) explanations (Table 1).

The Gill-Oxygen Limitation Theory (GOLT) presents a unifying theory-- based solely upon first principles and their corollaries-- that explains growth and related phenomena in both marine and freshwater fishes and aquatic invertebrates. It should replace several *ad hoc* hypotheses common in ichthyology, limnology and marine biology

How the GOLT defines growth

The GOLT builds on concepts developed by von Bertalanffy (1934, 1938, 1949, 1951, 1960, 1964), who built on earlier work by Pütter (1920), and whose main feature is that organic growth (dw/dt) can be seen as the difference between two processes, i.e.,

$$dw/dt = Hw^d - kw \qquad \ldots 1)$$

where the two terms on the right are usually called anabolism and catabolism, respectively, and where $d < 1$. That is, an increase of body mass (dw/dt) is the difference between body mass that is newly (Hw^d) synthesized and the body mass (kw) that becomes unusable. As simple as Equation (1) seems to be, considerable confusion exists regarding the definition of the two terms on the right.

In the GOLT, anabolism refers to the synthesis of body tissues (including gonad material); the process requires an amino acid pool to provide building blocks for proteins and ATP to provide the 'energy' required for synthesis. Here, ingested food is not 'energy'; rather, food is oxidized (i.e., 'burnt') to generate ATP, which may be considered to be 'energy' (Cox and Nelson 2008).

Thus, the process of anabolism requires oxygen, which must enter the body through some permeable surface. Therefore, in fish, the parameter d in Equation (1) is equivalent to the exponent (d_G) of a relationship linking gill surface area (G) to body weight of the form $G = a \cdot W^{d_G}$, and which determines how much anabolism can occur. For this reason, the oxygen consumption of fish scales with body weight with a factor (d_{O_2}) should be and is near d_G (De Jager and Dekker 1975). As we shall see below, d_G – and hence d_{O_2} as well – drops below 1 once fish have grown past a certain body mass (and past metamorphosis in teleosts).

In contrast, catabolism, as defined in the GOLT, is directly proportional to body weight because it consists of the spontaneous denaturation of the proteins and other molecules contributing to that weight. Protein molecules can fulfill their function (e.g., as enzymes) only if they maintain their native quaternary structure. In the long term, they cannot maintain that structure because, notably, they are constantly subjected to Brownian motion (Brandts 1967; Goldberg and St. John 1976; Hawkins 1991). Thus, all such molecules have half-lives, which become shorter when temperature increases (Somero 1995). Spontaneous loss of quaternary structure by molecules occurs throughout the body and requires no 'energy' (beyond the kinetic energy of Brownian motion). Thus, catabolism as defined in the GOLT requires no oxygen either. It is therefore weight-proportional even if the process of denaturation proceeds at different rates in different molecule types because the ratios between molecule types would not change much in the course of ontogeny (at least past the larval stage).

Integrating the differential equation in (1) is straightforward, and when d in that equation is set equal to 2/3, this yields the von Bertalanffy Growth Function (VBGF), which for length has the form:

$$L_t = L_\infty\left(1 - e^{-K(t-t0)}\right) \qquad \ldots 2)$$

where L_t is the mean length (however measured) at age t of the WBE in question, L_∞ their asymptotic length, i.e., the mean length they would attain after an infinitely long time, K a growth coefficient (of dimension time^{-1}) and t_o is the (usually negative) age they would have had at a length of zero if they had always grown in the manner predicted by the equation (which they usually have not; see e.g., Pauly 1998). Combining this equation with a length-weight relationship (LWR) of the form $W = a \cdot L^b$ leads to a version of the VBGF that can express growth in weight, i.e.

$$W_t = W_\infty(1-e^{-K(t-t_o)})^b \qquad \ldots 3)$$

where W_∞ is the mean weight attained after an infinitely long time, and all other parameters are as defined previously.

When $d \neq 2/3$ but is still <1, the integration of Equation (1) yields what may be called the generalized VBGF; for length, this is

$$L_t = L_\infty(1-e^{-KD(t-t_o)})^{1/D} \qquad 4)$$

where $D = 3(1-d)$. Note that here, the exponent of the LWR is equal to 3, as is (nearly) the case in the overwhelming majority of fish (Froese 2006; see also www.fishbase.org) and invertebrate species (see www.sealifebase.org).

For weight, the generalized VBGF is

$$W_t = W_\infty(1-e^{-KD(t-t_o)})^{b/D} \qquad 5)$$

where $D = b(1-d)$, which makes Equation (5) more versatile than Equation (3).

When $d = 0.75$ (and thus $D = 0.75$), Equation (4) is equivalent to the "general model" of West *et al.* (1997) which, however, is not general because the value of d does vary between taxa (Pauly 1981, 2019). Note that whether one uses the standard VBGF or its generalized versions (including versions which account for ubiquitous seasonal growth oscillations; Pauly 2019c), a reasonably good fit to length/age data pairs is obtained, including estimates of asymptotic lengths (L_∞) that are close to observed maximum lengths (L_{max}). Important exceptions are tuna and other large WBE with relatively high values of d (i.e., $0.90 \leq d \leq 0.95$, and hence $0.3 \geq D \geq 0.15$). In such cases, the estimates of L_∞ that are obtained are much higher than L_{max} (Figure 1).

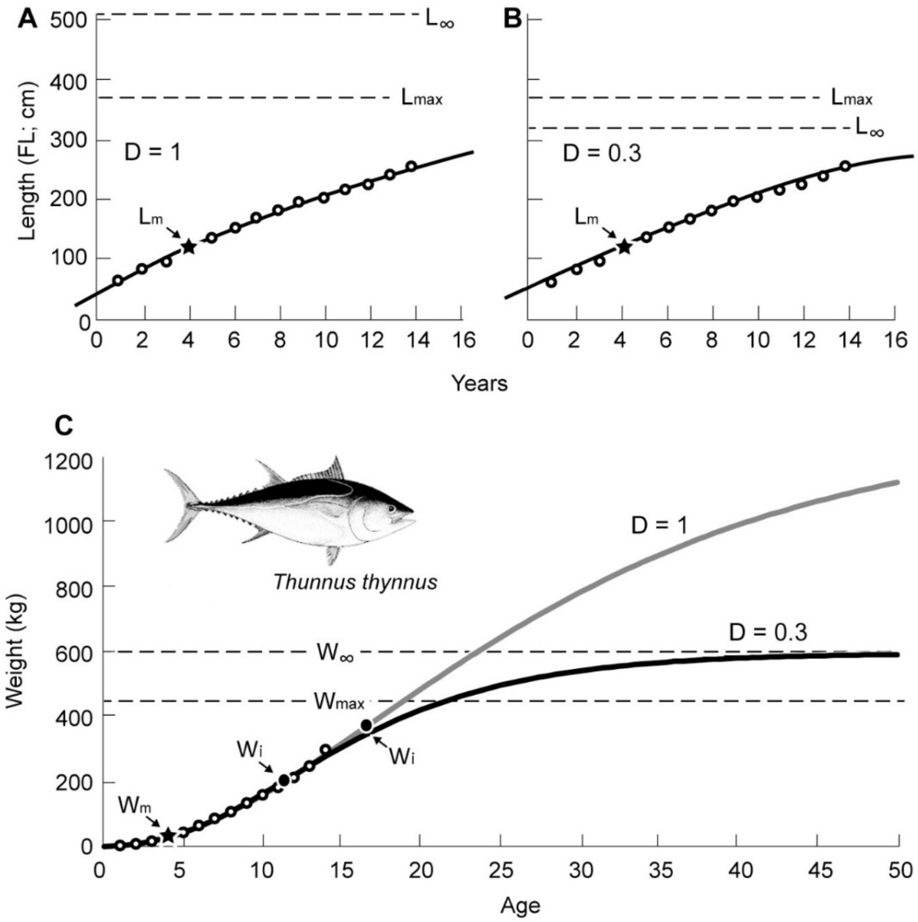

Figure 1 Different forms of the von Bertalanffy growth function. The VBGF fitted to bluefin tuna (*Thunnus thynnus*) length-age data pairs of Sella (1929). **A:** The standard VBGF (Equation 2), which assumes $d = 2/3$, and hence $D = 1$ (which thus can be omitted). **B:** The same length-at-age data, fitted by Equation 4, with $b = 3$ and $D = 0.3$, corresponding to d = 0.9 (Muir and Hughes 1969). **C**: Two versions of the generalized VBGF for weight (Equation 5), with D=1 and D = 0.3, with weights converted from lengths using $W= 0.0182 \cdot L^3$ (from FishBase), where W is in g, and (fork) length is in cm. Note the position of L_m (from Corriero *et al.* 2005) relative to L_{max} and L_∞ and W_m relative to W_{max} and W_∞, and that the weights at inflection points of the growth curves (*Wi*) are much higher than W_m, i.e., that bluefin tuna growth is still accelerating when they reach maturity.

The scope of the GOLT

If one can agree with the above definitions and constraints, the various predictions of the GOLT (Table 1) follow logically, while being empirically verified. Indeed, most natural scientists other than some fish physiologists, once informed of the points above, tend to accept the elements of Table 1 as straightforward corollaries. This is important given two massive challenges related to the respiration of WBE in an age of global warming, i.e., the accelerating deoxygenation of the oceans and freshwater bodies and the increasing role of aquaculture in supplying global seafood markets.

Studying the effect of temperature increases and deoxygenation requires a robust theory of why WBE, particularly old/large (and hugely fecund) individuals, are as sensitive as they are to such changes (see, e.g., Johansen et al. 2014; Messmer et al. 2017; Rodnick et al. 2004). Similarly, for the insights of physiologists to be able to assist in increasing aquaculture production, the theory that guides them has to be compatible with the fact that the aquaculture industry spends large sums to aerate the ponds in which WBE are raised (Figure 2).

Table 1. Some physiological and related differences between young/small and older/larger WBE of the same species, with item number (1) being the cause of all others. 'Relative' stands for 'per unit weight'.

No.	Young/small WBE	Older/larger WBE	Source(s)
1	Relative gill surface area is high.	Relative gill surface area is low.	See text
2	Thus, relative O_2 supply is high.	Thus, relative O_2 supply is low.	See text
3	Growth in weight is accelerating	Growth in weight is decelerating	See Figure 1C and 3B
4	High temperatures and thus shallower habitats are preferred.	Low temperatures and thus deeper habitats are preferred.	Heincke (1913); Messmer et al. (2017).
	In *C. macularius*, a temperature of 30 °C is "*optimal only up to an age of 22-28 weeks*".	In older *Cyprinodon macularius*, "*the temperature optimum shifts gradually to 22-26 °C*".	Kinne (1960); see text for other species.
5	Relative food consumption is high.	Relative food consumption is low.	Palomares and Pauly (1998)
6	Food conversion efficiency is high.	Food conversion efficiency is low, trending toward zero.	Gerking (1952, 1975); Pauly (1986)
7	Young adult fish may skip spawning, but spawn during the next season.	Adults do not skip spawning; large adults may spawn repeatedly in a spawning season.	Morbey and Shuter (2013) ; Rideout et al. (2005); Jørgensen et al. (2006); Pauly (2019c)
8	Enzymes in tissues are mainly oxidative.	Enzymes in tissues are mainly glycolytic.	Davies and Moyes (2007); also see text.
9	Fish otoliths contain proteinaceous substances.	The external layers of fish otoliths are purely crystalline.	Morales-Nin (1986a, 1986b)
10	Clear daily 'rings' are formed in otoliths of fish and statoliths of invertebrates.	Daily 'rings' in otoliths or statoliths are blurred, later disappear altogether.	Pannella (1971, 1974); Ralston (1985); Pauly (2019c)
11	Extensive seasonal migrations are not undertaken.	Extensive, often temperature-driven seasonal migrations are undertaken	Pauly and Keskin (2017);
12	Fat content is low	In fish, fat content is high, particularly when seasonal temperature oscillations are high.	Shul'man (1974), Pauly (2019c, p. 79-81)

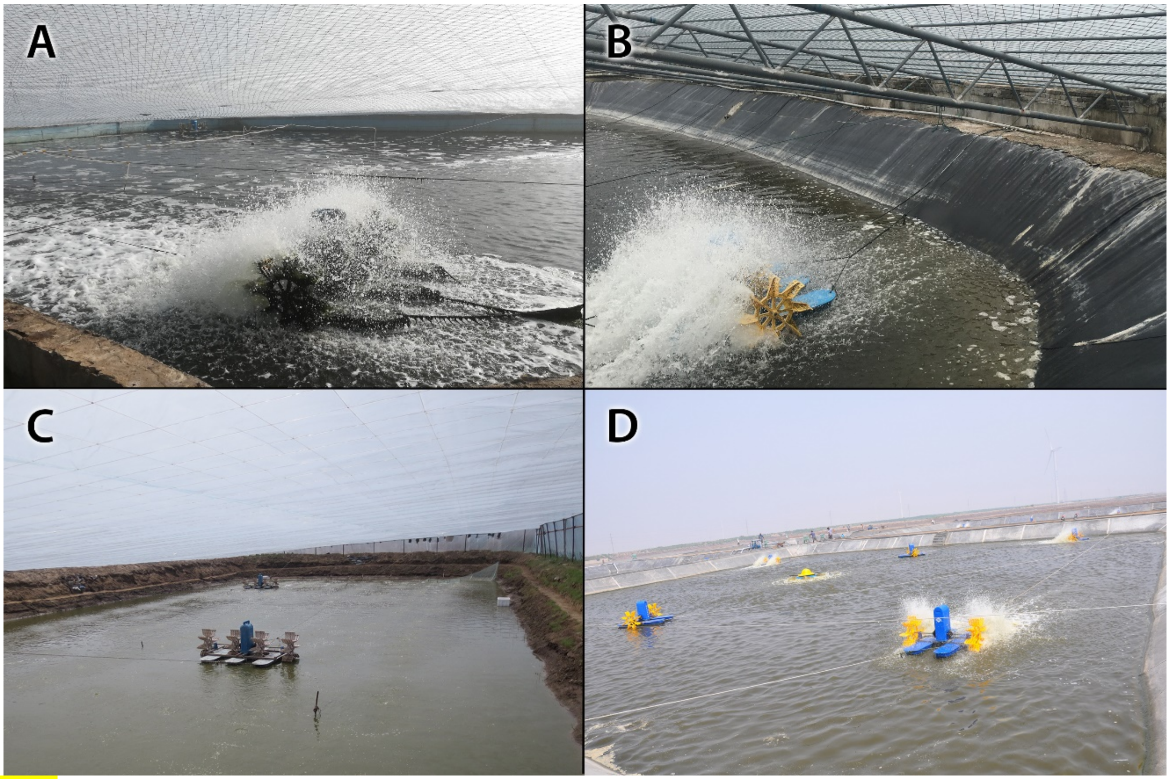

Figure 2[9]**. Aerating systems add oxygen to the water of fish farming ponds**. Such systems are common wherever intensive aquaculture is practiced. **A-C**: Photos by Mr. You Zhou, Ningbo University, 2019; near Ningbo, China (by permission); **D:** Photo by Ms. Liping Zhang, Lijin Ocean and Fishery Bureau, July 2019; near Dongying, China (by permission).

COUNTERARGUMENTS TO THE GOLT

The terms of the debate

So, what are the objections? They are presented here in a series of tables briefly stating the objections and their sources and providing a brief refutation, along with a reference to one or several articles presenting the evidence cited as refutation.

Each table addresses a different class of arguments, i.e.:

I. The gill surface area of WBE either does (or could) grow as required to keep up with a growing volume, i.e., with body weight;
II. Some WBE contradict key tenets of the GOLT (d_G >1, or large size in tropical waters);
III. What is the cause of the decline in metabolic rates, and what is the effect?
IV. Different definitions of 'anabolism' and 'catabolism'; and
V. Miscellaneous discipline-related and/or philosophical objections.

Gill lamellae *versus* book pages

The first group of objections (Table 2) is also the most important. In fact, if any of these objections were tenable, then the GOLT would be eviscerated. These objections refer to gills functioning as a surface, and thus being limited by the geometric constraint that they cannot keep up with the 3-dimensional growth of the bodies that they supply with oxygen.

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[9] This figure was deemed "gratuitous" by a reviewer, and was replaced by two references on the need for fish pond aeration.

Some authors believe that this is a simple problem, i.e., that if their gill surface area is too small, WBE can simply enlarge it, i.e., grow bigger gills. However, these authors do not perceive the underlying geometric problem. So far, only Lefevre et al. (2017) have tackled this problem head- on, based on two arguments, and stated that:

1. The surface area of gills is similar to the surface area of the pages of a book, which can increase in proportion to its volume. Thus, gill surface area can always keep up with body weight; and
2. The oxygen requirement of fish declines as they grow older/larger, and thus, these fish do not need to maintain the gill surface area/body weight ratio occurring in young/small fish.

The *raison d'être* of books is to be read, i.e., opened. The transfer of knowledge from their pages through the readers' eyes to the brain is analogous to the transfer of oxygen from the water flowing past the gills to the blood of a WBE. In a 3-dimensional context, only one layer of paper can be read at a time. Similarly, despite appearances to the contrary, in fish, only one 'layer' of gill lamellae stands in the path of a flow of water across gills (Figure 3).

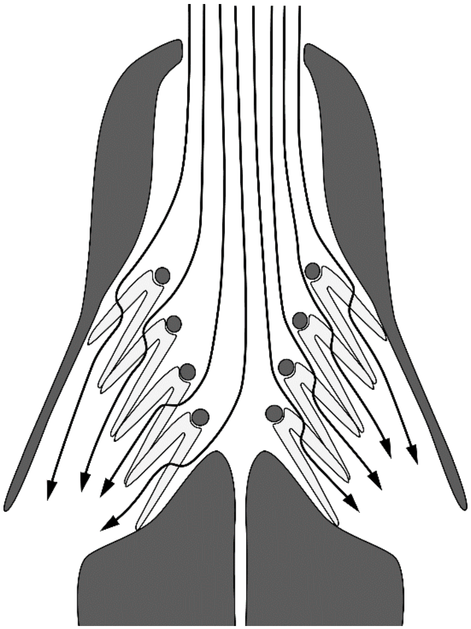

Figure 3. **Schematic representation of water flows across the gills of a fish**. Note that once water has flown between lamellae (which extracted most of O_2 it contained), there is no point for this water to flow through another set of lamellae. Hence gills function as a surface, even though their arrangement in 3-D space may suggest otherwise.

Given the efficiency of gills at extracting oxygen from flowing water, there would be little to be gained by putting subsequent layers (i.e., 'pages') of lamellae behind the first one. Hence, gill surface area, as complex as it may appear, functions like a sieve, perpendicular to the water flowing through the gill chamber. This implies that in a WBE, gill surface area cannot grow in 3 dimensions and thus cannot keep up with the 3-dimensional body that it supplies with oxygen.

The entire argument of Lefevre et al. (2017), who claim that the GOLT assumes gills to behave like spheres, is strange. It becomes even stranger when one notes that their argument that WBEs are able to maintain the same gill surface area/body weight ratios as their weight increases is backed up with only two astonishing references. The first is a contribution on the gill area of spangled perch, *Leiotherapon unicolor*, with a scaling factor of d_G=1.04 (Gehrke 1987) and, second, the bivalve, *Solemya velum*, with reported scaling factors of 1 between gill surface area and gill *mass* and d_G= 0.85 between gill surface area and body weight (Scott 2005).

The choice of the Gehrke (1987) citation is suspicious, as there are several reviews, jointly covering over 150 species, showing that typical scaling factor for fish gill surface area range from d_G = 0.6 to 0.9 (Muir 1969; Muir and Hughes 1969; Hughes 1970; De Jager and Dekker 1975; Palzenberger and Pohla 2002). Indeed, for "*medium-sized*" fish (200 g), De Jager and Dekker (1975), based on data from well over 200 papers covering 121 fish species, computed a mean value of d_G = 0.811, very close to their mean estimate of the scaling factor of metabolic rate vs. body weight, d_{O2} = 0.826, which confirmed the classical results of Winberg (1960). They then averaged these two values to obtain a robust estimate of $d_G = d_{O2}$ = 0.82, assuming that d_G *causes* d_{O2}. This was based on Fick's Law of Diffusion, which states that the total amount of oxygen which can diffuse into the circulatory system of a WBE is

$$Q = dP \cdot U \, \mu \, G \cdot WBD^{-1} \qquad \text{...6)}$$

where Q is the oxygen uptake (ml·h^{-1}). Here, dP is the difference between the oxygen partial pressure on either side of the membrane (in atm); U is Krogh's diffusion constant, that is, the amount oxygen (in ml) which diffuses through an area of 1 mm^2 in one minute for a given type of tissue (or material) when the pressure gradient is one atmosphere of oxygen per μ (micron); G is the surface area of the gills (total area of the secondary lamellae); and WBD is the Water-Blood Distance, or the "*water-capillary distance*" of Graham (2006), i.e., the thickness of the tissue between water and blood in μ (De Jager and Dekkers 1975).

By contrast, Lefevre et al. (2017) argue that, while fish could grow gill surface area such that d_G = 1 is maintained, they do not need to do so because, they suggest, *the activity of oxidative enzymes falls with body mass in fishes (Davies and Moyes 2007)"*. This argument is problematic, for two reasons, the first obvious, the second less so:

i) It begs the question why growing fish -- if not forced by a declining relative O_2 supply -- should have evolved to reduce their O_2 consumption and shift from relying on oxidative to glycolytic enzymes, the latter catalyzing metabolic processes that are far less efficient than the former; and

ii) It attributes to fish biological features (i.e., gill lamellae) that they could multiply but whimsically choose not to, making its claims about fish physiology unfalsifiable. Thus, Lefevre et al. (2017) can assert that d_G<1 in the overwhelming majority of fish species so far studied does not refute their claim that gill surface areas can grow according to d_G = 1. At the same time, single (and questionable) cases with d_G = 1 (e.g., Gehrke 1987) 'confirm' that gill surface area can keep up with body weight.

Argument (*i*) mistakes cause and effect (Pauly and Cheung 2018). The physiologists who documented that the preponderance of oxidative enzymes in the tissues of small/young fish is replaced in large/old fish by a preponderance of glycolytic enzymes were well aware that this shift contradicts standard hypotheses about fish physiology (Burness *et al.* 1999; Davies and Moyes 2007; Norton *et al.* 2000; Somero and Childress 1980). Thus, Somero and Childress (1980) titled the report of their findings: *"A violation of the metabolism-size scaling paradigm: activities of glycolytic enzymes in muscles increase in larger size fish"*. Note, however, that this feature is not only compatible with the GOLT, but is one of its inescapable consequences.

Argument (*ii*) evidently points to Karl Popper's 'decision criterion,' that claims which cannot be falsified in principle are not part of science (Popper 2002).

Regarding the bivalve *Solemya velum,* the fact that Scott (2005) reports a value of d =1 for the scaling factor between gill surface area and gill mass misses the point. What matters here is the scaling factor between gill surface area and the weight of the entire body, which at $d_G = 0.85$ (Scott 2005) is relatively high for a bivalve, but well under 1, as required by the GOLT. Other bivalves have values of d_G and d_{O2} ranging between 0.5 and 0.8 (see Vakily 1992) and thus suffer from "ontogenic anaerobiosis" (Lutz and Roads 1977. An exception may be the giant clams of the family Tridacnidae, which are phototrophic and thus produce their own oxygen (Klumpp and Griffiths 1994).

Note that despite the argument that gill surface area grows under the constraints of a surface, it does not mean that this growth should be proportional to length squared, i.e., isometric growth, with $d_G = 2/3$, though von Bertalanffy (1964) thought so. Indeed, he erroneously referred to instances of $2/3 < d < 1$ as growth that is *"intermediate between surface and weight proportionality*".

However, values of $d_G \approx 0.67$ seem to occur only in very small fish such as the guppies von Bertalanffy (1951, 1964) used to illustrate his theory of growth. An even lower estimate of $d_G = 0.60$ was obtained for *Mistichthys luzonensis*, in which an adult does not reach more than 25 mm and a weight of about 0.5 g (Te Winkel 1935; Pauly 1982). The other extreme appears to occur in bluefin tuna (*Thunnus thynnus*), in which a well-documented value of $d_G = 0.90$ for adult specimens has been published (Muir and Hughes 1969).

The matter with exceptions, or exceptions matter

As stated above, the GOLT is falsifiable, i.e., it would be refuted if well-founded estimates of $d_G \approx 1$ or worse $d_G > 1$ were shown, for example, via a meta-analysis, to routinely occur in the *adult* stages of WBE (and excluding air-breathing taxa).

So far, credible estimates of $d_G >> 1$ have been found to occur only in teleost larvae (De Sylva 1974; Bochdansky and Legget 2001; Oikawa and Itazawa 1985), while estimates of $d_G \approx 1$ have been reported from juvenile fish transiting from the high d_G values in larvae to the values of $d_G < 1$ typical of the adults (Bochdansky and Legget 2001; Oikawa and Itazawa 1985).

There will be a tendency for published estimates of d_G to be on the high side when, as is often the case, only the small representative of a species is studied. In the case of Gehrke (1987), the published estimate of d_G =1.04 pertained to juvenile fish reaching at most 30 % of the maximum weight typically attained by the species in question (see Table 3). This was similar to the specimens of icefish (*Chaenocephalus aceratus*) collected by Holeton (1976), who also published a value of $d_G \approx 1$ (after correction from 1.09 due to the inappropriate use of a 'Type II' regression; Ricker 1973). Pauly (2018) discusses a few more cases of this sort.

Thus, while this may appear as special pleading, in view of their theoretical importance, it may be recommended that d_G values should preferably pertain to adults (i.e., larger than a third of the maximum weight typically reached by the species in question). In the future, it would be fair to expect criticisms of the GOLT to take account of existing meta-analyses rather than search for isolated estimates that differ from the results of meta-analyses but seem to support one's point.

Table 2. Arguments raised against the GOLT: claims by S. Lefevre and associates

No	Arguments	Refutations
2.1	Fish could, if needed, grow new gill lamellae to maintain the ratio gill surface area/body weight constant. However, they don't need to, i.e., *"gill surface area can scale proportionally with body mass, and if it does not do so, it is because oxygen demands are reduced with body size…"* (Lefevre et al. 2017, particularly their Figure 1A).	It is actually impossible, as any book on geometry will confirm, for gill lamellae, which must function as 2-D surfaces (Figure 3), to keep up with the growth of the 3-D bodies they supply with O_2 (Pauly and Cheung 2017b) . Also, the suggestion that large fish could increase their gill surface if they wanted, but somehow don't, makes the claims of Leferve et al. (2017) effectively unfalsifiable.
2.2	*"Weatherley and Gill (1987) […] had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes…"* (Lefevre et al. 2017).	Weatherley and Gill (1987) actually wrote that: *"[t]here is little doubt that the relative size of the gills may be important in influencing growth and size of fish, but Pauly's claim that his hypothesis 'offers a single, simple explanation to a whole set of growth-related phenomena…' seems extravagant."* Thus, Weatherley and Gill (1987) disputed the scope of gill limitation, not the idea itself.
2.3	Here is another version of the above citation: *"…Blier et al. (1997) had already concluded that there was no evidence that capacity for gas exchange or gill surface area could limit growth performance in fishes, and their analysis remain valid today"*.	No, it is no longer valid. Following an exchange with P.U. Blier, he agreed that *"under natural conditions, particularly when fish have to move at the same time as they feed or digest, it is very probable that aerobic scope, i.e., the oxygen supply through the gills, acts as a limiting factor"* (pers. comm., March 16, 1998, translated from French; Pauly 2010, p. 150).
2.4	Lefevre et al. (2018) asserted that *"Pauly and Cheung [2017a] seem to suggest that when the gill area grows, it will eventually deplete the water of oxygen, and more surface area will be useless. However, an increase in body and gill size will of course coincide with a proportional increase in water and oxygen movement, so a doubling of surface area effectively doubles the capacity for oxygen uptake"*.	They didn't. Pauly and Cheung (2017a) suggested that the growth of gill surface area can proceed only by making the gill 'sieve' higher and wider (2-D) but not deeper (3-D), as this would put the new gill lamellae *behind* the first 'layer' of lamellae. Lamellae that were so placed would indeed be *"useless"*, as the first layer of lamellae would reduce the water flowing across the gills of O_2, leaving the second layer (and any subsequent layer) with little to nothing to do (see Figure 3, and Figure 2.14 in Pauly 2019c).
2.5	*"…a fundamental pillar of the GOLT – that geometrical constraints hinder the gills and their surface from growing at the same pace as the fish body – is not supported by existing data and knowledge"*. (Lefevre et al. 2018).	On the contrary, the GOLT has the support of an immense amount of data, stemming from numerous anatomical studies, physiological experiments and ecological surveys. The points are that this evidence had never been assembled into the coherent picture that the GOLT provides, and that this picture requires a rethinking of old assumptions.

Table 3. Arguments raised against the GOLT: issues regarding gill surface areas

No	**Arguments**	**Refutations**
3.1	Leferve et al. (2017) assert that *"in morphometric studies where both total lamellae area and gill mass have been measured, a linear scaling relationship (scaling exponent of 1.0) has been found in fishes (Gehrke 1987) as well as bivalves (Scott 2005). Consequently, there is no geometric constraint that prevents an increase in body size (mass or volume) from being accompanied by a corresponding increase in gill mass and hence respiratory surface area. In other words, gill surface area can scale proportionally with body mass and, if it does not do so, it is because oxygen demands are reduced with body size".*	Several meta-analyses of gill surface area covering hundreds of fish species exist; they report scaling exponents ranging overwhelmingly from 0.7 to 0.9 (e.g., De Jager and Dekker 1975; Palzenberger and Pohla 1992 and see text) and mention the difficulties in obtaining accurate values when a small range of body sizes are included (see also Hughes 1984). Thus, the value of 1.04 reported by Gehrke (1987) is not representative of fish in general and a likely overestimate, due to the largest specimen considered being only 12% of the maximum weight reported in *Leiopotherapon unicolor* (see www.fishbase.org). The scaling exponent between gill surface area and bivalve body weight appears to range from 0.51 to 0.80 (Franz 1993; Vakily 1992, Table 5.2), with 0.85 in *Solemya velum* (Scott 2005). The scaling exponent of 1.0 linking gill surface area to gill *mass* in *S. velum* is irrelevant to the O_2 supply to its *body*. Also note that the last sentence of the argument precludes falsification.
3.2	The presence of very large fish in warm tropical waters, e.g., Goliath groupers (*Epinephelus itajara* and *E. quinquefasciatus*), sunfishes (*Mola mola*), billfishes and other scombroids, giant manta ray (*Manta birostris*) and especially the largest extant fish, the whale shark (*Rhincodon typus*) refutes the GOLT, which postulates that high temperatures tend to reduce the size of fish (Lefevre et al. 2017). [This issue was a genuine challenge to the GOLT, and its successful resolution (see adjacent column and main text) widened its scope]	Pauly (2019c), following an extensive review of the biology of the species in question, concluded that rather than being invalidated by large fishes occurring in the tropics, the GOLT can be used to classify their response to the challenge that high temperatures pose to their metabolism. Thus, in addition to breathing air, as often occurs in tropical freshwater fishes, three types of increasingly complex adaptations occur, none mutually exclusive: *i*) Placid behavior, combined with ambush predation (e.g., groupers) or filter-feeding (e.g., whale shark); *ii*) Yo-yo-type swimming between the warm surface and colder, deeper water layers and feeding mainly near the surface (bluefin tuna, whale shark), or at depth (swordfish, billfish), the latter cases involving heating systems to keep their huge eyes and brain *warm*; and *iii*) Huge anatomical changes from the ancestral fusiform shape, turning the body into a shell around a cavernous mouth and oversized gills (giant manta ray) or a mass of inert jelly surrounding specialized locomotory muscles (*Mola mola*).
3.3	O'Dor and Hoar (2000) believe that squid respire through their skin, and that by having tubular bodies, squid have such large respiratory area that they cannot be O_2-limited. Also, their changed shape as they grow increases the surface area of their body hyperallometrically.	Squid do not breathe though their skin (Birk et al. 2018), and even if they did, it would not matter, because their body surface (even when multiplied by 2 because of their tubular nature and even after changing from roundish to lanceolate in the course of their ontogeny) is much smaller than that of their gill surface area.
3.4	The demonstrably asymptotic growth of *Growing Sealife*™ plastic squids implies that asymptotic growth does not require a limiting surface (Lipinski and Roeleveld (1990).	A detailed analysis of what occurs in plastic squids which 'grow' when placed in water shows that, actually (and surprisingly), it is a surface that limits their growth (Pauly 1998, 2019c).

TWO MAJOR CHALLENGES TO THE GOLT

Fish growth vs. reproduction

One of the main issues in ichthyology, though it is not often perceived as such, is the relationship between growth and reproduction. The majority of authors writing on this topic repeat the usual belief that the relationship between growth and reproduction is explained by stating that "the growth of fish slows down upon reaching maturity because their energy is redirected from growth to reproduction", or a variant of this phrase (Hubbs 1926; van Oosten 1923; Jones 1976; Lagler et al. 1977; Sebens 1987; Day and Taylor 1997; Charnov 2008; Quince et al. 2008). This notion implies a "*biphasic growth*" (Quince et al. 2008) with a rapid growth phase before the length at first maturity is reached and a slower phase thereafter, as illustrated by Figure 4A.

What is not realized, however, is that this phrase, like all statements about complex phenomena, is a hypothesis. Moreover, this hypothesis is contradicted by 4 sets of observations:

1. Fish kept in aquaria and that never mature and spawn also have asymptotic growth curves;
2. In most fish species, the females are larger than the males, although they devote more 'energy' to reproduction;
3. Growth in weight is more rapid after maturity is reached than before, and
4. Mean length at first maturity correlates tightly with the maximum length that can be reached in a given environment.

Regarding item (1), many of the salt or freshwater fish kept by home aquarists never mature and spawn. Yet, even though they are fed *ad libitum*, they stop growing at some point. Also, triploid and thus sterile fish exhibit growth patterns largely similar to those of their diploid brethren (Maxime 2008). This should suffice to kill the notion that it is reproduction that causes growth to cease. However, it has become a zombie idea: it does not die.

Similarly, regarding item (2), in over 80% of fish families where females and males look alike, it is the females that eventually reach larger sizes (Figure 4B), even if this growth dimorphism can become attenuated in certain circumstances (Morbey 2018). This strong female dimorphism should lead to a rethink of the notion that the cost of reproduction causes growth to decline. However, some authors, when confronted with this evidence, have doubled down and suggested that males have the higher reproductive cost.

One such case was Ursin (1967; see Table 5, No. 5.2). Also, Marshall & White (2019) suggested, in an effort to refute Pauly (2019b), that males had the higher reproductive effort, citing in support of this claim a figure from an unpublished thesis that did not even compare male and female reproductive *output* (see Table 6, No. 6.2). In reality, females are, by definition, the sex with the higher reproductive output, which also can be shown empirically in almost all groups of animals reproducing sexually (see, e.g., review by Parker et al. 2018). There are a few exceptions (e.g., parental care by male seahorse), but they are not pertinent here.

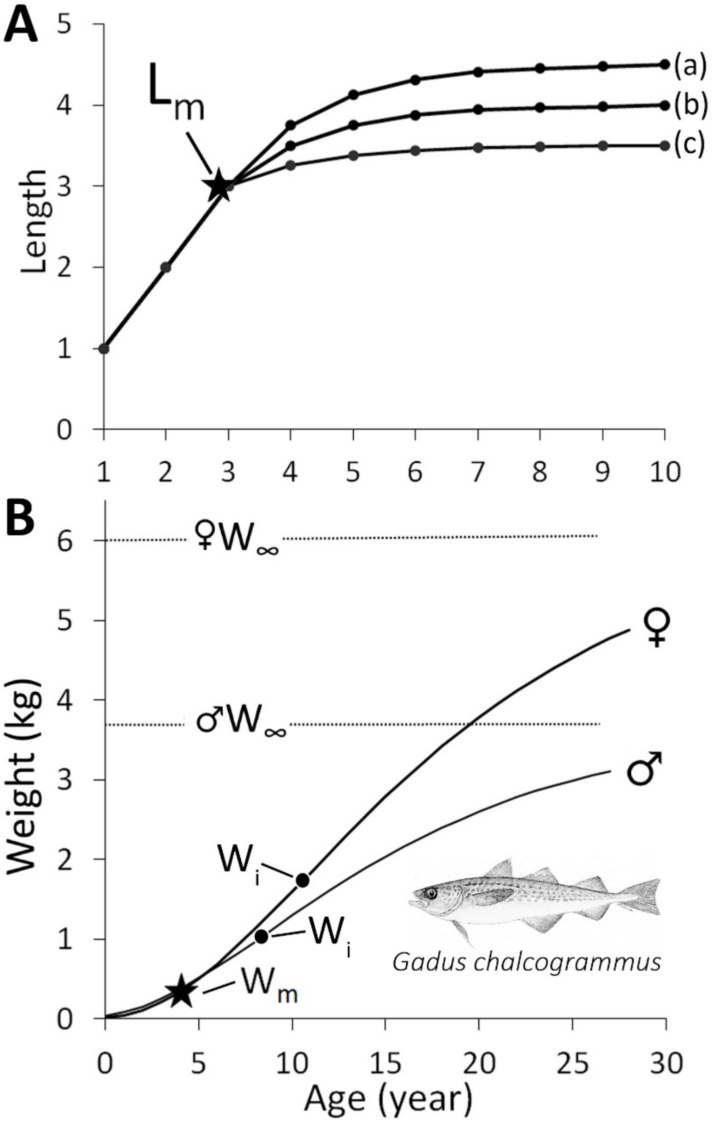

Figure 4. Two views of the relationship between size at first maturity and maximum size. **A**: the traditional view, where 'linear' growth slows down when length at first maturity (L_m; black star) is reached, with growth then continuing at a reduced pace depending on circumstances (i.e., a, b or c; redrawn from Quince et al. 2008). **B**: a more appropriate but uncommon view, with growth expressed as change in body weight (in line with Equation 1). This shows not only that weight at first maturity in females and males (W_m; black star) is reached when growth is still accelerating (i.e., $W_m < W_i$, the inflexion point of the curve), but also that females grow faster and reach larger weights than the males despite investing more in reproduction (see also text and Table 6). Graph based on length growth parameters, a length-weight relationship and lengths at first maturity for Alaska pollock (*Gadus chalcogrammus*) in FishBase (www.fishbase.org), which contains hundreds of similar data sets.

Table 5. Arguments raised against the GOLT: different definitions of anabolism and catabolism

No	Arguments	Refutations
5.1	Von Bertalanffy's hypothesis of a surface limiting fish growth (which is a key element of the GOLT) is wrong because the absorptive surface area of the gut is not in permanent contact with food. See Beverton and Holt (1957, p. 32), Ricker (1958, p. 196; 1975, p. 224).	Von Bertalanffy (1934, 1938, 1949, 1951, 1960, 1964) did not state that the surface limiting growth was that of the gut. He thought that "*the actual surface responsible for growth of an organism is in general unknown*" (von Bertalanffy 1938). However, he clearly favored a link to respiration (albeit without explicitly mentioning gill surface area).
5.2	Ursin (1967, p. 2359) suggested that *"Apparently, it was overlooked that although catabolic processes are going on all over the body, the necessary oxygen supply has to be introduced through some surface or the other, mainly the gills. With our basic assumption of isometric growth, this 2/3 means that catabolism is proportional to $w^{2/3}$".*	This was not overlooked. In the GOLT, the catabolic processes 'going on all over the body' do not require oxygen. They consist of the (temperature dependent) spontaneous denaturation (=loss of the quaternary structure) of protein molecules. This process is proportional to weight; the denatured proteins must be re-synthesized, which requires ATP and hence O_2. However, this is part of anabolism, not catabolism.
5.3	Morais and Bellwood (2018) *"…anabolism is proportional to the area of the circulatory network rather than to gill surface area (West, Brown and Enquist, 1997)".*	If this were correct, the scaling factor of anabolism to weight in fish and invertebrates would always be 0.75. This, however, is emphatically not the case (Glazier 2006; Pauly 2010, p. 132; Pauly 2019c, p. 140).
5.4	Brander et al. (2013), critique of Cheung et al. (2013a) included: *Methodological shortcomings include (i) assimilated consumption (the 'anabolic' part of the growth equation) is assumed to be proportional to oxygen, but oxygen is only a limiting factor for growth not a controlling factor, i.e. it only affects growth if the oxygen concentration is below a critical value (Brett 1979), and the equation is not documented in their reference, which is an unrefereed book".*	Cheung et al. (2013b) wrote that *"[w]hile Brander et al. cite Brett (1979) to suggest that oxygen is a limiting factor for growth, and not a controlling factor, there is abundant theoretical and empirical support in the peer-reviewed literature for oxygen being both a limiting and controlling factor for the growth of fish and aquatic invertebrates (Pauly 1981; Peck and Chapelle 2003; Kolding et al. 2008; Pörtner 2010; Pörtner and Peck 2010; Verberk and Bilton 2011; Verberk et al. 2011)".*

Regarding item (3), Figures 1C and 4B show that, in fish, the ratio of weight at first maturity (W_m) to asymptotic weight (W_∞) is much lower than the corresponding ratio for length (L_m/L_∞), which is frequently not realized because the overwhelming majority of growth curves drawn reflect growth in length (Figure 4A).

From length growth curves, one can indeed get the impression that spawning strongly affects growth, and hence the name "*reproductive load*" for the L_m/L_∞ ratio (Cushing 1975). However, growth is a process primarily involving mass (see Equation 1), as reflected in weight growth curves. Weight growth curves have marked inflection points in which growth rate (dw/dt) is highest (at W_i), and thus the question may be asked if $W_m > W_i$ or, on the contrary, $W_i > W_m$. Taking the 2nd derivative of generalized VBGF for weight growth (Equation 5) and setting it equal to zero allows identifying W_i, where the growth rate changes from increasing to decreasing:

$$W_i = W_\infty(1-(D/b))^{b/D} \qquad \text{....7)}$$

As may be seen from Figure 1C and Figure 4B, the weight at the inflection point of these curves is higher than the mean weight at first maturity of the population in question (i.e., $W_i > W_m$). This result, which can easily be reproduced for multiple species of (larger) fish, implies that as fish reach maturity, their growth in weight is still accelerating, which refutes the reproductive load hypothesis.

The question thus arises: if the reproductive load concept does not hold, i.e., if reproduction does not cause growth to decline, what then is the relationship between reproduction and growth in fish, and by extension, in other WBE?

Equation (1) with $d < 1$ implies that the heavier fish get, the less O_2 per unit weight they will get, which should imply – other things being equal - more frequent occurrences of respiratory stress. All we need to assume, therefore, is the existence of a threshold weight (W_m) at which the high frequency of respiratory stress events triggers the hormonal cascade that leads to maturation (Pauly 1984). Thus, one can define

$$A = (W_\infty^{1/b}/W_m^{1/b})^D \qquad \text{8)}$$

From which $$W_m = W_\infty \cdot (1/A)^{b/D} \qquad \text{...9)}$$

with A being the ratio of gill surface area (or O_2 supply) at W_∞ over the gill surface area (or O_2 supply) at W_m (Pauly 1984, 2019c).

A first estimate of $A = 1.365$ was obtained by Pauly (1984; and see Figure 5C), whose 95 % confidence interval is C.I = 1.218 – 1.534, as estimated using the method of Fieller (1940) applied to the data of Table S1. These data covered 56 pairs of L_m and L_∞ in 34 different fish species ranging from guppies to tuna and raised to the of power 3/(1-d), which here substitutes for weights (see Supplementary Material).
Since $A^{-1} = 0.733$, combining with Equation (7) and rearranging (see Liang 2021; Supplementary Material) leads to the conclusion that $d > 0.733$ implies $W_i > W_m$; $d \approx 0.733$ implies $W_i \approx W_m$ and $d < 0.733$ implies $W_i < W_m$. Thus, in small fishes, which usually had small values of d (e.g., 0.6 in the diminutive goby *Mistichthys luzonensis*; Pauly 1982, 2019c), $W_m > W_i$, while the opposite, $W_m < W_i$, applies to larger fishes (e.g., bluefin tuna, see Figure 1C and 3B).

This also aligns with the result of Froese and Binohlan (2000), who investigated the relationships between L_m and L_∞ (with and without additional variables) in 265 fish species in FishBase (www.fishbase.org), covering 88 Families and 27 Orders, with an average scaling factor of ≈ 0.9 emerging. Thus, the simplest of their empirical relationships is:

$$\log(L_m) = 0.898 \cdot \log(L_\infty) - 0.0782 \qquad \text{...10)}$$

when L_m and L_∞ are in cm.

Equation (9) implies that fish with an asymptotic length of 10 cm reach maturity at a length of 6.6 cm, while fish with asymptotic lengths of 100 and 1000 cm reach maturity at 52 and 412 cm, respectively. These values, when converted to weights, are well within the confidence interval of the value of W_m predicted by Equation 7 (Table 7).

Table 7. Theoretical vs. empirical predictions of weight at fish maturity. Comparing 'theoretical' predictions of W_m based on the GOLT (Equation 9) to the empirical equation of Froese and Binohlan (2000; Equation 10) and their relationship to growth curves' inflexion point (W_i; Equation 7).

#	L_∞ (cm)	L_m (cm)	W_∞ (g)[a]	d[b]	W_m (% of W_∞)[c] Equation 10	W_m (% of W_∞)[a] Equation 9	W_i (% of W_∞) Equation 7
1	2	≈ 2	0.08	0.6	47	46 (34 - 61)	28
2	10	6.6	10	0.7	29	35 (24 - 52)	30
3	100	52	10^4	0.8	14	21 (11 - 37)	33
4	1000	412	10^7	0.9	7	4 (1 - 14)	34

a) Assuming the length-weight relationship $W = 0.01 \cdot L^3$, corresponding to a trout-like (i.e., 'average') fish when cm and g and used for L and W, respectively;
b) Estimated from W_∞ (g) and $d \approx 0.6742+0.03574 \cdot \log W_{max}$ in Pauly (1981, 2019c), with $W_\infty \approx W_{max}$;
c) The error term corresponds the 95 % confidence interval of A = 1.365, i.e., 1.218 - 1.534 (see text).

Unfortunately, Equation (9) does not work below 1.3 cm, i.e., it predicts $L_m > L_\infty$. Indeed, it can be hypothesized that such small fish are semelparous, i.e., will spawn only once before they die, as documented in minute gobies (Caputo et al. 2003). It doesn't work either with large semelparous species such as Pacific salmon (*Oncorhynchus* spp.), whose reproductive strategy, however, is a derived trait connected with their diadromous life history (Crespi and Teo 2002).

Finally, regarding item 4 above, there is the huge environmental plasticity of fish, which can manifest itself both in individuals used for aquarium experiments (Kinne 1960; Kolding et al. 2008) and in the wild. Thus, Randall et al. (1993) noted that "*tropical fishes living near the limit of their tolerance for low temperature grow to larger size at such temperatures.*" In such cases, i.e., when the maximum length (L_{max}) or the computed asymptotic length (L_∞) changes, the mean length at first maturity (L_m) also changes in the same direction, such that the ratio L_m/L_{max} or L_m/L_∞ remain approximately constant.

The GOLT provides an explanation for the near constancy of L_m/L_{max} or L_m/L_∞ by postulating that spawning is induced by the same mechanism that also causes growth to decline (i.e., with asymptotic growth). As fish grow in weight, their gills, whose surface area has grown with the scaling factor $d < 1$, deliver less O_2 per unit of body weight (Figure 5A).

Thus, growing fish will gradually experience more respiratory stress, and a stress level is finally reached that initiates the hormonal cascade leading to maturation (Bass 1993; Bhattacharya 1999; Pauly 1984). Thus, gonadal products are elaborated, often by using fat accumulated in the summer and fall as energy sources (Shul'man 1974). In spring, the gonadal products are released, the gill surface area/body weight ratio increases again, and summer growth can resume, etc.

With time, however, the fish grow heavier despite generating an increasing reproductive output and the ratio of gill surface area/body weight declining further (Figure 5A). Thus, growth gradually ceases, but life (and reproduction) does not need to, as exemplified by adult whitefish (*Coregonus* spp., Salmonidae) that can live a decade or more after they have ceased to grow (Johnson 1976). The same occurs in a number of coral reef fishes, for example, in the families Acanthuridae and Scaridae (Choat and Axe 1996; Choat et al. 1996).

The threshold gill surface area and hence the relative metabolic rate at which spawning is initiated is similar among different fish families (see Figure 5C and Supplementary Material) because such a critical threshold would be conserved through evolutionary time. Thus, when the growth of teleosts causes their metabolic rate to drop to about 1.3 to 1.4 times their maintenance metabolic rate (i.e., something that fish can monitor in real time), then sexual maturation is initiated. Figures 5D-F provide further examples of this generalization (see also Meyer and Schill (2020).

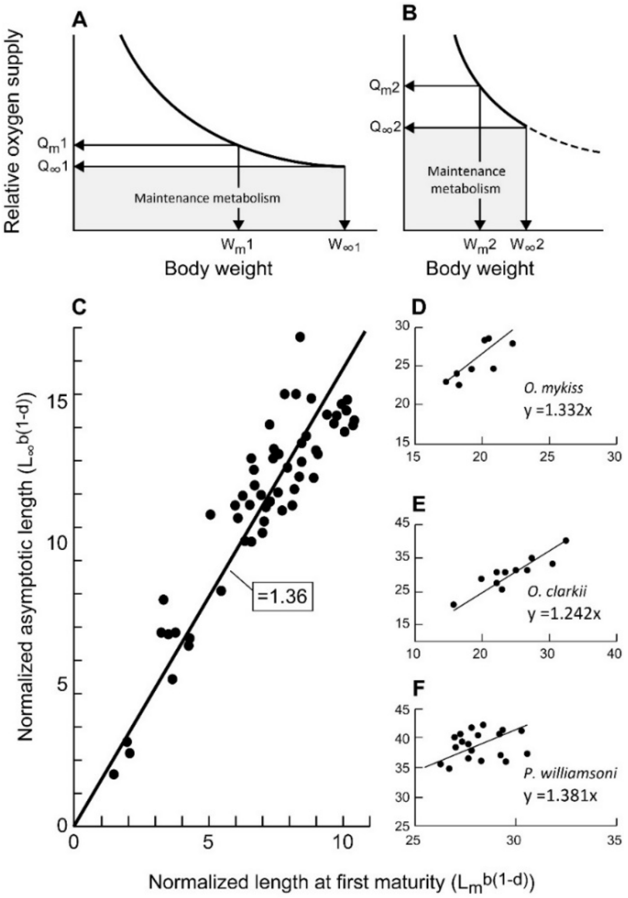

Figure 5. Growing fish mature when their relative gill surface area reaches a threshold. A: In the ontogeny of fish, when their relative gill surface area declines, their oxygen supply declines as well; when the latter reaches 1.3-14 times the oxygen supply required for maintenance and routine activities, i.e., as fish increasingly get 'out of breath', they initiate the hormonal cascade leading to gonad maturation and spawning. **B**: if the same fish are in a stressful, e.g., warmer environment, causing oxygen demand to be elevated, the same 1.3-1.4 threshold will cause them to mature and spawn at smaller sizes. **C**: The plot, whose 56 point represents the 34 fish species ranging from guppies to tuna (see Supplementary Material) that Pauly (1984) used to estimate the average threshold value of 1.36 (with 95% confidence interval: 1.218-1.534). **D**: the same plot, but for different populations of redband trout (*Oncorhynchus mykiss)*; **E**: ditto for Yellowstone cutthroat trout (*Oncorhynchus clarkii*) **F**: ditto for Mountain whitefish (*Prosopium williamsoni*).

Table 6. Arguments raised against the GOLT: spawning vs. growth and vice-versa

No	**Arguments**	**Refutations**
6.1	Old/large adult fish do not stop growing because of a declining O_2 supply, but because all their 'energy' goes to reproduction (see, e.g., Charnov et al. 2001).	Well-fed, non-reproducing fish (e.g., in aquaria) stop growing at some point. Also, the females of >80% of fish species grow to be larger than the males (see www.fishbase.org and section on 'Fish growth vs. reproduction').
6.2	*"Pauly's assumption that female fish have higher reproductive output than male fish is unsupported by data. There is no pattern of female fish investing more in reproduction than males in fish (or other water-breathing ectotherm [Parker et al. 2018]". Indeed, for the species given by Pauly [2019a], females invest relatively less in reproduction than males as a proportion of body mass (see figure 5.5 in G.A. Sarre, PhD thesis, Murdoch University, 1999).* (Marshall and White 2019). Note that "*figure 5.5*" is a plot of ova stages vs. body weight in female (only) black bream (*Acanthopagrus butcheri*), which does not deal with the female-to-male comparison at hand; it is likely that the authors meant figure 5.6, which compare the gonosomatic index (GSI) of females and male black breams. Also, Ursin (1979), in a context similar to that above, claimed in a funny *ad hoc* hypothesis that the greater reproductive investment of the female is more apparent than real, i.e., "*[t]he male gonad often weighs less than the female gonad. This does not mean smaller spawning loss in males because sperm, consisting almost entirely of DNA, RNA and lipoids, is likely to be the most expensive substance in the fish body.*"	Hayward and Gillooly (2011) in a review of 168 mammal, 97 bird, 3 reptile, 100 amphibian, 98 fish and 16 invertebrate species concluded that, overall, the cost of egg production was up to 3 orders of magnitude higher than the cost of sperm production. This confirms Gould (1985, p. 59), who wrote "*[s]perm is small and cheap, easily manufactured in large quantities by little creatures. A sperm cell is little more than a nucleus of naked DNA with a delivery system. Eggs, on the other hand, must be large, for they provide the cytoplasm (all the rest of the cell) with mitochondria […]), and all other parts that a zygote needs to begin the process of embryonic growth…*". Parker et al. (2018) state in their abstract that sessile invertebrates (not "*fish*") are *"subject mainly to selection on gamete selection and gamete success and so high gonad expenditure is expected in both sexes. […] We review the literature on gonadosomatic index (GSI) […], which we use as a proxy for gonad expenditure. […] When GSI is asymmetric, female GSI usually exceeds male GSI, as least in echinoderms. […] Intriguingly, higher male GSI also occur in some species […] of gastropod molluscs"*. If these authors had found that male investment routinely matches that of females, they would not have used the word '*intriguingly*'. As for figure 5.6 in G.A. Sarre's unpublished thesis, it shows male GSI to be occasionally higher than female GSI. However, GSI is an index relating the gonads *weight a given time* to the weight of the body, not the *rate of production* of gonad tissue, which alone relates to reproductive costs, which are always much higher in females (see above).
6.3	Brander et al. (2013), critique of Cheung et al. (2013a) included: *"the bioenergetic model assumes that the term scaling directly with weight is due to catabolism, but the there is a strong case that reproductive investment is the principal factor (Day and Taylor, 1997; Charnov et al. 2001; West et al. 2001)"*.	Cheung et al. (2013a) replied: *"Brander et al. argue that fish growth is inversely proportional to reproductive investment. However, this […] cannot explain why female fish (which have a much larger reproductive investment than male fish) reach larger sizes than male in the majority of fish species, and why sterile fish […] grow asymptotically. Moreover […] diploid (reproductively active) and triploid (sterile) fish show very similar growth patterns despite large differences in reproductive investment (Maxime 2008)"*

Temperature and maximum sizes

To compensate for Lefevre et al. (2017), who critiqued the contribution of Cheung et al. (2013a), but did not propose their own hypothesis as to why fish should remain smaller at higher temperatures, the contribution of Audzijonyte *et al.* (2018) is examined in some detail here, as these authors attempt to answer the question of whether "*oxygen limitation in warming waters is a valid mechanism to explain decreased body size in aquatic ectotherms*" (Figure 6A).

Answering this question would also solve the riddle posed by Kinne (1960), who was baffled by his observation, based on guppies raised at different temperatures, that *[t]he results indicate that the differences in growth rate established in young fish do not persist throughout life. Initially slow-growing fishes may surpass initially fast-growing fishes, and finally reach a greater length-at-age"*, as reported and illustrated earlier by Pütter (1920; Figure 6B).

Audzijonyte *et al.* (2018) presented and discussed six potential explanations, as documented in their figure 1 (with the quotes all extracted from its caption), which are here summarized and commented upon. All but the first of these potential explanations can be viewed as implicit alternatives to the GOLT:

a) The GOLT (or 'GOL hypothesis' in Audzijonyte et al. 2018).

The GOLT, based on the inherent properties of gills as 2-D surface that must remain exposed to an oxygen-laden water flow, assumes that they will provide decreasing amount of oxygen per unit weight to the bodies of growing WBE. Hence, increased temperatures, which increase oxygen demand, will force them to remain smaller (Figures 6C; see also Cheung et al. 2013a). However, the fish kept at higher temperature may at first experience a more rapid growth than those kept at low temperature, which also explains the above quote from Kinne (1960).

Note also that many inferences on the growth of fish and other WBE are based on juveniles, whose growth is usually accelerated by temperature increases, and not on adults, whose growth is often depressed by increased temperature (Table 1). The preference of researchers for working with juvenile fish is understandable (they require smaller aquaria, require less food, etc.), but it often leads to more confusion, as illustrated by the above quote of Kinne (1960), one of the few aquatic biologists who raised fish (albeit small ones) under different temperatures from larvae to adults.

b) "Different temperature dependence of DNA replication (development) results in smaller cells and faster division at warmer temperatures."

Fish that remain smaller at higher temperatures have, to the author's knowledge, never been shown to possess smaller cells. And if they did, this would be the reason for their smaller size in warm water only if they had the same number of cells, as do, e.g., tardigrades and small nematodes. This, as well, has never been demonstrated.

Hypothesis (b) is probably another case of cause and effect being inverted (similar to the case documented above; Table 4), as often happens when things correlate (Pearl and Mackenzie 2018). Some of the largest fish, e.g., tuna, have very small cells, while the much smaller lungfish have large cells (Hinegardner and Rosen 1972; Thompson 1972; Cavalier-Smith 1991). Indeed, it seems that, in fish at least, cell size is linked with DNA content and activity level but not with size (Pauly *et al.* 2000). On the other hand, the higher cellular turnover implied by "*faster cell division at warmer temperatures*" would be associated with a higher rate of protein denaturation, which is a central tenet of the GOLT (see above).

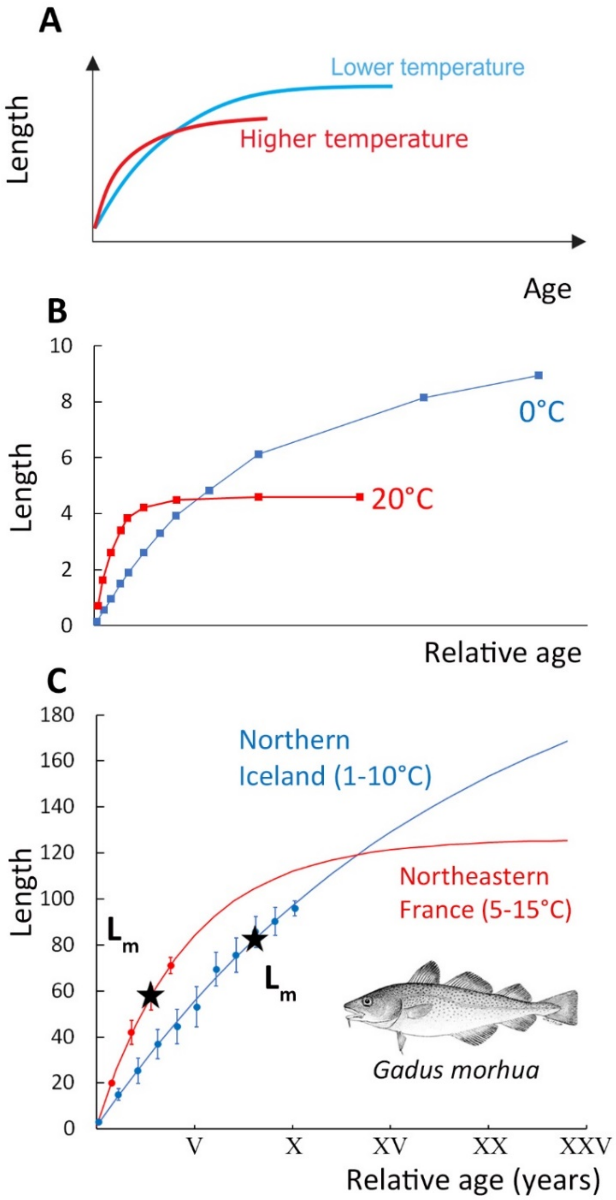

Figure 6. Fish, at higher temperatures, tend to grow fast toward smaller maximum sizes. **A**: The "Observed phenomenon" that needs to be explained (adapted from an insert in Figure 1 of Audzijonyte et al. 2018); **B**: A simplified version of figure 1 in Pütter (1920), who derived it from principles later elaborated upon by von Bertalanffy (1934 and beyond); **C**: Atlantic cod (*Gadus morhua*) has wide geographic and temperature ranges; in Eastern Iceland (1-10 ^{o}C), they reach much larger sizes than in French waters (8-18 ^{o}C); based on data in Saemundsson **(**1923) and Le Franc (1966).

Table 4. Arguments raised against the GOLT: mistaking cause and effect

No	Arguments	Refutations
4.1	Lefevre *et al.* (2017) suggested that since *"the activity of oxidative enzyme falls with body mass in fishes (Davies and Moyles 2007"* larger/older fish need less oxygen anyway. Thus, it is not necessary to maintain a high O_2 supply.	This is mistaking cause and effect: fish shift from oxidative to glycolytic enzymes *because* their relative O_2 supply declines. This was understood by Somero and Childress. 1980), who attributed the shift from oxidative to glycolytic enzymes, if tentatively, to "*[l]imitation on aerobic metabolism [which] may derive from surface-volume relationships…*"
4.2	Lefevre et al (2017) write: *"In our field, it is generally accepted that a species' oxygen demand determines the size of their [sic] respiratory surface area, not the other way around".*	Something being "*generally accepted*" within one's field is not evidence of its validity. Thus, e.g., Plate Tectonics was not mentioned in geology textbooks and generally not accepted by geologists… until it was (Oreskes 2013).
4.3	In their abstract, Lefevre et al. 2017) claimed that there is *"a large body of evidence demonstrating that respiratory surface areas in fishes reflect metabolic needs, not vice versa, which explains the large interspecific variation in scaling of gill surface areas".*	There is no such body of evidence; rather, the O_2 consumption of fish is generally *assumed* to reflect their '*needs*'. What is missing are tests of whether the *supply* of O_2 by the gills to the body (always) satisfies the O_2 *demand* of the fish tissues. It does not in large adult fish, which is the reason that they switch from oxidative to glycolytic enzymes

c) "Decreasing growth efficiency at higher temperatures means that less energy is converted to growth."
This is not an explanation because it shifts that which must be explained from 'reduced growth when temperature is high' to 'decreased growth efficiency', which is a restatement of the issue at hand.
The GOLT explains 'decreased growth efficiency' (i.e., K_1 = growth increment/food ingested; Gerking 1952, 1971) by pointing out that when WBE are exposed to higher temperatures, more of their oxygen supply is diverted to basal metabolism, leaving less available to assimilate food. Hence, the amino acid pool of fish spills over and "*is excreted by the gills and kidney as incompletely oxidized nitrogenous compound*" – the latter point quoted from Webb (1978), who cites the works of Forster and Goldstein (1969); Savitz (1969, 1971); Olson and Fromm (1971) and Niimi and Beamish (1974); see also Kajimura *et al.* (2004).

d) "Higher size-specific allocation to reproduction at higher temperatures […] leaves less energy for growth."
No evidence is presented by Audzijonyte *et al.* (2018) that fish and/or aquatic invertebrates devote more resource to reproduction at high temperatures. Besides[21], the argument is irrelevant because the effects of temperature on growth manifest themselves well before fish mature (see Figure 6A-C).

e) "Faster increases in energy demand (metabolism, activity cost, etc.) compared with food availability leaves [less] energy for growth and reproduction in […] warmer environments."
This complex hypothesis, which implies that tropical ecosystems make less food available to consumers than colder ecosystems, would be hard to test. Fortunately, there is no need to test it, because experiments can be and have been conducted *in vitro* in which food is provided *ad libitum* and in which fish kept at

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[21] Deleted at the suggestion of a reviewer.

cooler temperatures grow to be larger than those at higher temperatures (Kinne 1960; Liu and Walford 1966, 1970).

The only reason this point is perhaps not obvious is that laboratory growth experiments are difficult to run with large/old fish, and thus are mostly conducted with juvenile fish, with the initial growth acceleration due to higher temperatures leaving the strongest impression. Only when small, short-lived fishes are monitored over their entire life-spans does the phenomenon, which so puzzled Kinne, appear (1960; see above quote).

f) *"Increased predation mortality at higher temperatures drives an evolutionary response of higher net energy allocation to reproduction versus growth."*
This is hypothesis (d) in another guise. Evoking a complex "evolutionary response" is not an explanation of anything because, as was said so elegantly, "*nothing in biology makes sense except in the light of evolution*" (Dobzhansky 1973). The point, rather, is to identify the mechanism in question. However, it will be quite difficult, given that, as stated for (d), fish grown under experimental conditions and without opportunity to spawn remain smaller at higher temperatures (Kinne 1960; Liu and Walford 1966, 1970). The critique of items (b) to (f) is serious: proposed hypotheses should be able to withstand a confrontation with common-sense observations. Moreover, several of these hypotheses were only complex restatements of the issue at hand (Figure 7).

In contrast, the GOLT proposes a mechanism for the reduced body size of fish and invertebrates under global warming that is simpler than what needs to be explained and that is based on consensual knowledge – including that gills cannot be perceived as Escher-like objects *à la* Lefevre et al. (2017). Also, the GOLT makes numerous predictions pertaining to domains that, at first glance, appear to be unrelated to temperature affecting the size of fish.

This is because the constraints on the surface area of gills are real: their surface area was optimized in the course of evolution to allow their owners to reach first maturity relatively fast, after which growth can gradually slow down.

The notion that gill surface area cannot be limiting because lamellae can be added as required, as suggested by Lefevre et al. (2017), is false because gills function similar to a sieve, i.e., and must be perpendicular to the flow of water that flows through them. This means that they can grow in height and in breadth but not in depth – they cannot grow in the 3rd dimension, and thus 3-D bodies must experience a declining oxygen supply as they grow. Moreover, as Audzijonyte et al. (2018) emphasize, gills are a favorite site for parasite infestation, and thus fish and aquatic invertebrates have good reasons to keep them as small as possible (see also Nilsson et al. 2012). Thus, gill surface area is not limiting to young/small fish, but they are limiting to big adults.

The GOLT offers a coherent framework for exploring these phenomena and a vast number of related observations. This is not the case for just-so hypotheses.

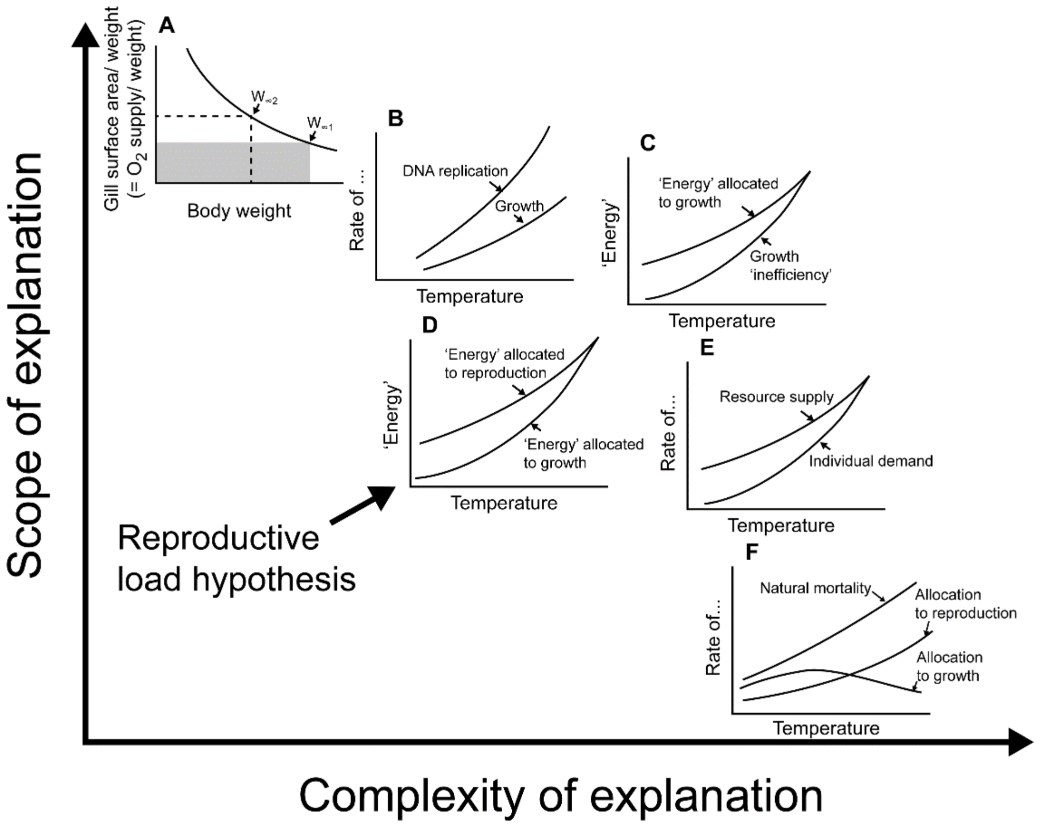

Figure 7. **Simplicity vs. scope in explaining why higher temperatures lead to smaller sizes**. The 6 explanatory models are adapted from Audzijonyte et al. 2018), who presented them in two columns, as 'intrinsic mechanisms' (**A**, **B**, **C** and **D**), and 'extrinsic mechanisms' (**E** and **F**). Here, they are arranged according to the perceived complexity of the mechanism(s) they require its (or their) generality or 'scope' (see text).

DISCUSSION

The nature of explanations

The physicist Wolfgang Pauli is supposed to have said, "*God made the bulk; surfaces were invented by the devil*" (Jamtveit and Meakin 1999, p. 21). When thinking about the explanations provided by the GOLT, which is concerned primarily with the 'tension' between volumes and surfaces (and the arguments denying such tensions that have been advanced against the GOLT's explanations), it is appropriate to recall what is meant by an 'explanation'. Rather than pedantry, an exercise is required to define the terms of the debate and the criteria that are applied below.

To become widely accepted, scientific explanations, in addition to being (obviously) congruent with the facts at hand, must be:

1. Consilient with underlying scientific disciplines;
2. Parsimonious, i.e., as simple as possible;
3. Independent from the observer and/or standpoint; and
4. Productive, i.e., make unexpected predictions.

The first of these, building on Wilson (1998), is the notion that the different scientific disciplines, while autonomous in their investigations of the phenomena upon which they focus, cannot accept explanations that violate constraints established by other scientific disciplines (or by logic and mathematics). Thus, biological organisms must comply with physical laws, and the processes comprising their metabolism must comply with constraints studied by chemists.

An explanation consists, therefore, of 'mapping' a phenomenon observed by the practitioners of a given discipline onto constraints, rules, or 'laws' that are parts of an underlying discipline. For example, 'Bergmann's Rule' (Bergmann 1847) explains why high-latitude mammals and birds tend to have bigger bodies and shorter appendages (ears, limbs, tails) than their congeners in more temperate climes. It states that, while they generate heat in their bodies (a volume, which tends to grow according to length *cubed*), mammals and birds radiate (i.e., lose) heat through their body surface (proportional to length *squared*). Hence, increasing body weight and reducing the size of appendages through evolutionary time will reduce heat loss by reducing body surface per unit volume. Bergmann's Rule relies on consilience, specifically on facts of geometry and physics, to make a case concerning the biology of homeotherms.

The key feature of this type of explanation is that it avoids infinite regress: an observation is explained once it is mapped onto a more basic framework i.e., there is no need to map the basic framework onto an even more basic one. Thus, in the example above, there is no need for biologists to explain why heat loss is proportional to a surface – though it has been, for a while at least, a legitimate research question for physicists (Boltzmann 1884).

Parsimony is the requirement that an explanation should be 'small' relative to the 'size' of what needs to be explained (Dawkins 2006). Parsimony is another term for 'Ockham's razor', the rule that among competing hypotheses, the simplest one is (generally) to be favored (Kelly 2004).

The third requirement of a scientific explanation is that it must be non-local, i.e., it must not favor a privileged observer, or standpoint (Feynman 1985). For example, we should not project our homeotherm biases (notably our mammalian preoccupation with the food we require to maintain our elevated temperature) onto WBE, which require far less food, but to which the extraction of oxygen from their surrounding medium is a challenge that air-breathers often find difficult to imagine.

Finally, a successful hypothesis should not only explain the facts at hand, and map them parsimoniously onto the fabric of a more basic discipline, but it should also make successful predictions, i.e., make sense of facts that it was not designed to explain.

Some real issues with the GOLT

While the GOLT can obviously deal with objections that are beside the point (Table 8), there are several areas in which this theory is deficient. One of these issues is that the GOLT is still largely a qualitative theory, frequently unable to make quantitative predictions. For example, while the GOLT met the challenge posed by whale shark – the largest extant fish – occurring in warm tropical waters by evoking their yo-yo type "cooling dives" (Table 3, No. 3.2), it would at present provide no quantitative constraints for a model that could predict the duration of such dives as a function of whale shark size and depth-temperature gradients. Such a model could be tested using the data on whale sharks occurring in the Persian Gulf (which is both warm and shallow; Chao et al. 1992) and the Red Sea (whose deeper waters are very hot and briny; Swift et al. 2012).

At present, it can only be stated that the GOLT is not refuted by the presence of whale shark in these extreme environments, even though cooling dives are not possible because these whale sharks are juveniles and young adults below 10 m in the Gulf and below 7 m in the Red Sea (Berumen et al. 2014; Cochran et al. 2016; Rezzolla and Storai 2010; Robinson et al. 2017). Fully grown whale sharks, those assumed to require frequent cooling dives, are reported to exceed 18 m (McClain et al. 2015).

Another example is the experiment explicitly conducted by Kolding et al. (2008) as a test of the GOLT, which predicts that fish raised in (mildly) hypoxic conditions should reach maturity at a smaller size than fish raised in normoxia. The GOLT passed this test while alternative hypotheses did not (Kolding et al. 2008), but its prediction concerned only the type of response and not its strength.

Another deficiency of the GOLT is assuming that the WBE in question always get enough food to grow (i.e., the converse of most studies that deal with food limitation) but tacitly assuming the oxygen needed to turn ingested food into 'energy' is always available, and at no cost. This issue is obviously related to the investment required to produces ova and sperms by mature WBE, whose reproduction can be understood only by considering seasonal growth oscillations, a topic not considered here (but see Pauly 2019c).

Clearly, the GOLT will have to be assimilated into a bioenergetics model or vice versa. However, the intellectual effort this represents will be undertaken only if oxygen supply to the bodies of WBE is perceived as the constraint that it is, and hence this contribution.

The GOLT and Evolution

How a further elaboration of the GOLT would look cannot be anticipated, at least not by the author. However, such elaboration, if successful, may influence the way we view the evolutionary process. It may lead to a realization that evolution has two ways of handling challenges, depending on their nature. In the first, the challenge is met head-on by an adaptation (for example when its grazers neutralize a toxic substance in the leaves of a plant, or when a parasite gradually becomes a symbiont). In the second, the challenge (e.g., gravity, oxygen requirements, heat buildup) cannot be overcome by a metabolic or behavioral trick. In the latter case, all that can occur is what may be called a set of 'accommodations.'

The 'dimensional tension' (Pauly and Cheung 2017a) between the gill (or other respiratory) surface of a WBE and its body weight results in the accommodations that are made explicit by the GOLT. These should not be perceived as adaptations. Indeed, when the challenge posed by geometric or physical constraints cannot be accommodated, the corresponding region of morphological space remains unoccupied. This is why neither the huge spiders stalking Frodo and Sam in *Lord of the Rings* nor even beetle-shaped insects of more than 18 cm (Kaiser et al. 2007) can exist. As for fish, this is why the megatooth (*Megalodon*) could not reach more than twice the length of the great white shark (i.e., 20 m), implying a weight nearly 10 time greater, as claimed in a Discovery Channel 'documentary' film.

The GOLT requires that these two types of evolutionary challenges be recognized and distinguished, lest colleagues continue to believe that if fish suffer from warmer temperature and deoxygenation, they will just grow larger gills.

Table 8. Arguments raised against the GOLT: miscellaneous, mainly normative arguments

No	Arguments	Refutations
7.1	O'Dor and Hoar (2000) claimed that "*There is a fundamental flaw in examining Pauly's surface area limited growth scheme by plotting two different sets of units (m^2 and m^3) on the same graph and then making quantitative conclusions. Not only is [the resulting figure] messy, it violates a rule of physics and engineering (Vogel 1981)*". The rule alluded to here is probably: *"For an equation to have any applicability to the real world, not only must the two sides by numerically equal, but they must also be dimensionally equal"* (Vogel 1981, p. 6).	The GOLT involves no equation with dimensionally unequal sides. Its presentation, however, may include graphs with two ordinates axes with different units, as in figure 6.8, in Vogel (1981, p. 96), who therefore is not likely to have suggested that such figures violate the rules of physics and engineering. In fact, plots with two (or more) ordinate scales are common in science (see e.g., Crawley 2009, p. 868). The key issue, in any case, is that anything proportional to the 3rd power of length will outgrow anything that remains proportional to its 2nd power, whatever the units and the starting values (Figure 4b).
7.2	Lefevre et al. (2017) claimed that in Cheung et al. (2013a), the GOLT predicted a strong size reduction of fish with temperature because a key parameter was deliberately set too low (d = 0.7)	When the parameter in question was set at higher values (d = 0.8-0.9), the size reduction caused by increasing temperature actually *increased* (Pauly and Cheung 2018).
7.3	Ecophysiological arguments should not be used to explain physiological processes, as implied by the title of Jutfelt et al. (2018) which implicitly criticizes H.-O. Pörtner's 'Oxygen and Capacity Limited Temperature Tolerance' (OCLTT) hypothesis (which partly overlaps with the GOLT; Pörtner 2010; Pörtner et al. (2017, 2018).	No biological sub-discipline can assume *a priori* a monopoly in answering a specific scientific question. In fact, scientific problems are nowadays best tackled using interdisciplinary approaches (Ledford 2015). Pörtner et al. (2018) suggest that "*to connect closely to ecological changes, studies need to consider the long-term consequences of subtle functional constraints. […] Indeed, such requirements are rarely met in purely physiological studies*".
7.4	Jutfelt et al. (2018) suggest that H.-O. Pörtner's OCLTT hypothesis *"incorrectly [considers] aerobic scope or oxygen delivery capacity as the 'energy' available to animals, when in fact it is only a permissive factor compared with other constraints (e.g., food availability)"*.	Animals – including fish -- deprived of oxygen die within minutes. Also, the chemical energy embodied in their food becomes available to them only when that food is combined with oxygen, i.e., 'burnt'. Thus, considering oxygen to be one of several '*permissive*' factors of metabolism in order to score a few points against a colleague takes us back to the times before the discoveries of Lavoisier (1743-1784).
7.5	Here is another argument against H.-O. Pörtner's OCLTT hypothesis *"it is hard to imagine why animals would allow tissue hypoxia to become severe enough to inflict performance decline at moderate levels of activity when possessing the functional capacity to significantly increase oxygen delivery to tissues"* (Jutfelt et al. 2018).	That none of the 28 authors of Jutfelt et al. (2018) could imagine why animals can't operate all the time at peak performance is itself hard to imagine. However, it bears repeating here: peak performance extracts a massive toll on all organ systems and is used only to escape predators or life-threatening situations (Priede 1985; Pauly and Cheung 2017a). Repeated peak performance, as forced in experiments, renders the tested animals unfit for life in the wild.
7.6	Lefevre et al (2017) write: *"The idea that insurmountable geometric constraints on the size of the gills could determine the metabolic rate of fishes has never, as far as we know, been pursued as a valid hypothesis among respiratory physiologists. It is for example not mentioned in Schmidt-Nielsen or in Evans and Clairborne, two sources for overviews of animals and fish physiology.*	This meta-argument about the authority of textbooks such as Schmidt-Nielsen (1997) or Evans and Clairborne (2006) is a strange one to make in the 21st Century, though it could have been made in the Middle Ages with reference to species not mentioned in Aristotle's *Historia Animalium* (Thompson 1910) or in the writings of Plinius the Elder (Cotte 1944).

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Supplementary Materials

Relationships between W_m and W_i

Given:

$W_i = W_\infty \cdot (1-(D/b))^{b/D}$ ...(1)

$W_i / W_\infty = (1-(D/b))^{b/D}$ ... .(2)

$A^{-1} = (W_m{}^{1/b} / W_\infty{}^{1/b})^D$ (3)

$A^{-1} = (W_m / W_\infty)^{D/b}$ (4)

$W_m = W_\infty (1/A)^{b/D}$ (5)

By combining equation (2) and (5), we get

$W_i / W_m = (1-(D/b))^{b/D} / A^{-b/D}$ ...(6)

When $W_i > W_m$, we also have:

$(1-(D/b))^{b/D} > A^{-b/D}$ ....(7)

which implies

$(1-(D/b)) > A$ ...(8)

Given that $D = b \cdot (1-d)$, then:

$d > A^{-1}$ implies $W_i > W_m$

$d \approx A^{-1}$ implies $W_i \approx W_m$

$d < A^{-1}$ implies $W_i < W_m$

Derivation courtesy of Dr. Cui Liang,
Chinese Academy of Science, Qingdao, China

Table S1. Data on 34 fish species (f = female; m = males) used to infer the underlying relationship between their length at first maturity (L_m; cm) and their asymptotic length (L_∞; cm); 'a·100' is ; see Figure 5Ca)

No.	Species	L_m	L_∞	a·100	W_∞ (g)	Db)	L_m^D	L_∞^D	Source
1	*Clupea harengus*	24	30	0.75	203	0.73	10.2	12.0	B&H'59
2	*Clupea harengus*	28	34	0.75	295	0.71	10.7	12.2	B&H'59
3	*Clupea harengus*	25	34	0.75	295	0.71	9.83	12.2	B&H'59
5	*Coregonus clupeaformis*	27	50	1.7	2125	0.62	7.72	11.3	B&H'59
6	*Cottus gobio* (f)	5	6.5	1.55	4	0.91	4.33	5.49	B&H’59
8	*Cottus gobio* (f)	4.6	7.2	1.55	6	0.89	3.89	5.79	B&H'59
7	*Cottus gobio* (m)	5	6.5	1.55	4	0.91	4.33	5.49	B&H'59
9	*Cottus gobio* (m)	4.2	7.3	1.55	6	0.89	3.59	5.87	B&H'59
10	*Euthynnus affinis*	45	100	1.6	16000	0.53	7.52	11.5	M.'70
11	*Euthynnus alletteratus*	38	102	1.6	17000	0.52	6.63	11.1	B&H'59
12	*Gadus chalcogrammus*	31.2	55	0.8	1300	0.64	9.04	13	M.'70
13	*Gadus microcephalus*	55	94	1.3	11000	0.54	8.71	11.6	M.'70
14	*Gadus microcephalus*	60	105	1.3	15000	0.53	8.76	11.8	M.'70
15	*Gadus morhua*	85	134	0.85	20450	0.52	10.1	12.8	B&H'59
16	*Gadus morhua*	70	105	0.85	10000	0.55	10.3	12.9	M.'70
17	*Gasterosteus aculeatus*	3.6	6.7	1	3	0.93	3.29	5.86	B&H'59
18	*Hippocampus erectus*	7	14	0.5	14	0.85	5.23	9.42	B&H'59
19	*Hippocampus erectus*	2	2	0.5	0.04	1.13	2.19	2.19	B&H'59
20	*Hippoglossus hippoglossus* (f)	132	250	1.8	281250	0.39	6.71	8.61	B&H'59
21	*Hippoglossus hippoglossus* (m)	95	170	1.8	88434	0.45	7.76	10.1	B&H'59
22	*Katsuwonus pelamis*	46.5	106	2.6	31000	0.5	6.82	10.3	M.'70
23	*Katsuwonus pelamis*	70	180	2.5	140000	0.43	6.21	9.33	B&H'59
24	*Katsuwonus pelamis*	55	157	2.5	95000	0.45	6.07	9.73	B&H'59
25	*Labidesthes sicculus*	7	9.2	1.2	9	0.88	5.54	7.05	B&H'59
26	*Leuresthes tenuis* (f)	11.9	18.4	1	60	0.79	7.07	9.98	B&H'59
27	*Leuresthes tenuis* (m)	11	17.8	1	55	0.79	6.65	9.72	B&H'59
28p	*Limanda aspera*	23	50	1.2	1500	0.64	7.44	12.2	M.'70
29	*Melanogrammus aeglefinus*	26	60	0.75	890	0.66	8.59	14.9	B&H'59
30	*Merluccius merluccius* (f)	27	60	0.75	1620	0.63	7.98	13.2	B&H'59
31	*Merluccius merluccius* (m)	23	44	0.75	640	0.18	8.43	13.1	B&H'59
32	*Phoxinus phoxinus*	4	9	1.1	8	0.88	3.39	6.91	B&H'59
33	*Pleuronectes platessa*	48.5	68.5	1	3200	0.6	10.3	12.6	M.'70)
34	*Poecilia reticulata*	1.9	2.36	0.9	0.12	1.08	2.00	2.53	U.'69
35	*Poecilia reticulata* (m)	1.4	1.5	0.9	0.03	1.14	1.47	1.59	S.'43
36	*Pollachius virens*	71	107	0.95	11640	0.54	9.99	12.5	B&H'59
37	*Pseudopleuronectes americanus*	32	44	1.6	1365	0.64	9.19	11.3	B&H'59
38	*Pungitius pungitius*	3.7	4.3	0.5	0.4	1.02	3.8	4.43	B&H'59
39	*Rastrelliger brachysoma*	17	22	1.2	128	0.75	8.37	10.2	B&H'59
40	*Rheinhardtius hippoglossoides*	60	90	1.8	13000	0.54	9.12	11.4	M.'70

Table S1. (continued)

No.	Species	L_m	L_∞	a·100^b)	W_∞ (g)	$D^{c)}$	L_m^D	L_∞^D	Source
41	*Sardinops sagax*	18.5	26	1	176	0.74	8.66	11.1	B&H'59
42	*Scomber japonicus*	32	40	1	640	0.68	10.6	12.3	B&H'59
43	*Scomber japonicus*	30.5	46	1	975	0.66	9.54	12.5	B&H '59
44	*Sprattus sprattus*	13	16	0.7	29	0.82	8.19	9.71	B.'63
45	*Sprattus sprattus*	10.5	14	0.7	19	0.84	7.21	9.18	B.'63
46	*Sprattus sprattus*	9	12.5	0.7	14	0.85	6.47	8.56	B.'63
4	*Sprattusprattus*	10	13	0.7	15.4	0.85	7.08	8.85	B&H'59
47	*Thunnus alalunga*	90	124	1.9	36000	0.49	9.07	10.6	M.'70
48	*Thunnus alalunga*	89	136	1.9	48000	0.48	8.62	10.6	M.'70
49	*Thunnus alalunga*	86	160	1.6	65000	0.47	8.11	10.9	B&H '59
50	*Thunnus albacares*	100	190	1.6	110000	0.44	7.59	10.1	M. '70
51	*Thunnus maccoyii*	120	190	2	140000	0.43	7.84	9.55	M.'70
52	*Thunnus obesus*	95	180	2	120000	0.44	7.42	9.82	B&H'59
53	*Thunnus obesus*	92	170	2	100000	0.44	7.31	9.58	B&H'59
54	*Thunnus tonggol*	48	105	1.6	18500	0.52	7.49	11.2	B&H'59
55	*Trisoperus minutus* (f)	13	24	1	138	0.75	6.85	10.8	B&H'59
56	*Trisopterus minutus* (m)	11	20	1	80	0.77	6.34	10	B&H'59

a) Data used previously (Pauly 1984), but not publicly available;

b) The **a**-values refer to length-weight relationships of the form $W=\mathbf{a}\cdot L^3$;

c) The estimates of D stem from D = 3(1-d), with d = 0.6742+0.03574·log(W_∞); W_∞ in grams (Pauly 1981, 2019c)

d) B.'63 = Beverton (1963); B&H'59 = Beverton and Holt (1959); M.'70 = Mitani (1970); S.'43 = Svärson (1943); U.'69 = Ursin (1969)

RESPONSES TO REVIEWERS

Dear Editor,
Please find below my responses to the two generally positive reviews (*in italics*) that my original submission of 'The Gill-Oxygen Theory (GOLT) and its critics' received.

To facilitate your evaluation that I have taken the reviewers' comment seriously, I have added to the responses new line numbers to the line numbers in the original submission that were mentioned by the reviewers[22].

Cheers
Daniel Pauly

Reviewer: 1

> *1) General: This is an interesting article that makes several important points and contributes to the debate around size/growth relationships in fishes, especially as it relates to global warming. it provides a detailed, point by point refutation of an important hypothesis. The rebuttal is extremely thorough and detailed. As such, it makes important contributions to the literature.*

I thank the reviewer for this positive assessment.

> *2) However, I have a couple of serious concerns. First, the author ignores the blood side of the equation (literally and figuratively). This is exacerbated by the simplistic analogy of the gill as a page of paper in a book. In this analogy, the gills are static, and all that can change about the gills to improve gas exchange is to add more "pages".*

This is a misunderstanding. The analogy of gills (of rather gill lamellae) with pages in a book was not made by me, but by my critics (Lefevre et al. 2017, p. 3450), who argued that the surface area of the page of a book would increase in proportion of its volume (length x height x depth), that gills, which they claimed behave like the page of a book, could not be limiting oxygen supply. Thus, they wrote "*A simple way to explain the geometry of the gills is by analogy to a book, where pages correspond to lamellae. It is easy to grasp that if you double it's the thickness of a book (thereby doubling its volume and mass), you can fit in twice the number of pages and, therefore, the total surface area of the page is also doubled*".

As this was their only attempt at a coherent argument, I cannot avoid dealing with it, and deal with books as well, by pointing out that you can't read through a book, but that it must be open to be read and thus used. I have now rephrased this argument so it will hopefully be understood as their, not mine.

As for blood, the volume of blood in fish (and other animals that have blood) scales with the volume of their body, as stated in Schmidt-Nielsen's classic, which does not mention changes of blood volume during their ontogeny. Thus, blood is not a limiting factor for growth as defined here. The dimensional

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[22] The line numbers have been left here, although they do not appear in the above version of the article.

tension that is at the heart of the GOLT, moreover, must also apply to WBE which lack gills (despite the first letter of GOLT…) and blood (see also Point # 4).

> 3) *Nothing is said of how the gill could improve gas exchange performance by changing the pattern of perfusion of the lamellae (e.g. sending more or less blood to peripheral channels) or changing blood residence time by altering branchial blood flow.*

A sentence dealing with these two processes has been added between lines 184 and 185 (now lines 185-188). It states that neither of them scales such that they could offset the dimensional tension between the cumulative surface area of the gill lamellae and the volume of a growing fish (or another water-breathing ectotherm).

> *4) …nor is discussion made of longer-term performance changes by actually remodeling to reduce water-blood diffusion distance. To be fair, this has rarely been considered in the GOLT community. Yet, such changes could allow gas exchange to keep pace with body size, even though the morphometric values were not.*

Unfortunately, there is not yet a 'GOLT community' (though hopefully, there will be once this paper is published). Therefore, it is still up to me to argue that reducing the water-blood diffusion distance cannot reduced at will, and that such reduction wouldn't scale, even if it were possible (see line 209 [now 212] and also argument (3) above.

> *5) Second, and I admit up front that this is a matter of style rather than content, the author, in an effort to make his (reasonable) points, resorts to hyperbole and unfortunately uses words like "astonishing", "suspicious", "strange", "baffled", and "whimsical" to describe the actions and attitudes of those who oppose the GOLT. In doing so, he only undermines his own credibility.*

Agreed; these words were all replaced by less-charged terms. Thus, 'astonishing' was replaced by 'very questionable', 'suspicious' by 'unfortunate' (as suggested by this reviewer, see below), 'strange' by 'disconcerting', 'baffled' by 'surprised', and 'whimsical' by 'somehow'.

> *6) Specific Comments. Line 2. Title: Why emphasize only critics, excluding supporters?*

If the editor insists on a change of the title, I will have to go along. I would do so very reluctantly, however, because at present, the GOLT has fewer supporters than critics. I explain in the Introduction that I think the GOLT will be examined fairly (i.e., rigorously tested) only after scurrilous critiques are dealt with (which this article does). I assume that if it were published, the number of its supporters will begin to outgrow the critics.

> *7) Line 12. WBE not defined.*

Thanks for pointing out this oversight. This is now rectified in line 11 (now line 14).

> *8) Lines 22-33. This section is largely superfluous, and should be curtailed or eliminated. By defining what "this attitude" is in a phrase, the article could easily start on Line 34.*

Agreed; this section was curtailed, as suggested (see new line 25). Completely eliminating this section doesn't work because it introduces the concept of atheoretical '*ad hoc'* hypotheses which are a running theme in this article.

9) Lines 38. Not clear. Do you mean that the GOLT is being introduced to the readers who don't already know about it?

This article is meant to introduce the GOLT to colleagues what don't know it and re-introduce it to colleagues who may have casually dismissed it (see new line 38-39). I have slightly modified Line 38 to express this.

10) Lines 45. Discredit is a better than "knock down"

Agreed; changed as suggested (see new line 45).

11) Lines 53-55. This seems to me to be seriously overstated. How is the distribution of almost all marine fishes (or fishes in large lakes, for that matter) dependent on oxygen and (once below the surface waters) temperature? I suggest toning this down.

Here, I must respectfully disagree, as these lines can be seen as summarizing the whole paper. However, I should have cited here an important review of oxygen as a 'resources' which very much backs claim in Line 53-55 (see Kramer, D.L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes* 7: 47-55). This is now done (new line 53).

Line 158. Point III is a not an argument, as the points in the rest of the list, but rather a question. Rephrase.

Agreed; done (see new line 158).

12) Line 170-174. This is an interesting section, but it doesn't address certain aspects of gill remodeling – i.e. more lamellae (definitely not like pages of a book) or even a decrease in the water-blood diffusion distances. Moreover, it doesn't address the perfusion side. What about changes, especially increases, in the rate of blood flow and the residence time of RBCs in the lamellae themselves?

As explained above (Item 2), the book page analogy was not mine. Equation 6 in Line 202 (now line 205) includes the 3 factors which determine how much O_2 can diffuse through gill lamellae into the blood of fish, or through the integument of a small, gill-less WBE[23]. The water-blood distance (or the integument thickness) cannot continuously decline as the volume of a WBE increases. Accelerating the flow of blood through the gill lamellae would not help either, as the rate of O_2 diffusion is the limiting factor, and not the removal of the O_2 that has diffused through the lamellae. Thus, even if the venous O_2-free blood entering the gill were flowing at high speed through the gills (i.e., with a small residence time), this fast-flowing blood could still only pick up the oxygen that had diffused across the water-blood distance, and not more.

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[23] As, e.g., in the case of lancelets (Pauly and Chu 2021) [Note added in January 2021]

13) *Line 175-176. Ditch the analogy, which is weak at best.*

As stated above, the gill-lamellae-as-book-page analogy is not mine. It is however, the most serious attempt by others to refute the core tenet of the GOLT, based on a (flawed) dimensional argument. If I don't deal with it here (new line 175-179), it will continue to haunt all discussions about the GOLT.

14) *Line 188. Replace astonishing with another adjective.*

Agreed; done (new line 192).

15) *Line192. Replace "suspicious" with "unfortunate".*

Agree; done (new line 196).

16) *Line 259. Not only are larvae small representatives of the species, but they are physiologically different from adults, even deriving some gas exchange across their integument.*

Agreed; it is now stated (new line 264) that teleost larvae breathe through their integument, and a supporting reference was added.

17) *Line 281-287. You mention 4 sets of observation that contradicts the hypothesis. Given the importance of these, you should provide references for each of them.*

Each of these 4 set of observations is commented further below in one or more paragraphs that present the evidence for them (see new lines 297, 306, 319 and 374 for the start of the presentation of the evidence for each of the 4 sets of observations). The presentation of this evidence requires a context; simply adding references after each of the 4 sets wouldn't do them justice.

18) *Line 288-289. Aquarium fish can hardly be held up in any way as representative of broader populations. They don't breed for a myriad of reasons – type of food, photoperiod, temperature, density, etc. etc… and etc. You should be careful of criticizing authors who at least cite references while not similarly supporting your observations the same way.*

Agreed: aquarium fish may not spawn for a variety of reasons. However, the point that was made was not about the reasons they have not to spawn, but about the fact that they stop growing (i.e., reach a maximum size and maintain it) in spite of not having spawned. Given the high frequency of such occurrences (i.e., non-reproducing fish reaching a maximum size similar to that of reproducing fish despite food given to them *ad libitum*), we simply cannot maintain that it is spawning which limits the size of fish.

Two aquarium books are now cited (from the dozens that could be used for such purpose) which report maximum sizes reached in aquarium that are similar to the maximum size of the reproducing conspecifics in the wild. (See new lines 297-301).

> 19) *Line 445. You criticize by saying "no evidence if presented….". This places an additional burden upon the author to substantiate with references as many of his points as possible. (E.g. see my comment immediately above.)*

Agreed. The sentence starting with 'No evidence in presented…'was deleted because it was not a good argument to make (absence of evidence of not evidence is <u>really</u> not absence of evidence!). Also, the second argument is sufficient to counter the hypothesis in question (See new line 459-460). See response to Point 15 for the "comment immediately above".

> 20) *Line 497-503. This takes on the feel of being lectured at. I suggest softening.*

Agreed; this was rewritten in fewer words as a continuous sentence (new lines 510-512).

> *21) Figure 2. This figure seems gratuitous to me. What does this add other than fish farms are aerated? Of course they are. Delete figure.*

I agree to delete the figure, but very reluctantly, as I still thinks that confronting the readers with batteries of (undoubtedly costly) aerating devices would have helped them realize that fish farmers know something that biologists often do not seem to care about, i.e., that oxygen is really needed for growth. I have replaced the nice figure by two references, cause this argument must still be made (new line 148).

> *22) Table 2. "It is actually impossible, as any book on geometry will confirm, …" This subtle ad homonym*[24] *insult is complete unnecessary. In my opinion there is no place in scientific discourse for such an approach.*

Agreed; I have deleted the words 'as any book on geometry will confirm'.

Reviewer: 2

> *23) The gill oxygen limitation theory has been set up to explain body size limitations during growth in fish, relating it to gill surface area in relation to body size. The backbone is represented by the von Bertalanffy growth equation which has an empirical basis. What is appealing about the theory is its empirical logic, building on patterns observed.*

I thank the reviewer for this positive valuation; and yes, the GOLT relies on patterns in large data sets, for which explanations are presented.

> *24) Evidence is mostly indirect. In light of multiple components potentially contributing to oxygen limitations the link to gill surface area may just be correlative or represent one of several system components involved. Opponents have developed their own rationale why such reasoning focusing on gill surface area may not work. I will not go into who is right or wrong and focus on where I see gaps in the storyline of GOLT and where the narrative needs tightening.*

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[24] Here, I did not dare to mention that insults are never 'ad homonym', but rather *ad hominem*.

Agreed; when, as is attempted here, a theory such as the GOLT is to challenge (or overthrow) a set of explanations for various phenomena by another set of explanations thought to be more 'correct' (for lack of a better term), what one does (1) assemble correlative studies that are compatible with the new explanations, (2) hope that these new studies and their interpretation survive successive tests

> *25) What is missing on both sides of the argument is a step by step full traceability of the evidence. This leaves the impression of a debate on interpretation of empirical observations.*

This article is indeed part of "*a debate on interpretation of empirical observations*". A mountain of empirical observations on the growth, respiration distribution, behavior, etc. of fish and other water breathing ectotherms has been accumulated by diligent researchers in the last two centuries, and these observations have tended to be interpreted a certain way. I now propose to interpret these observations in a different way: through the GOLT. If colleagues accept that this new way of interpreting the evidence before us is plausible, they can subject the GOLT to more and more stringent tests. If the GOLT survives these tests, it will gradually seep into textbooks, then be used widely to interpret new empirical observations. If not, the present interpretations will continue to have currency, or a better set of hypotheses will emerge. This is how science progresses.

> *26) I fully share the call for a theoretical basis which should be at least somewhat unifying. However, acknowledging deficiencies, limitations and open questions should be part of this and need to be called out to allow the reader to evaluate limits to understanding, the confidence / uncertainties around any conclusions and to formulate open questions. The specific examples discussed (536 to 587) are somewhat illustrative but do not provide such insight to overcome the limits in understanding. In general, the text would need explanatory notes with full traceability to literature reporting underlying evidence.*

I could cite far more references supporting the various claims in this article. However, the number of references already cited exceeds by far the limit suggested in the guidelines of *Science Advances*. Thus, I cited my 2019 book on the GOLT for issues dealt therein at length, and which the present contribution need not duplicate.

> *27) While elegantly written this paper is full of assertive statements which would need to be amended / worded differently, e.g. 51 to 57 "…for water-breathing ectotherms (WBE, i.e., most fish and aquatic invertebrates), life is shaped more by the distribution and concentration of dissolved oxygen, and the temperature of the water surrounding them than by the availability of food, which is more important for endotherms (birds and mammals)" A physiologist would clearly say this differently as this comparison is simply inappropriate… Both groups need food and oxygen.*

Agreed, both groups need food and oxygen. However, the whole point of the GOLT and of this paper is that oxygen is far more difficult to extract from water than from air (due to the specific density and viscosity of the two media, and to the latter containing far more oxygen than the former). On the other hand, mammals and birds consume far more food per unit weight than WBE, except perhaps for tuna and some sharks, which can also maintain body temperatures above that of their surrounding medium.

As mentioned in Point 11 of Reviewer 1, I have added to the paragraph in question the reference to a review arguing that oxygen in fish should be treated as a ‘resource’ (like food) and which thus support my point (see new line 53).

> *28) As to the basis, 72 to 74: an increase of body mass (dw/dt) is the difference between body mass that is newly (Hw^d) synthesized and the body mass (kw) that becomes unusable…. The term unusable is not defined.*

Agreed; the term ‘unusable’ was replaced by ‘degraded (see new line 73)’ with ‘below’ refereeing to paragraphs immediately following.

> *29) 82 to 87: When looking at the energetic basis the paper essentially introduces an allometric exponent but does not discuss the related wider literature and open questions, as well as its value. The background of the allometric coefficient would be worth exploring, also associated energetic patterns which also relate to body size. Such allometric patterns are not only found in water breathers but across the animal kingdom.*

The article introduces a number of exponents, e.g., *d* in equation 1, or b in equation 3, can be isometric (e.g., when d = 2/3, or b =3) or allometric. For all the equations presented, the allometric cases is discussed along with the isometric case. Thus, unless the reviewer is asked to specify which ‘allometric coefficient’ is meant, I can’t respond to this comment.

> *30) 88 to 93: The description of protein denaturation is not up to speed with the literature.*

The description of denaturation (new lines 87-93) is not meant to be exhaustive. Rather, it only addresses the question whether the loss of the quaternary structure of proteins (which renders protein molecules ‘unusable’) requires ATP (and hence O_2) or not. Or put differently, it interprets denaturation as a two-step process: the first, i.e., the loss of quaternary configuration is spontaneous, requires no ‘energy’ input, and is temperature-dependent, while the second, i.e., the breakdown of molecules having lost their quaternary configuration requires ATP.

I have added to the references I originally provided the reference to a biochemistry text which support this two-step interpretation (28; D. L. Nelson, M. M. Cox, *Lehninger Principles of Biochemistry* (Freeman and Company, San Francisco, 7th edition, 2017).

> *31) Line 121: the exponent of the length-weight relationship is equal to 3…? so briefly, what is the explanation?*

The explanation is that when its exponent is 3, a fish or other WBE maintains the same relationships between its linear dimensions (length, height and depth), i.e., growth is isometric. When b < 3, growth is negative allometric (i.e., the WBE gets thinner); when b > 3, growth is positive allometric (i.e., the WBE gets thicker). The exponent b in fish differ between species and between their populations, and also seasonally. Overall, b has a bell-shaped distribution, with b = 3 as the mean and the mode. The reference cited to that effect (34; Froese 2006; new line 121) is the best of which I am aware.

> 32) *140 to 142: There is one statement which shows that GOLT is a first and useful but not sufficiently deep grinding approach to explaining the patterns observed: talking about …"massive challenges related to the respiration of WBE in an age of global warming, i.e., the accelerating deoxygenation of the oceans and freshwater bodies…" leading to the question whether and to what extent reduced oxygen solubility during warming is indeed a constraint at constant oxygen partial pressure. Verberk and Spicer would argue otherwise. This clearly has to be distinguished from a situation where oxygen partial pressure falls.*

Agreed: I also do not believe that the reduction of oxygen solubility with increasing water temperatures is the main problem facing water-breathing ectotherm (WBE). Rather, it is the fact that WBE are ectotherms whose oxygen requirements increase with temperature and their own size. This is the core of this paper and of the GOLT, which, however, must end somewhere. Thus, I can't elaborate here on the physics and chemistry of dissolved oxygen, and the deoxygenation of the ocean. I just show why WBE are so sensitive to it.

> 33) *214 to 223: I am supportive here but while I appreciate the effort of the author to counter the arguments of the opponents the question is what counts. Most empirical data clearly show an allometric exponent below 1 and this is what needs to be explained. If the opponents want to construct a hypothetical case, they can do so but should not confuse it with reality. The picture is complex and any one sentence explanation such as the one on glycolytic enzymes becoming more important will be insufficient and will need a wider context, e.g. considering mode of life of the growing adults as well as the allometric scaling of metabolic rate.*

The reason why the exponent d is below 1 in adult fishes and other WBE is that it pertains to a surface (S), and that surface, even when growing allometrically (i.e., S ∝ L^a, with a>2), d cannot come too close to 3 – because a surface can become a solid (i.e., S ∝ L^3) and function as a surface, e.g., for gas exchange.

> 34) *267 to 269 fully supported.*

Glad we agree on this – the cherry picking is annoying.

> 35) *327 to 328, 373: This is one of the cases where the paper operates with educated guesses: …. "more frequent occurrences of respiratory stress and hypercapnia." An allometric time series of the respective data would be needed for such statements to be made.*

Let's agree that these are at least well-educated guesses. The decline of weight-specific gill area with increasing weight is inescapable if d < 1. In any WBE, this must result in less O_2 being available, given equation 6. Another line of evidence is provided by the finding of Somero and Childress (1980), Norton et al. (2000) and Davis and Moyes (2007) whom I cite, and who showed, much to their expressed surprise, that the tissue of the larger specimens of a given species contain predominantly glycolytic enzymes (i.e., catalyzing reactions in the absence of O_2), while smaller specimens, contain predominantly oxidative enzymes (i.e., catalyzing reactions in the presence of O_2). This is the reason why Somero and Childress (1980) concluded that "*Limitation may derive from surface- volume relationships*", a theme that they did not pursue, but which is at the heart of the GOLT.

> 36) *328 to 330, ditto: "…assume, therefore, is the existence of a threshold weight (Wm) at which the high frequency of respiratory stress or hypercapnia events triggers the hormonal cascade that leads to maturation (79). Thus, one can define…." This comes across as a speculatory statement that needs to be tested by measurements of the actual process in relation to size threshold. This gap is glaring, especially, as this hypothesis has been repeated by the author for quite some time… Correlation with a certain fraction of maximum body size is quite natural to expect for different reasons but does not necessarily represent causation.*

We all agree that "*correlation […] does not necessarily represent causation*", or more precisely, that it is a necessary, but not a sufficient condition for causation. However, if a growing number of lines of correlative evidence keep pointing to the same relationship, there is a point the burden of proof must shift. The best example of this is the correlative evidence pointing to cigarettes as the cause for cancer, which became compelling long before the cellular mechanism was elucidated which explained, in agonizing details, how the tar from cigarette smoke affects the DNA of lung cells. Similarly, evolution through Darwinian natural selection became widely accepted before population genetic (not to mention genomics) provided the underlying mechanisms. Indeed, if this argument became a reason not to publish this article, there would be no reason for physiologists to search for the trigger of the hormonal cascade that the GOLT requires to exist.

> 37) *Fig. 5 does not present evidence for the hypothesis described.*

This must be a misunderstanding, as Figure 5 (now Figure 4) is the illustration of the section of "Fish growth vs. reproduction" (starting on new line 280), which is entirely devoted to presenting (and citing) the considerable evidence presented for that very figure. For what it is worth, however, I have added a few words and a citation to a paper just accepted in the *Journal of Fish Biology* which rigorously tested the hypothesis inherent in Figure 5C (new line 401).