



Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins

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ABSTRACT

This contribution presents time series of the ‘fishery biomass’ of fish populations, defined as the weight (whole-body, wet weight) of the in-water part of a fishable population, i.e., that part of a population (also called ‘stock’) that is exposed to fishing gears. Detailed data of this type are only available for a limited number of species that are targets of the fisheries in the waters of economically developed regions, such as Europe, the USA, Canada or Australia. However, similar fishery biomass assessments are generally lacking for developing countries, even for many of their most heavily fished species. Here, an estimation of the long-term fishery biomass trends of 1320 fish and invertebrate populations for 483 species exploited by fisheries in the 232 coastal Marine Ecoregions (MEs) around the world was undertaken. Fishery biomass trends were derived using the Bayesian CMSY stock assessment method applied to the global fisheries catch database for 1950–2014 as reconstructed by the *Sea Around Us* for every maritime fishing country in the world. Overall, the results suggest a consistent decline in the fishery biomass of exploited populations, in virtually all climatic zones and ocean basins in the world. The only zone with currently higher fishery biomass than in 1950 is the northern Pacific polar-boreal zone, likely due to environmental changes that occurred in the region positively affecting fish populations, combined with prudent management of the fisheries. For populations in MEs that are known to have highly questionable catch statistics, the results suggested smaller declines in fishery biomass than likely occurred in reality, implying that these results do not exaggerate declining trends in fishery biomass. This study used informative Bayesian priors to improve the trend analyses in areas where systematic stock assessments were conducted. The use of these independent assessments reduced the uncertainty associated with the findings of this study.

1. Introduction

Since at least the 1990s, there has been a widespread decline in marine populations, driven largely by fishing (Pauly et al., 2002) and reflected in a marked decline in global fisheries catches (Pauly and Zeller, 2016a). This crisis of fisheries really started in the 1880s with the deployment around the British Isles of steam trawlers, which were immensely more powerful than the rowed or sailed fishing vessels of the time. This led to these trawlers quickly exhausting the coastal resource around the British Isles and forcing them to move offshore into the open North Sea and later into the North Atlantic (Roberts, 2007). A similar expansion in terms of both power and geography occurred around the coasts of all industrialized countries to the extent that in 1902, the International Council for the Exploration of the Sea was founded to explore the decline of fish resources around European waters. Although temporarily halted by WWI and later WWII, this expansion of fishing from the waters of developed countries continued southward until the

1990s when new fishing grounds in the distant waters of developing countries, such as the Patagonian Shelf or the Sunda Shelf, ceased to be available for fisheries development (Swartz et al., 2010). Thus, since 1996, the world’s global catch is declining (Pauly and Zeller, 2016a).

This expansion went along with tremendous build-up in fishing effort (Tickler et al., 2018), and massive declines of fisheries biomass (Costello et al., 2016; Watson et al., 2013) defined as the weight (whole-body, wet weight) of the in-water part of fish (and invertebrate) populations that is vulnerable to fishing gears (henceforth referred to as ‘biomass’). This generally excludes the miniscule component represented by larval and small juvenile stages. This decline in biomass of demersal species went along with an often radical modification of the ecosystems and habitats in question. Notably, the large, long-lived high trophic level demersal species were depleted and replaced by smaller short-lived low trophic level species (Liang and Pauly, 2019, 2017; Stergiou and Tsikliras, 2011; Pauly and Palomares, 2005; Pauly et al., 1998; see also www.fishbase.org). Another fishery-induced change in marine ecosystems is the

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flattening of the sea floor caused by trawling, which has become a major geological force modifying the sea floor globally (Martin et al., 2014; Watling and Norse, 1998).

Fisheries for the non-demersal, large pelagic species (tunas, billfishes and sharks) are not affected by ecosystem and habitat impacts as demersal populations are. Nevertheless, many of these pelagic species are or have experienced overfishing and the associated strong declines in biomass. Juan-Jordá et al. (2011) found an average decline of nearly 60% across tunas over the 52-year period assessed. These declines, exacerbated by their so-called highly-migratory and straddling stock nature (UN, 1995) with extensive presence in waters beyond national jurisdiction, i.e., the High Seas (UN, 1982), showed that most of the various Regional Fisheries Management Organizations with management responsibilities for large pelagic fisheries did not perform their given tasks very well (Cullis-Suzuki and Pauly, 2010, 2016). Recent studies suggest pathways for improvements in management, which should be driven by clearly set and agreed total allowable annual catch limits accompanied by strong enforcement (Pons et al., 2017, 2018). For many countries, especially in the developing world, this may remain a substantial financial challenge to implement.

There are numerous estimates of biomass in different ecosystems (for example, Whitfield, 2016). However, detailed stock assessments are available for only a few species that are major fisheries targets in the waters of developed regions (as in Europe, the USA, Canada or Australia). This was most recently highlighted for Australia by Edgar et al. (2018, 2019), including a lack of appropriate data for harmonising ecological and fisheries assessments.

There are many reasons for the scarcity of stock assessments in the waters of developing countries, notably: (1) a long-standing lack of local technical expertise, slowly alleviated through dedicated stock assessment training workshops (Palomares and Froese, 2017; Venema et al., 1988); (2) the frequently cited “lack of data”; and (3) until recently, a dearth of methods to generate preliminary biomass time series with the limited data that are available in most regions of the world. Issue (1) remains a real problem, particularly for the developing world which in recent decades has seen the most pressure on fish populations due to fishing (Alder and Sumaila, 2004; Atta-Mills et al., 2004; Pauly and Zeller, 2016a). However, issues (2) and (3) have been increasingly mitigated over the last two decades, by addressing the perceived “lack of data” through comprehensive reconstructions (Zeller et al., 2016) of global marine fisheries catch data (Pauly and Zeller, 2016a, Pauly and Zeller, 2016b), and the development and refinement of relatively easily understood but computer-intensive methods relying mainly on fisheries catch time series to estimate biomass trends over time (Froese et al., 2017; ICES, 2014, 2015; Martell and Froese, 2013; Rosenberg et al., 2014).

The data reconstruction process for marine catch data of the *Sea Around Us*¹ correct several of the challenges associated with the global fisheries landings database disseminated by the Food and Agriculture Organization of the United Nations (FAO), which is largely based on data submissions by its member countries (Pauly and Zeller, 2016b). Notably, the reconstructed catch data complement officially reported data on landed catches with comprehensive time series estimates of catches and discards (Zeller et al., 2018) that are not included in the national data reported by individual countries to the FAO. Also, *Sea Around Us* data distinguish between the four major fishing sectors: industrial, artisanal, subsistence, and recreational (Zeller et al., 2016). At present, the reconstructed catch data of the *Sea Around Us* that complements the data provided by FAO on behalf of member countries cover 1950 to 2014, with data updates to 2018 currently in progress. These data illustrate that global marine catches peaked in the mid-1990s and have been on a consistent declining trend ever since (Pauly and Zeller, 2016a). Some of these reconstructions (see for example, Al-Abdulrazzak

and Pauly, 2014b; Belhabib et al., 2014) received some critical comments (Chaboud et al., 2015; Garibaldi et al., 2014) that were subsequently refuted (Al-Abdulrazzak and Pauly, 2014; Belhabib et al., 2015). Overall, however, the declining global catches have now been confirmed by the FAO (FAO, 2018), after some initial reservations (Pauly and Zeller, 2017a, Pauly and Zeller, 2017b; Ye et al., 2017).

Perhaps most importantly, these reconstructed catch data are spatially allocated to ocean space at an ecologically relevant scale (Palomares et al., 2016; Zeller et al., 2016). This spatial allocation process allows marine catches to be assigned to spatial entities much smaller than the 19 very large, and ecologically uninformative Statistical Areas that FAO uses to report their marine landings data. For example, FAO Statistical Area 57, the ‘Eastern Indian Ocean’, ranges from Bangladesh in the North to the Antarctic Convergence in the South. Thus, due to its ecologically meaningful spatial allocation to smaller spatial units, *Sea Around Us* data can be readily assigned, for instance, to the 64 defined Large Marine Ecosystems (NOAA, 2018; Pauly et al., 2008; Sherman and Duda, 1999) or the 232 Marine Ecoregions identified by Spalding et al. (2007).

Marine Ecoregions (often referred to as MEOW, Spalding et al., 2007; but here labelled as MEs) are defined as ocean areas which cover coastal and continental shelf waters to 200 m depth, and are driven by biogeographic assessments of the benthos and overlying water column. Marine Ecoregions roughly correspond to our general understanding of ecosystems (communities of plants, animals and other living organisms), which, along with the non-living components of their environment, can be found in particular habitats and which interact with each other. Given their ecological representativeness and their utility for conservation efforts (Halpern et al., 2008; Spalding et al., 2007), MEs can serve as generalized ‘spatial units’ for the assessment of biomass trends for the major exploited fish and invertebrate populations in the coastal and shelf waters in each climatic zone around the world (Fig. 1). Marine Ecoregions do not necessarily overlap with all distinct populations of exploited species, but the ecology-based geography MEs provide are more realistic at the global scale, especially when grouped to account for ‘straddling’ and highly-migratory fish populations (UN, 1995). This is especially so compared to the ecologically arbitrary political boundary-based spatial entities of Exclusive Economic Zones or EEZs (Pauly and Zeller, 2016a), the considerably larger Large Marine Ecosystems concept (Pauly et al., 2008; Sherman and Duda, 1999; Sherman and Hempel, 2008), or the extremely large and ecologically artificial FAO Statistical Areas used for some global fisheries stock assessments (see for example, Costello et al., 2012). Note that, here, stock assessment is defined as the estimation of fishery biomass trends to provide reference points for fisheries management (see Haddon, 2001).

Global climatic zones are defined by a variety of factors that may include annual average temperature and temperature ranges, sunlight hours, rainfall volumes and seasonal variations therein, and more. These factors are generally heavily influenced by the latitudinal location of a given area. Ocean climatic zones are roughly parallel to the zones of sea surface temperatures, although they may be influenced or modified by major ocean circulation and prevailing ocean current patterns. Water temperature, a main determinant of climatic zones, is also a major species distribution factor, which determines and influences the species composition and hence biodiversity patterns in the ocean. Various such climatic classification systems exist, but most match closely in their general boundary locations. Here we follow the ocean climatic zones as described and presented in Anonymous (1991), but simplified it by combining the sub-polar (boreal) and polar zones into single polar zones in each hemisphere (Fig. 1). We also use a single tropical zone, which combines the equatorial and the northern and southern tropical zones distinguished in some other schemes (see for example, The Trustees of Indiana University, 1999–2007).

We here present long-term biomass trend estimates for major exploited populations of fishes and invertebrates by MEs, climatic zones and ocean basins. These biomass trends are presented as changes

¹ All *Sea Around Us* data are freely available from www.seaaroundus.org.

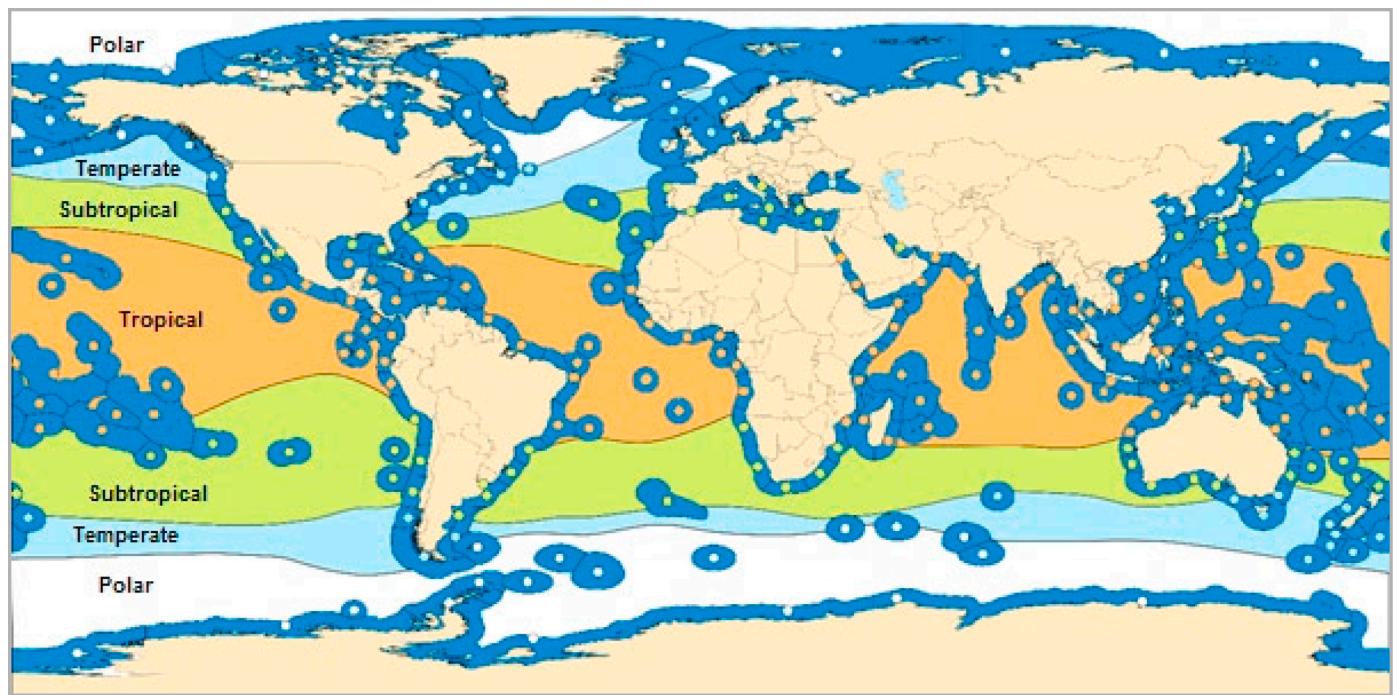


Fig. 1. The global system of Marine Ecoregions (ME in dark blue, Spalding et al., 2007) overlaid over climatic zones of the world (Anonymous, 1991). Centroid colour in each ME indicates the climatic zone to which each ME was assigned. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

relative to biomass levels in 1950 (i.e., at the start time of global fisheries catch data reporting) and were derived using a population biomass estimation method borrowed from fisheries science (i.e., a 'stock assessment' method). This method was applied to fish and invertebrate populations that have species-level fisheries catch data by MEs. The analysis includes so-called 'straddling stocks' that may spend part of their life cycle outside ME areas.

2. Methods

2.1. Standardized underlying data

The most widely available fisheries data with the most comprehensive temporal (since 1950) and global spatial coverage for estimating biomass trends for the major exploited species are fisheries catch data in whole-body, wet-weight (FAO, 1948, 2018; Garibaldi, 2012). The catch time series data used for the present study are based on FAO data, restructured and complemented through a procedure called 'catch reconstruction' documented in Zeller et al. (2007, 2016). These catch data reconstructions were largely performed through over 200 individual studies documenting the catch data reconstructions in 273 EEZs or parts thereof (Pauly and Zeller, 2016b). These reconstructions were documented individually either as technical reports (summarized in Part II of Pauly and Zeller, 2016b) or in well over 100 peer-reviewed scientific papers (e.g., Abudaya et al., 2013; Ainley and Pauly, 2014; Cashion et al., 2018; Derrick et al., 2017; Freire et al., 2020; Khalfallah et al., 2016; Piroddi et al., 2015; Popov and Zeller, 2018; Seto et al., 2017; Vianna et al., 2020; Zeller et al., 2011a; Zeller et al., 2015; Zeller et al., 2011b), and are all freely available, as are the associated data via www.seaaroundus.org.

The difference between reconstructed catch data and officially reported landings data, i.e., as reported by the FAO on behalf of member countries, can be substantial. For example, small island states in the Pacific emphasize their industrial tuna catches, but neglect to comprehensively document and report catches of nearshore reef fisheries for artisanal and subsistence purposes, which contribute substantially to

their food security (Vianna et al., 2020; White et al., 2018; Zeller et al., 2015). Recreational fisheries catches, despite being requested by FAO for inclusion in country data reports (Garibaldi, 2012), are also commonly absent from reported catch statistics (Freire et al., 2020).

In addition to accounting comprehensively for otherwise under- and unreported catches, both landed and discarded catches (Zeller et al., 2018), all reconstructed catch data are spatially allocated, i.e., they are distributed to 150,000 $\frac{1}{2}$ degree latitude x $\frac{1}{2}$ degree longitude ice-free grid cells, with the allocation accounting for the biological distribution of each taxon in the data (Palomares et al., 2016) as well as the access fishing countries may have to waters of other countries (Zeller et al., 2016). This spatial allocation of global catches to ecologically and politically relevant grid cells permits the examination and analysis of catches at a large variety of spatial scales and geographic frameworks. These grid cell level catch data can, therefore, be assembled and analyzed at geographic scales of, e.g., EEZs, Large Marine Ecosystems (LME; Pauly et al., 2008; Sherman and Hempel, 2008) or Marine Ecoregions (ME) as used here. Thus, the spatial allocation of the *Sea Around Us* reconstructed catch data facilitates ecosystem- and population-scale assessments.

The current version of the *Sea Around Us* reconstructed catch database contains catch data in total wet-weight tonnes for over 3300 taxonomic entities, of which 1446 are species. For purposes of the present biomass trend estimation, only reconstructed catch data that were disaggregated to the species level were used. These species-level data account for approximately half of all global catches, and thus the present biomass trend evaluation represents a substantial proportion of the most heavily impacted populations of marine fishes and invertebrates around the world.

2.2. Marine Ecoregions

Marine Ecoregions (MEs) are biogeographic entities along the world's continental shelves and coasts (Spalding et al., 2007), and geographic data and GIS shapefiles for MEs are available from a joint WWF/Nature Conservancy project (http://maps.tnc.org/gis_data.html).

Marine Ecoregions have clearly defined boundaries and definitions, and are smaller and more numerous than Large Marine Ecosystems, the other widely used marine ecosystem classification (Sherman and Duda, 1999; Sherman and Hempel, 2008). Marine Ecoregions were derived to represent and spatially group ecological patterns of species and communities in the ocean. They serve as a tool for conservation planning worldwide (Spalding et al., 2007), and are ideally suited for ecologically driven evaluations of biomass trends for populations impacted by fisheries. In order to maintain internal consistency in the global spatial data system of the *Sea Around Us*, some ME boundaries were modified to better correspond to existing EEZ boundaries, which represent the political control, resource ownership and hence impact on exploited marine fish and invertebrate populations that are reflected in the catch data (Zeller et al., 2016). Thus, the ME boundaries as used in the present study (Fig. 1) differ only slightly, if at all, from the ME shapefiles available from WWF/Nature Conservancy (http://maps.tnc.org/gis_data.html). The very small differences in the ME boundaries are mainly due to different map projections used by the Geographic Information System being used.

These MEs were then assigned to major ocean climatic zones (Anonymous, 1991) and can be grouped by ocean basins (Fig. 1). In cases where a given ME 'straddles' two climatic zones, the ME was assigned to that climatic zone where most of its area is found. In cases where this area-based definition could not be applied, the climatic zone was determined using the centroid of the ME (Fig. 1). These geographic groupings (ocean basin and climatic zone) were used to group the results of the biomass trend assessments that were undertaken at the scale of MEs.

The presently available ME system focuses on coast and shelf areas and does not consider open-ocean pelagic or deep-ocean benthic environments. The *Sea Around Us* anticipates that parallel but distinct systems for pelagic and deep benthic biotas can be integrated and assessed in the future, likely leaning on the Pelagic Provinces concept of Spalding et al. (2012), and/or the biochemical provinces of Longhurst (1998, 2007).

2.3. Climatic zones

We grouped the marine ecoregions described above into seven climate zones (Polar/Boreal, N. Temperate, N. Subtropical, Tropical, S. Subtropical, S. Temperate, Antarctic) drawn from Anonymous (1991) mainly on the basis of temperature regimes. The areas of these climate zones largely overlap with the robust marine ecosystem clusters derived by Zhao et al. (2019) based on 19 environmental variables distributed over 5.7 million valid spatial cells.

2.4. Biomass trend assessment: the CMSY method

In traditional fisheries science, the term 'stock' has long been used for a population of exploited fish. However, there is a gradual recognition among many fisheries scientists that fish are not only a commodity of which we 'take stock' (hence the term 'stock'), but actually wild animals, which have 'agency', i.e., they do things. Therefore, as we would never talk about the 'stock' of deer in a given forest, we should abandon the word 'stock' for populations of fish as well. Here, we refer to populations instead of 'stocks', except in established expressions used in fisheries science. For the purposes of fisheries 'stock assessments' to derive biomass trends for populations of species that are exploited by fisheries, the 'stock' or exploited population is defined as that part of the total biological/ecological population *in situ*, i.e., in the water body, that is vulnerable to the fishing gears used and hence potentially exposed to fisheries exploitation. Thus, larval stages and small juvenile stages that are too small to be captured and retained by the fishing gear are excluded from the concept of exploited population for the purposes of fisheries 'stock assessment' biomass estimations derived here. Hence our use of 'fishery biomass', or simply 'biomass' which we treat as

synonymous with the fisheries 'stock' term. The 'biomass' or tonnage of the exploited population that is actually caught and killed by the fishing gear is referred to as catch.

To derive biomass trend data for 1950–2014 from the global reconstructed catch data as allocated to MEs, we used the now well-established data-limited Bayesian CMSY method of fisheries 'stock assessment', an earlier version of this method was first proposed as 'Catch-MSY' method by Martell and Froese (2013), but it has been further operationalized and refined in Froese et al. (2017) and applied, e.g., for European 'stocks' (Froese et al., 2018). The Bayesian CMSY approach has been independently evaluated by FAO (Rosenberg et al., 2014) based on the earlier Martell and Froese (2013) version, and described as "...overall best performer..." and especially "...suitable for fisheries in developing countries..." among the data-limited 'stock' assessment methods that were evaluated. Since Froese et al. (2017), this method has been continuously updated and improved, and is now available as CMSY+ (Froese et al., 2019).

To test the robustness and reliability of the CMSY method, Froese et al. (2017, 2018) included a large number of analytical comparisons between the results obtained by the CMSY method and independent, traditional 'stock' assessments conducted by other fisheries scientists. These comparisons showed clearly that the CMSY method works well and its results are robust and reliable.

Like the Maximum Sustainable Yield (MSY) concept from which its name is derived, the CMSY method is based on an approach initially formulated by Schaefer (1954, 1957, see Fig. S1) to describe, generalize and understand fish population dynamics in a fisheries context. This approach, also known as 'surplus-production' modeling among fisheries scientists, assumes that a given ecosystem has, for any animal population, a specific average carrying capacity (k , usually set equal to unfished biomass), and that if the biomass of this population is reduced through an external event (e.g., fishing), the population will tend to grow back towards its carrying capacity. Thus, there is always a relationship between biological production or population biomass growth and fishery yield or catch (Schaefer, 1957).

Herein, population growth will be determined by the attributes of the individuals of the population in question (individual growth rate, age at first maturity, natural mortality, fecundity, etc.), and by the current biomass (B) of the population. Thus, the biomass of a very small population cannot grow by a large amount, even if its growth rate is relatively high, and neither will a population that is near its carrying capacity k , because in this case, growth is close to zero (Fig. S1). In other words, the maximum population growth rate occurs at the intermediate biomass level of $k/2$ or half the unfished biomass. Note that the decline in population growth rate at high levels of biomass is not necessarily caused by density dependence of adults, but of recruits (due to a 'hockey stick' stock-recruitment curve, Barrowman and Myers, 2000). Therefore, at carrying capacity or unfished biomass levels k , loss of adult biomass due to natural mortality (as by definition for k there is no fishing) is replaced by recruit biomass, and thus recruit biomass and adult natural mortality (M) determine k . We follow the convention in the ecological literature to use r for maximum population growth rate.

Thus, human extraction of parts of the population biomass as catch via a fishery can in principle maintain a given population at any given biomass level, by removing from it, every year, as catch, an amount equivalent to the natural growth of that population. The CMSY fisheries stock assessment method is built on this conceptual framework. It essentially consists of tracing, for any given exploited population, multiple trajectories of its likely biomass time series and identifying those trajectories that remain viable while accommodating the catches taken from this population over this time period and a few other constraints (Froese et al., 2017). Here, 'remaining viable' means a population that is not going extinct because catches are excessive, given a pair of k and r values. The constraints (or 'priors' in Bayesian terminology) are the assumed biomass reductions caused by fishing, a range for the carrying capacity (k) for the species under study in the ME in question, and a

range of likely values of r , the species maximum intrinsic rate of population growth (see Fig. S2). Qualitative measures of r , i.e., resilience (as defined in Musick, 1999; and refined in Musick et al., 2000), were taken from FishBase (www.fishbase.org) for finfishes and from SeaLifeBase (www.sealifebase.org) for invertebrates. For most exploited species, FishBase also provides r priors from a range of biological parameters, especially natural mortality (M , year⁻¹), the von Bertalanffy growth parameter K (year⁻¹), generation time, maximum age, and fecundity.

For practical applications, the CMSY method amounts to producing a multitude of potential biomass trajectories, given a catch time series and a large range of paired growth rate–carrying capacity (r and k) estimates. The method then identifies the mean of the r and k value pairs that produce the most likely biomass trajectories, or viable trajectories (trajectories excluding population collapses) which also comply with any constraints on relative biomass (e.g., a substantial decline) on the terminal exploited population biomass (Froese et al., 2017).

Constraints must also be provided about the likely reduction of population biomass by fishing from carrying capacity (in % relative to k) at the start of the time series, here usually 1950, or the year when the fishery was opened if that is known. This applies, for example, in the case of various populations of orange roughy, *Hoplostethus atlanticus*, which began to be exploited only in the 1970s. We recognize that there are many fish stocks, e.g., around the North Atlantic, that have been strongly fished prior to 1950.

Such independent knowledge about relative population depletion can be obtained from general knowledge about a given fishery (“good”, “not as good as it used to be”, “bad”, “very bad”; see Table 1) and is translated into very wide percentage or fractional ranges relative to carrying capacity (k). For example, for a “good” terminal biomass we assigned 0.8–0.9· k , i.e., 80%–90% of the unfished biomass level k , while for “bad” we assigned 0.2–0.4· k .

The version of the CMSY model used here (Froese et al., 2017) also implements a Bayesian version of the full Schaefer surplus-production model (BSM; Schaefer, 1954, 1957), which uses pre-existing and independently derived time series of relative population biomass, e.g., based on catch per unit of fishing effort (CPUE) data from official fisheries stock assessments when available. This typically results in narrower and thus better estimates of changes in population biomass trends over time in the current assessments. See Table S1 for a summary of the assessments in each ME.

3. Results

The *Sea Around Us* reconstructed catch data for 1950–2014, disaggregated to species level accounts for 1446 species, which when categorized by the 232 MEs, make up 19,278 ME-populations. In this analysis, we only considered those populations within each ME that:

- 1) Had total catches that consisted to <20% of discarded catch; as discard data are often more poorly documented over time than landed catch and therefore result in uninformative time series (remaining $n = 17,229$ populations); and
- 2) Did not have catch data sets that were deemed to be highly uncertain and will require more in-depth review before they can be assessed (remaining $n = 11,966$ populations).

Table 1

Categories of the state of a fished population and corresponding ranges of carrying capacity (B/k ; percent). Note that healthy unfished populations would require B/k at 100%.

Relative state of the population	B/k assigned (%)
Good	80–90
Not as good as it used to be	40–80
Bad	20–40
Very bad	1–20

- 3) Cumulatively accounted for the top 90% of the total catch reported at the species level within each ME (remaining $n = 1320$ populations; 483 species).

All individual ‘stock assessments’ for each population in each ME are presented and can be accessed for each ME at www.seaaroundus.org. The populations we analyzed here mostly occur in the tropical (60%), northern subtropical (18%) and northern temperate zones (13%; Fig. 2). The least number of populations analyzed were from the southern and northern polar zones and the southern subtropical and temperate zones, all together representing the remaining 9%.

The last five-year averages (2010–2014) of current fishery exploited population biomass (B) relative to the biomass deemed optimal for achieving Maximum Sustainable Yield (B_{MSY}) for all the assessed populations suggest that only 18% of all the assessed populations might be deemed ‘healthy’, with exploited population biomass values above the level deemed optimal for maximum sustainable fisheries yield (Fig. 3). The rest of the populations, i.e., 82% of all assessed populations, are in various states of depletion relative to the biomass levels with regards to maximizing sustainable fisheries yield (i.e., B/B_{MSY} below 1.0 in Fig. 3), with slightly more than 8% of these populations currently in the “very bad” category with population biomass levels less than 20% of the level that might maximize sustainable fisheries catches.

The time-series of population biomass estimates resulting from the CMSY analyses were expressed as a percentage of the average total biomass of all assessed populations by climatic zone in each ocean basin at the start of the time series, i.e., the assumed unexploited or largely unexploited population biomass level (Fig. 4). These results suggest an overall declining trend across all oceans and climatic zones except two. The exceptions are the northern polar and temperate zones of the Pacific Ocean, with population biomass increases of about 800% and 150% since 1950, respectively (Fig. 4). For the other climatic zones, the declines in fishable population biomass range from about 50% in the southern polar Pacific Ocean and the northern temperate and subtropical Atlantic Ocean to about 10% in the southern polar Atlantic Ocean and in the southern temperate and polar Indian Ocean. While declines in population biomass of around 50% may be taken to represent biomass levels optimal for maximizing fisheries catch from the underlying populations, the fact that at least 10 of the 18 climatic zone-ocean basin groupings had average biomass declines well below 50% is reason for concern (Fig. 4).

4. Discussion

This contribution is the first global study of long-term trends (generally 50–60+ years) in the population biomass of exploited marine

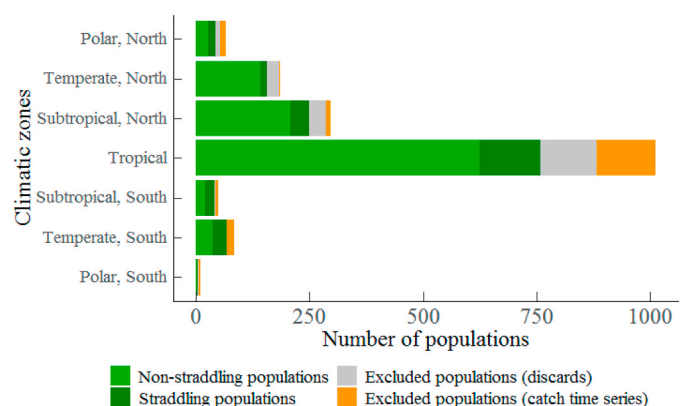


Fig. 2. Summary by climatic zone of the number of populations analyzed and the number of populations excluded from this analysis due to uncertainties in the underlying catch data or because more than 20% of the catch consisted of poorly monitored discards.

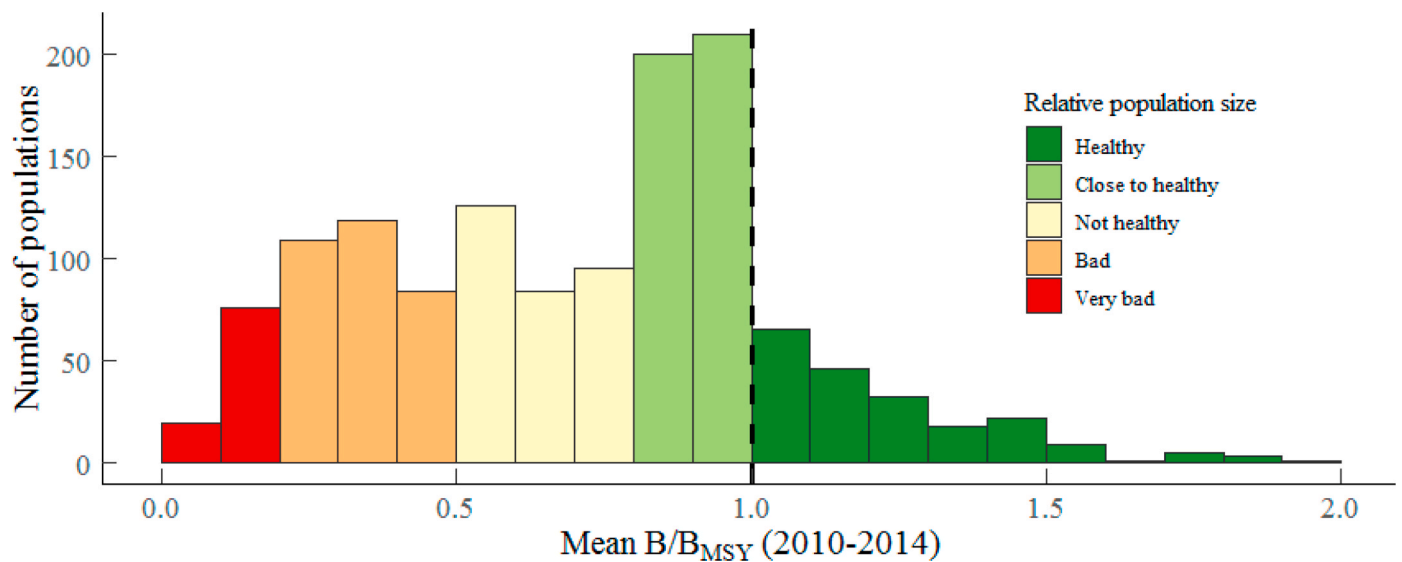


Fig. 3. Frequency distribution of the average fishery exploited population biomass status (B) over the most recent five-year period (2010–2014) relative to the optimal biomass level for Maximum Sustainable Yield (B_{MSY}) for the 1320 populations analyzed in this study.

fish and invertebrates for all coastal areas in the world, based on an established and tested data-limited biomass assessment method borrowed from fisheries science. Our results corroborate analyses conducted using other methods for estimating biomass of exploited populations with more limited spatial and population coverage. Thus, the general decline in biomass of exploited marine species reported by Myers and Worm (2003) was previously confirmed by a variety of studies using various approaches. For example, Tremblay-Boyer et al. (2011) used a global application of the EcoTroph model (Gascuel et al., 2011), Watson et al. (2013) used general catch/effort data, Christensen et al. (2014) used an array of Ecopath models, Costello et al. (2016) relied on the RAM Legacy Stock Assessment Database, and Ricard et al. (2012) used a method roughly similar to CMSY applied to the database of landings compiled and disseminated by FAO.

However, the present study is the first comprehensive evaluation of global biomass trends of exploited marine species based on a large number ($n = 1320$) of independent, individual single-species ‘stock’ assessments. The overall trends presented here for assessed populations can be assumed to be representative of the overall biomass trends of marine species targeted or affected by fishing.

There are some studies that suggest that fisheries sustainability, and hence population biomass trends seem to be improving worldwide (e.g., Worm et al., 2009). One needs to consider, however, that Worm et al. (2009), despite its title, was not a global study, but rather heavily biased by data and examples from a limited number of areas around the world (i.e., case studies) with near exclusive emphasis on data and examples from developed countries. This was clearly demonstrated in Fig. 2 in Pauly and Zeller, 2017a. A subsequent study by Costello et al. (2016), in which the “developing” or emerging economies in Asia, Africa and South America were better represented, correctly identified a globally declining trend of exploited biomass, i.e., global fisheries have not improved in sustainability. This demonstrates clearly that global studies on fisheries must be based on comprehensive representation of world fisheries, and not be based on a likely biased set of case studies from richer and likely well managed countries only. The effort to assess fisheries trends globally is also reflected in Hilborn et al. (2020) which argues that abundance is increasing in jurisdictions with effective management. However, their analysis based on the RAM global legacy dataset still excludes the vast majority of Asia and Africa, as well as ignoring the data on the expansion of fisheries into poorly regulated jurisdictions (Tickler et al., 2018). That much of the world’s catch from and in developing countries are ignored undermines the argument that

the world’s fisheries are recovering.

A similar point relates to studies that are regionally limited, and therefore cannot be viewed as representative of global conditions. For example, Fernandes and Cook (2013) and Zimmermann and Werner (2019) present the case that biomass declines of fished populations have been or are being reversed in the North East Atlantic due to improved management of fisheries. Both these studies support a clear point, namely that in some areas the status of some exploited populations seem indeed to be improving, in large part due to more effective management actions. This is also clearly illustrated by our results (Fig. 4, middle column top two panels), where the population biomass status in the Polar North Atlantic and Temperate North Atlantic are indeed showing an uptick in the last decade, which is good news if this trend continues. However, in a study on the status of European fisheries, Froese et al. (2018) recently demonstrated that nearly 70% of the stocks assessed in Europe were still subject to overfishing and half of these stocks were outside of safe biological limits. Thus, even though progress seems to be made in Europe and the North East Atlantic, even the highly developed and managed fisheries in Europe continue to have substantial overfishing and overfished stock problems.

Climatic zones are key to understanding the ecology of marine species because of the massive difference between cold and warm climate. When temperatures are low, the dead phytoplankton sinks as marine snow (mainly as dead phytoplankton cells and as part of zooplankton fecal pellets) through the water column onto the sea floor and thus maintains, even at great depth, an abundant marine macrobenthos that serves as the food of bottom fish. Thus, in cold climates, fisheries exploit predominantly demersal fish, even at great depths and far from the coast (Ursin, 1984). In contrast, in tropical regions, the higher temperatures allow bacteria to degrade marine snow within the photic zone and very little of it reaches the deeper sea floor. Thus, most fish biomass tends to be small-pelagic and high biomass are achieved mainly near coastal areas (Longhurst and Pauly, 1987; Ursin, 1984).

The differentiation by climatic zones and ocean basins undertaken here enabled the identification of an area of the world, the far North Pacific (temperate and polar), which differs from the global declining trend in population biomass. In contrast, it is characterized by strong increases of biomass, mainly of Alaska pollock, *Theragra chalcogramma* (recently renamed *Gadus chalcogrammus*). This is a major fisheries target species and is well managed, at least in US waters, but is also very sensitive to environmental changes (Ciannelli et al., 2005).

The other region of the world where the trend is not exclusively one

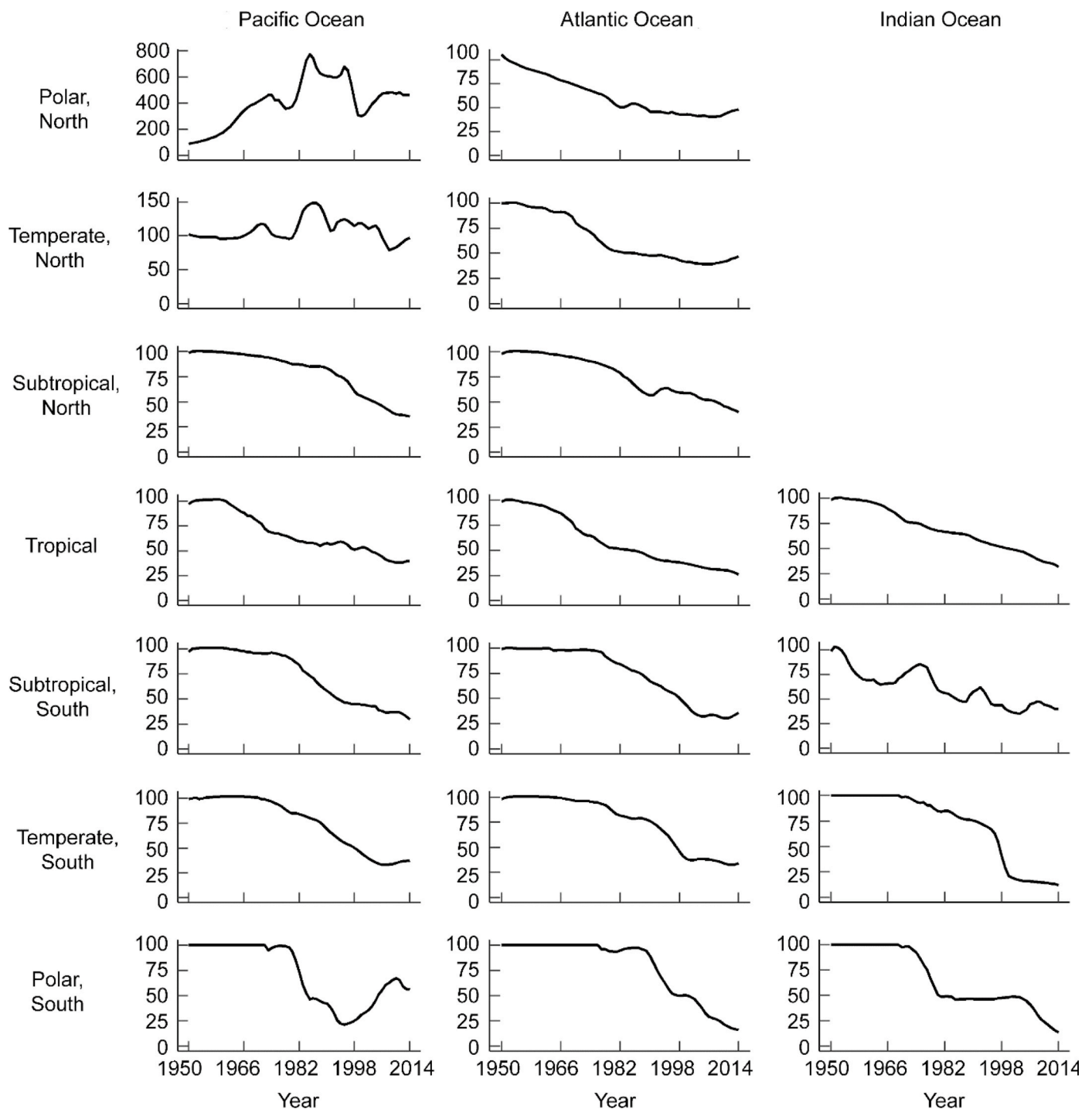


Fig. 4. Relative changes in population biomass of analyzed populations over time expressed as a percentage of the average biomass at the start of the time series (1950–1954), grouped by climatic zone and ocean basin. Note that the Indian Ocean is limited to the north by the Asian continent and thus does not have any northern subtropical, temperate or polar zones.

of decline (whether gradual or rapid), is the Pacific Ocean Antarctic waters (Pacific southern polar zone), where biomass, after massive declines in the 1980s, experienced a strong increase from the mid-1990s to the mid-2010s. However, this appears to be due mainly to a resurgence of krill (*Euphausia superba*), which is extremely sensitive to subtle environmental changes, and thus may not be an indication of a broad-based recovery of the few species reported to be exploited in that region (Ainley and Pauly, 2014; see also www.seaaroundus.org).

The fishery biomass estimation method used here, called CMSY (Froese et al., 2017), is based on a data-limited fisheries stock

assessment method developed to derive biomass estimates over time for fished populations with limited data availability. Several of these data-limited assessment methods have been evaluated by numerous studies (e.g., ICES, 2014, 2015; Rosenberg et al., 2014; Free et al., 2020). In most cases, these studies used either simulated stock data and/or the stock data from the RAM legacy stock assessment database (Ricard et al., 2012) as their test datasets. In these evaluations, the CMSY method as used here (Froese et al., 2017) performed quite well, with few comparative convergence failures (see e.g., Table S1 in Free et al., 2020 Supplementary Materials) and good match of biomass estimates to the

simulated data (see e.g., Fig. S2 in Free et al., 2020 Supplementary Materials). We recognize that it did not perform as well in comparison to the RAM legacy dataset, and we will be investigating in future research as to the reasons for this. The CMSY method used here has been evaluated against 128 real stocks, where estimates of biomass were available from traditional, full stock assessments, and provided good matches for well over 70% of these stocks (Froese et al., 2017). Furthermore, informative priors are crucial for effective application of the Bayesian CSMY method, and we could not find details on the use of informative priors in Free et al. (2020). In a Bayesian context, priors are part of the analysis and if they are wrong, the results are wrong. This makes the use of informative priors crucial. Note also that the process used for informative priors in CMSY as used here is more straightforward and transparent than the “fixing” of key parameters or model components (e.g., natural mortality rate M , or fisheries catchability coefficient q , etc.) in standard fisheries stock assessment models. In traditional least-squares statistics, the start values or start ranges for the parameters to be estimated need also to be specified. If these ranges are “uninformative”, typically the model does not converge or gets stuck in local optima that make no sense. Such start ranges use the most probable range of expected values based on experience, very similar to priors based on expert opinion. However, Bayesian priors force this practice into the limelight and make it more transparent and open to scrutiny. This is proper, as we should not forget that using expert knowledge is a well-established and well-accepted part of any analysis in science.

Here, we demonstrated wide-spread and strong declines in average population biomass for a large number of exploited fish and invertebrate populations in almost all areas of the world. Furthermore, in the majority of cases, these biomass estimates are well below the level deemed optimal for sustainable maximization of fisheries catches. This supports previous suggestions of systematic and wide-spread overfishing of the coastal and continental shelf waters in much of the world, and thus support calls to reduce the current level of overfishing globally (Pauly et al., 2003, 2002; Pauly and Zeller, 2016a; Zeller and Pauly, 2019) that is heavily driven by harmful fisheries subsidies (Sumaila et al., 2016). While it is possible that biomass has decreased because the productivity of the world ocean ecosystems has declined in the last 40 years (Zimmermann and Werner, 2019; Fernandes and Cook, 2013; Worm et al., 2009), it is likely that it is the fisheries that are the main drivers of these trends. In any case, our final conclusion is still that humanity is in the process of losing much of its marine biomass, and hence biodiversity across the world.

Declaration of competing interest COI

Palomares, MLD; Derrick, B.; Noël, S-L.; Tsui, G.; Woroniak, J.; Zeller, D. and Pauly, D. have no conflict of interest to declare.

We received funding primarily from Oceana for the biomass trends evaluations that form the basis of this study. Dr. Michael Hirshfield (former Oceana Chief Scientist) offered several suggestions, which improved the manuscript.

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Froese, R. and Meeuwig, J.J. have no conflict of interests to declare.

CRedit authorship contribution statement

M.L.D. Palomares: Supervision, Conceptualization, Methodology, Formal analysis, Writing - review & editing. **R. Froese:** Methodology, Validation. **B. Derrick:** Data curation, Formal analysis. **J.J. Meeuwig:** Writing - review & editing. **S.-L. Noël:** Data curation, Formal analysis, Visualization. **G. Tsui:** Data curation, Formal analysis, Visualization. **J.**

Woroniak: Data curation, Formal analysis. **D. Zeller:** Writing - review & editing. **D. Pauly:** Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106896>.

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