

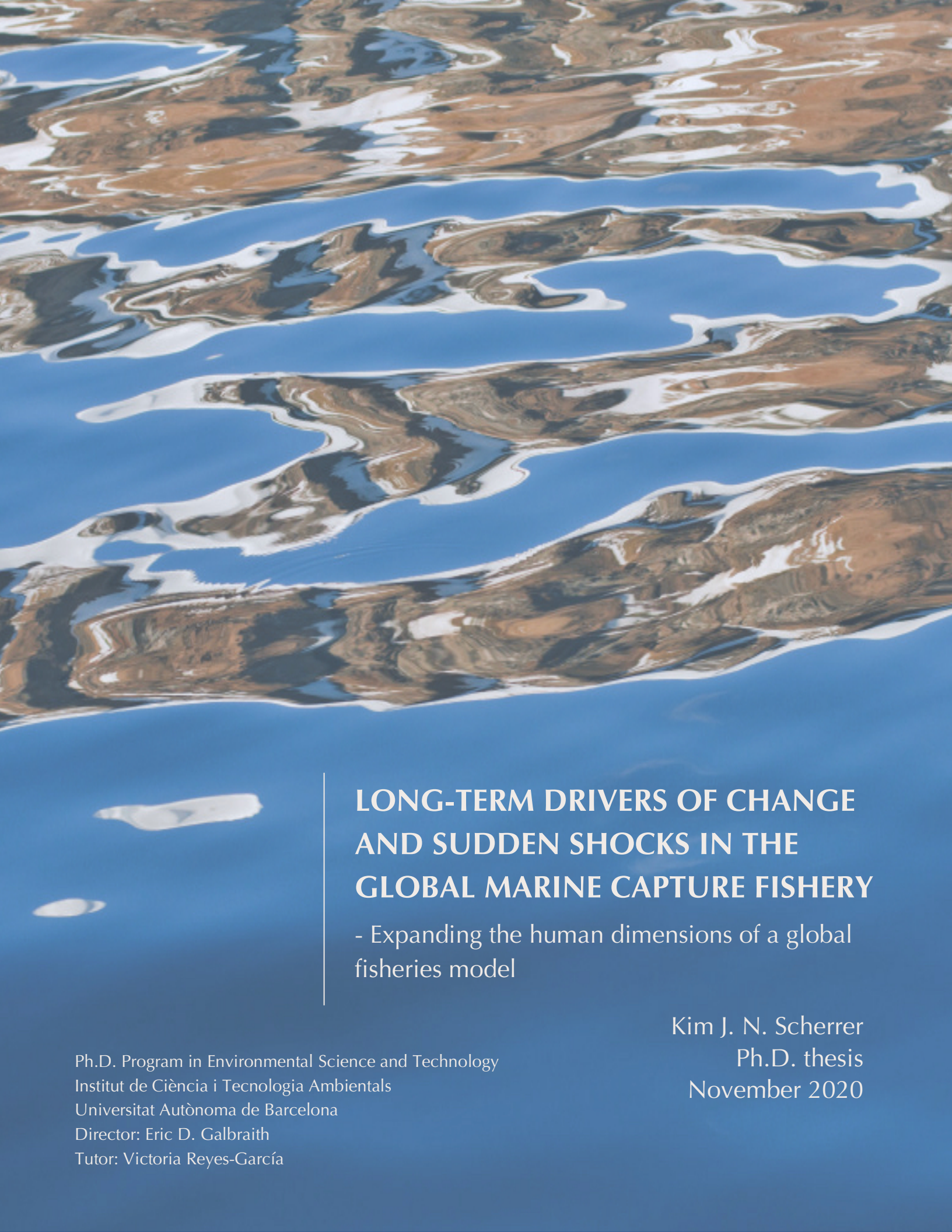


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LONG-TERM DRIVERS OF CHANGE AND SUDDEN SHOCKS IN THE GLOBAL MARINE CAPTURE FISHERY

- Expanding the human dimensions of a global
fisheries model

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Ph.D. thesis
November 2020

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– *expanding the human dimensions of a global fisheries model*

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Thesis for the degree of Philosophiae Doctor

Barcelona, November 2020

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Cover photo:
Surface patterns in Isfjorden, Svalbard, May 2015

Till Mikaela

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Table of contents

ABSTRACT.....	1
ACKNOWLEDGEMENTS.....	2
FUNDING ACKNOWLEDGEMENT.....	4
CHAPTER 1.....	5
1 INTRODUCTION.....	5
2 AIM AND SCOPE OF THESIS.....	8
3 BACKGROUND.....	10
3.1 TRENDS AND CHALLENGES IN THE GLOBAL WILD-CAPTURE FISHERY.....	10
3.2 TECHNOLOGICAL PROGRESS AS A DRIVER OF CHANGE.....	12
3.3 CLIMATIC IMPACTS ON FISHERIES.....	15
3.4 NUCLEAR WAR AS AN EXTREME CLIMATIC AND SOCIOECONOMIC PERTURBATION.....	17
3.5 LABOUR – A KEY HUMAN DIMENSION IN FISHERIES.....	19
3.6 GLOBAL FISHERIES MODELS AND THEIR USE.....	19
3.7 THE BOATS MODEL – AN OVERVIEW.....	21
CHAPTER 2.....	26
REGULATION STRENGTH AND TECHNOLOGY CREEP PLAY KEY ROLES IN GLOBAL LONG-TERM PROJECTIONS OF WILD CAPTURE FISHERIES.....	26
CHAPTER 3.....	38
MARINE WILD-CAPTURE FISHERIES AFTER NUCLEAR WAR.....	38
CHAPTER 4.....	50
GLOBAL FISHERIES EMPLOYMENT 1950-2015.....	50
1 INTRODUCTION.....	50

2	METHODOLOGY	53
2.1	EMPIRICAL DATA ON NATIONAL EMPLOYMENT	53
2.2	FLEET POWER DATA AND RATES OF LABOUR SUBSTITUTION.....	55
2.3	RELATIONSHIP BETWEEN GDP AND MECHANIZATION LEVEL	56
2.4	RECONSTRUCTING THE NUMBER OF FISHERS	59
3	RESULTS.....	61
3.1	LONG-TERM LABOUR SUBSTITUTION	61
3.2	RECONSTRUCTED EMPLOYMENT	62
4	DISCUSSION.....	66
5	CONCLUDING REMARKS	69
	CHAPTER 5.....	71
1	DISCUSSION AND CONCLUSION.....	71
1.1	ACHIEVING THE RESEARCH AIMS.....	71
1.2	CONTRIBUTIONS.....	72
1.3	LIMITATIONS	74
1.4	FUTURE WORK	76
	BIBLIOGRAPHY	78
	APPENDICES.....	92
	APPENDIX I – SUPPLEMENTARY MATERIAL FOR CHAPTER 2.....	92
	APPENDIX II– SUPPLEMENTARY MATERIAL FOR CHAPTER 3	93
	APPENDIX III – SUPPLEMENTARY MATERIAL FOR CHAPTER 4.....	113

Table of figures

Chapter 1

Figure 1. Reconstructed global marine fish catches by fishery type from Pauly and Zeller (2016; licensed under CC BY 4.0).....	11
Figure 2. An investigation of the importance of three key socio-economic drivers of change using the global fisheries model in this thesis work (Galbraith et al., 2017; licensed under CC BY 4.0).....	13
Figure 3. Estimates for the fishing effort in the world’s regions from Rousseau et al. (2019)...	14
Figure 4. The impact of a regional nuclear conflict between India and Pakistan on global agriculture production of the world’s major crops, from Jägermeyr et al., (2020; licensed under CC BY-NC-ND 4.0).....	18
Figure 5. Spatial distribution and temporal development of fish catch (harvest) in the BOATS model (Galbraith et al., 2017; licensed under CC BY 4.0).....	21
Figure 6. Schematic overview of the BOATS model modified with permission from Carozza et al. (2017) to reflect the additional drivers included in Chapter 2.....	23

Chapter 2

Figure 1. Modelled and empirical fisheries reference points in a well managed fishery.....	31
Figure 2. Simulated and empirical global catch (1950–2050).....	32
Figure 3. Simulated fisheries trajectories under continued technological progress.....	32
Figure 4. Simulated fisheries trajectories under stabilizing technology.....	33

Figure 5. Illustration of the impact of regulation strength..... 33

Figure 6. Hidden losses under weak regulation..... 34

Chapter 3

Figure 1. Prewar trajectories of global fisheries..... 40

Figure 2. Short-term impacts of nuclear war on global fisheries..... 42

Figure 3. Global fishery developments postwar..... 43

Figure 4. Spatial distribution of changes in fish catch..... 44

Figure 5. Country-level fish catch changes under the 5-Tg and BAU fishing scenario..... 45

Figure 6. Contribution of well-regulated fisheries to postwar food security 46

Chapter 4

Figure 1. Relationship between GDP and mechanization level.....58

Figure 2. Empirical ($n_{F,i}$) versus reconstructed ($n_{F,i}^*$) number of fishers for each country and year for the complete dataset.60

Figure 3. Long-term labor substitution in six fishing nations.....61

Figure 4. Reconstructed global fisheries employment 1950-2015.....62

Figure 5. Reconstructed number of fishers by region.....63

Figure 6. Reconstructed number of fishers and fisher fraction by country income group..64

Figure 7. Catch per fisher (metric tons) by country income group.....65

Table of tables

Chapter 2

Table 1. Examples of universal components of regulation systems in three diverse fisheries.... 29

Table 2. Overview of model forcing variables used in scenarios..... 30

Chapter 3

Table 1. Overview of nuclear-war–driven climatic perturbations 40

Table 2. Overview of modeled socioeconomic responses 41

Chapter 4

Table 1. Summary of available independent historical data on employment in fisheries. 54

Table 2. Statistics for multiple linear regression with log(GDP per capita) and one additional predictor. 58

Abstract

Marine wild-capture fisheries have supplied humans with food, income and a way of life for centuries. However, the past half century has seen a dramatic intensification of human impacts on the ocean, threatening the benefits provided by fisheries worldwide. Processes like technological progress, demographic shifts, marine management, climate change and mechanization will greatly influence future fisheries and those who live off them – but to what extent and with what consequences? This thesis aims to explore and untangle large-scale and multidecadal anthropogenic drivers of change in the global fishery. I develop new ways of representing key human processes in a global macroecological fish and fisheries model, and use the model to simulate the effect of both progressive and abrupt changes in key socio-economic and climatic factors. Where possible, I draw on existing theory, but to better understand the mechanisms of change in fishers, I also assemble and analyze new data. In the first study, I include fisheries regulation in the model, and use it to show that long-term sustainability in global fisheries hinges on a race between strengthened fisheries management and technology-driven increases in catch efficiency. My findings also suggest that this race can hide a progressive erosion of the global fish biomass. The second study investigates how the global fishery responds to a catastrophic climatic cooling event; a nuclear war. I find that while cooling somewhat decreases the potential fish catches from the ocean, proactive and precautionary fisheries management ahead of time can create a considerable supply of fish for emergency animal protein. The third study reconstructs the historical global employment in fisheries. It suggests that despite great regional differences, the fraction of the global human population working as fishers has been surprisingly stable and the increase in catch per fisher relatively small between 1950 to 2015. Altogether, the findings in this thesis provide new macro-scale understanding of processes in the global fishery that are important for long-term, strategic management of marine resources. They also lay out avenues for further research on the global fishery’s response to sudden shocks and on the long-term evolution of its human dimensions.

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Chapter 1

1 Introduction

The rate and spatial scale at which we technology-assisted humans are altering the environment is unprecedented. The world's oceans, on which many societies depend, are facing many, intensifying and rapidly evolving pressures. Many branches of science are endeavoring to keep up. The understanding of how oceanographic, climatic, biogeochemical and ecological processes determine the state of the ocean, and the marine resources that we depend on, is steadily growing. We know that currents – driven by physical processes such as wind, the Earth's rotation, and temperature and salinity gradients – distribute heat and nutrients in the global ocean. This distribution in turn creates the preconditions for the growth of photosynthesizing algae, the fuel for marine ecosystems, whose energy content is transferred to zooplankton, then to anchovies and herrings, then to cods and tunas (Lindeman, 1991). But in the past century, the impact of humans on these natural processes has intensified greatly. Modern humans now not only change the numbers of cod or tunas through fishing (Myers and Worm, 2005), but even alter the ocean's temperature and circulation (IPCC 2019). How will this evolution impact the oceans and the benefits that they provide us?

Due to its many interacting components and the rapidly evolving human societies, it is a great challenge to understand the global, coupled human-ocean system (Österblom et al., 2017). Many different parts of the human-ocean system are directly or indirectly linked, so a change in one variable may influence many other processes. Motorization, made possible through technological progress, allows increasing fishing pressure and the removal of a larger proportion of fish populations. At the same time, motorization produces much of the global greenhouse gas emissions that warm the atmosphere and seas. This warming indirectly affects fish populations by decreasing the amount of nutrients that well up from greater depths

(Steinacher et al., 2010), and by increasing the metabolic rates of ectothermic (cold blooded) marine organisms (Brown et al., 2004). To keep track of the myriad relationships, and their strengths, we can build and use numerical models of the oceans and their ecosystems. In these models, the relationships are represented quantitatively by differential equations that describe how much a change in one variable translates to change in another. If representing key processes in a sufficiently accurate way, these models can help us understand what different future developments in a range of variables would mean for different aspects of the human-ocean system.

To describe systems with models can seem increasingly challenging when going from physical to chemical, biological and societal systems. To many, predicting the aggregate macro-scale behavior of molecules appears easier than predicting the aggregate macro-scale behavior of human beings. This may in part explain why the most advanced components of large-scale global ocean models are the physical and bio-geochemical ones. Today's Earth system models (ESMs) – coupled climate models that also describe the flow of carbon through the Earth system – generally stop at describing the primary producers and microorganisms that govern Earth's biogeochemical cycles, leaving out larger animals, including humans. For the oceans, humans are represented in ESMs mainly by their emissions of greenhouse gases, estimated by separate so-called Integrated Assessment Models (Harfoot et al., 2014). This approach omits many other key human impacts and feedbacks between human societies and the oceans system (Donges et al., 2017; Müller-Hansen et al., 2017). Therefore, research on how to advance the representation of humans in global ocean models is needed.

This thesis focuses on the role of humans in marine capture fisheries in particular. Marine fisheries provide a source of nutrition and income for millions of people worldwide (Golden et al., 2016; Teh and Sumaila, 2013), but global catches have stagnated since the 1990's, after a century of astonishing growth (FAO, 2018a; Pauly and Zeller, 2016; Watson and Tidd, 2018). This development has been accompanied by a depletion of global fish biomass and widespread problems of overfishing (Costello et al., 2016; Myers and Worm, 2003; Palomares et al., 2020), as fishers have taken more fish than what is replenished. Efforts to reduce the

pressure on marine resources through a range of regulation measures have followed (Hilborn et al., 2020; Worm et al., 2009), but the effects of multiple processes, such as climate change, technologically boosted fishing techniques or rising demand from a growing human population, interact to create new challenges for sustainability. Therefore, we need a better mechanistic understanding of the long-term drivers of change in the global fishery.

Beyond the many “slow” drivers of change, the global fishery can also be greatly affected by sudden societal and natural disruptions, or shocks (Gephart et al., 2017). The impact of shocks on global fisheries has received relatively little attention and studies on the topic are often limited to regional climatic phenomena such as marine heat waves or cyclic climate oscillations (Caputi et al., 2016; Cheung and Frölicher, 2020; Lenanton et al., 2017; Ñiquen and Bouchon, 2004; Roberts et al., 2019). Yet, like the ongoing COVID-19 pandemic is currently illustrating (FAO, 2020a), unpredictable shocks could have profound effects on global fisheries and the benefits they provide.

Finally, the marine fishery is a good test system for investigating how to include humans explicitly in a gridded global model framework. Although extensive (Halpern et al., 2008), our activities in the ocean are less complex than on land, where humans have altered not only the fauna, but also the soil, vegetation and flow of materials on a major scale (Nyström et al., 2019). Marine capture fisheries are special in being the last major food production industry that is not based on domestication. But while reminiscent of humanity’s earlier way of hunting and gathering, capture fisheries have made a great transition from being a subsistence activity to becoming an industrial enterprise (Sahrhage and Lundbeck, 1992). Fisheries are also a classic example of a socio-ecological system of renewable natural resource use, where the benefits that humans can derive depend on the fishing pressure as well as the natural productivity of fish populations themselves (Gardner et al., 1990; Gordon, 1954). Thus, the feedbacks of overfishing become particularly noticeable. Altogether, this means that a global, spatially explicit model of marine fisheries can help illuminate how humans interact with ecosystems on a global and multi-decadal scale.

2 Aim and scope of thesis

The overarching goals of this PhD thesis are

- to advance the representation of humans and their activities in global marine ecosystem models
- to improve the understanding of how the global fishery responds to key macroscale drivers of changes

To achieve these goals, I build on a preexisting global macroecological, bioeconomic fisheries model. The question of how to represent key human processes in this global model is central, and I approach it in three different ways. First, I review the literature from a wide range of fields to identify key theories about regulation, and translate these theories into a new model equation. Further, through simulations with the new model development, I perform experiments with the human-ocean model system, exploring the importance of different drivers of change and human behaviors. Finally, for less explored processes I also collect and analyze data with the aim to identify the main mechanisms.

Humanity interacts with the ocean in many ways. This thesis focuses on fisheries, and on the macro-scale processes that affect them. However, for now, it leaves out the effects of many processes such as acidification, habitat destruction or plastic pollution. For many of these processes, the large-scale implications for global fisheries are still uncertain and general theories that can be applied in a macroecological model are lacking.

The thesis consists of an introduction and three main chapters, each of which treats some aspect of humanity's interaction with the ocean. I focus on three themes: 1) fisheries regulation, 2) global shocks and 3) labor. In Chapter 2, I develop a new regulation (management) component for the global model and use it to investigate the interactions between regulation effectiveness, technological progress and climate change in long-term future projections. In Chapter 3, I explore the effect of an extreme climatic and socioeconomic shock – a nuclear war – on global marine capture fisheries, assessing the potential contribution of fisheries in the event of a global food emergency. In Chapter 4, I

investigate the historical development of labor, a key human dimension in fisheries, by collecting data on fisheries employment and reconstructing the global labor force from 1950 to 2015. Chapter 5 concludes by discussing the contributions and limitations of the thesis, as well as future work.

3 Background

This thesis encompasses theories and concepts from a range of different fields. In this background section, I summarize fundamental knowledge and current research challenges in the areas of largest importance in the thesis.

3.1 Trends and challenges in the global wild-capture fishery

As outlined in the introduction, global marine capture fisheries have undergone tremendous changes in the past century and are facing many challenges. Although the reported global annual catch has remained relatively stable around 80 Mt yr⁻¹ since the 1990's (FAO, 2018a), data reconstructions of unreported, illegal and discarded catch suggest that global catches peaked at around 130 Mt yr⁻¹ in 1996 and has declined since (Figure 1; Pauly and Zeller, 2016). Data deficiencies, especially in many developing countries (e.g. Zeller et al., 2015), make the exact global development somewhat elusive. Yet even larger uncertainty surrounds what the catch trends tells us about the biomass of fish left in the ocean (Pauly et al., 2013). Declining catch can be a sign of overfishing and depletion of the underlying fish biomass, or could conversely be an effect of fisheries regulations that help limit the so-called fishing effort (often measured as the time spent fishing or the power used by fishing vessels). Data on fishing effort combined with catch data can help estimate biomass trends, but biomass trends are still poorly known at the global scale, particularly in the >50% of world's fisheries that lack fish stock assessments (Costello et al., 2016, 2012). Although management measures have been effective in many higher-income countries (Hilborn et al., 2020), recent analyses and advances in data reconstructions continue to raise concern about global fisheries sustainability (Ye and Gutierrez, 2017; Rousseau et al., 2019; Palomares et al., 2020).

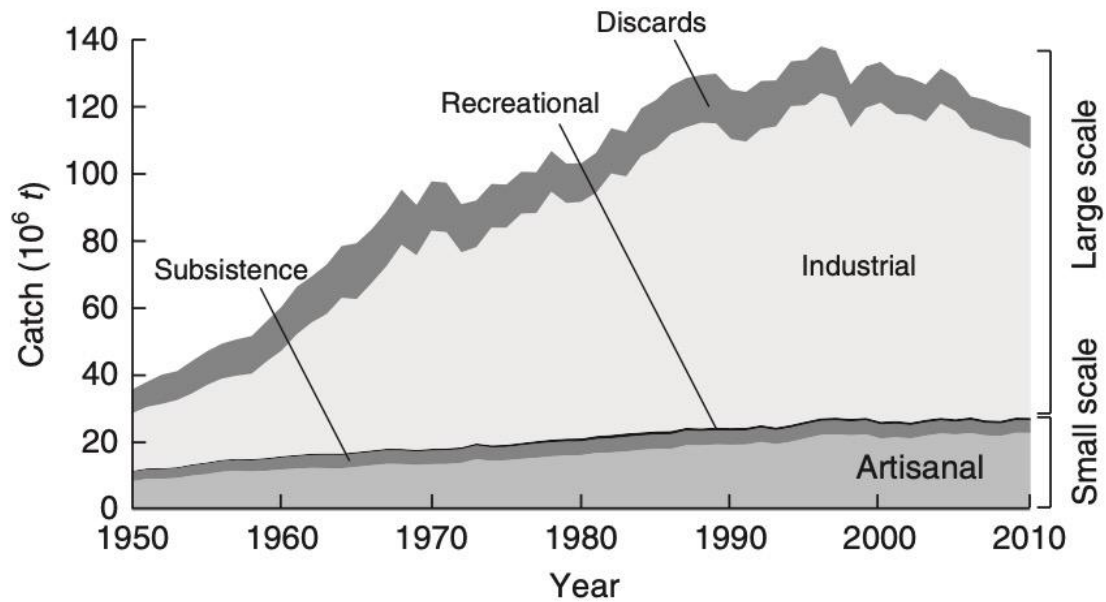


Figure 1. Reconstructed global marine fish catches by fishery type from Pauly and Zeller (2016; licensed under CC BY 4.0). Since the peak in the mid 1990's, reconstructions suggest that global annual catches have decreased significantly. The reasons for this decrease are debated, and the future trajectory of the curve will depend on many factors, including the effectiveness of fisheries management measures.

One of the main challenges in fisheries is to effectively regulate the amount of fish that is allowed to be taken from the ocean. The importance of fisheries regulations is the focus of Chapter 2 in this thesis. Humans have significantly altered populations of marine organisms through fishing, gleaning and hunting for hundreds or even thousands of years (Butler, 2001; Erlandson et al., 2008; Harris and Weisler, 2018; Jackson et al., 2001; Máñez et al., 2014; Roberts, 2007). Strategies and behaviors that prevent overexploitation may have an equally long history (Caddy and Cochrane, 2001; King, 1900; Toniello et al., 2019), but this need to regulate fisheries has accelerated greatly in the last decade. At the heart of the problem of sustainable fishing lies a social dilemma common to all systems with a “common” pool of a renewable resource (Ostrom, 1998). If resource users do not cooperate to keep the rate of resource extraction at a sustainable level and each user competes to get to the resource before someone else does, this kind of system can easily become subject to overexploitation, which is detrimental to all users (Hardin, 1968). This problem, often termed the tragedy of the (open

access) commons, can be overcome by coordinated collective action (Olson, 1971). Beyond the more general research on common-pool and open access resources, much research has focused explicitly on the overfishing problem, often with the aim to help fisheries management identify and implement the most effective regulation systems (see e.g. Botsford et al., 2009; Costello et al., 2008; Gutiérrez et al., 2011).

3.2 *Technological progress as a driver of change*

“I believe that it may be affirmed with confidence that, in relation to our present modes of fishing, a number of the most important sea fisheries [...] are inexhaustible”

T.H. Huxley, 1882

When investigating the evolution of the coupled human-ocean system, the rapid pace of technological progress over the past century is an ever-recurring matter. In the statement of zoologist T. H. Huxley above, who today epitomizes the idea that sea fisheries were impossible to exhaust, he indicates that this inexhaustibility depends on our “modes of fishing”. Since then, technological progress has enabled humans to increase global fish catches by about an order of magnitude (Watson and Tidd, 2018). It has also enabled us to seriously deplete the resources of the sea on a global basis (Costello et al., 2016; Palomares et al., 2020). Knowing about the extraordinary technological progress that ensued, from sail to motorized fishing (Engelhard, 2009), from natural to synthetic fibers (Martinussen, 2007), and with refined fish finding, fish aggregation and navigation techniques, the transition to viewing fisheries as exhaustible might perhaps not have surprised even Huxley himself.

While having a tremendous impact on how humans interact with the ocean, the steady progress of technology can go by quite unnoticed over shorter time-scales. Further, the mechanistic understanding of what determines the rate of technological progress is poor, making the future pace of technological progress highly uncertain (Nagy et al., 2013). This might explain why technology has not been included as a driver of change in some influential studies investigating the future of global fisheries (Costello et al., 2016; Gaines et al., 2018).

Yet, the importance of including estimates of how technological advances boost humanity’s fishing capacity has recently been demonstrated in several studies. Galbraith et al. (2017) tested the importance of three key socio-economic drivers of change – fishing costs, revenue and technology – in the global fisheries model used in this thesis work. They found that a creeping technology-driven increase in the “catchability” of fish (the ease by which fish is caught) could alone explain the first-order features of the 20th century development of global fish catches (Figure 2). Further, this technology-driven increase in catch efficiency greatly influences estimates of the catching power of the global fishing fleet (Figure 3; Rousseau et al., 2019). Chapter 2 in this dissertation investigates the importance of future technological progress and regulation effectiveness.

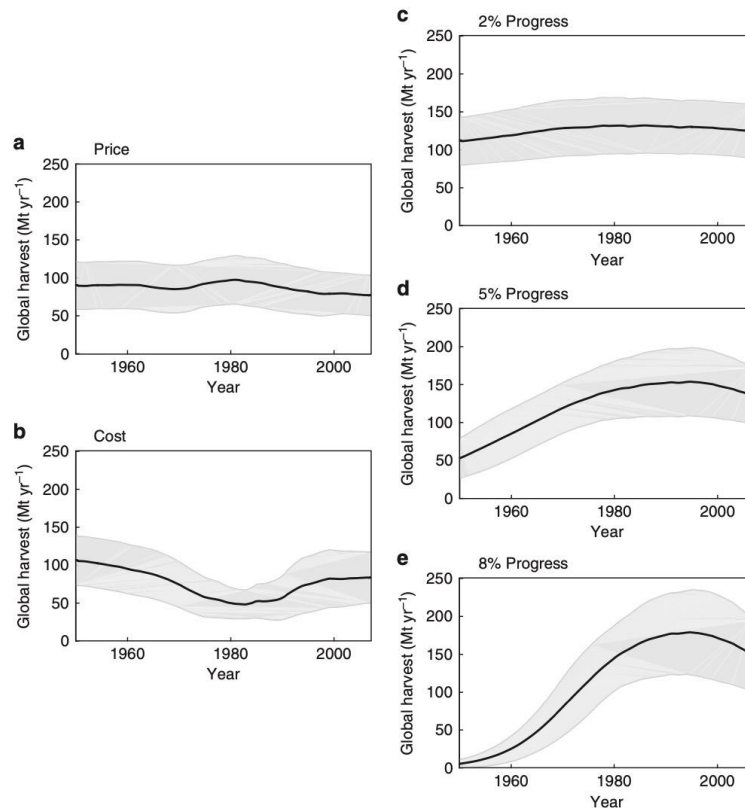


Figure 2. An investigation of the importance of three key socio-economic drivers of change using the global fisheries model in this thesis work (Galbraith et al., 2017; licensed under CC BY 4.0). When the model is run with reconstructed time series of historical global fish prices (a) and fishing costs (b) as inputs, it does not recreate the historical trends for fish catch as seen

in Figure 1. However, a steady exponential increase in technological progress (c-e), in particular an intermediate rate of 5 % yr⁻¹, creates an increase, peak and slight decline of catch, similar to observations.

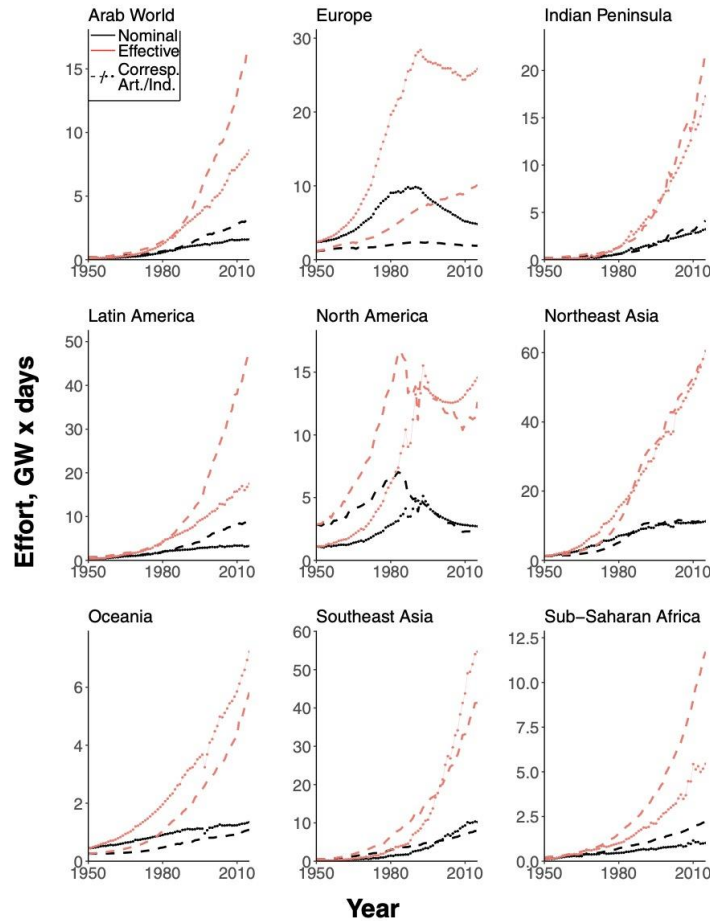


Figure 3. Estimates of fishing effort in the world’s regions from Rousseau et al. (2019). Technological progress multiplies the catching power of global fishing fleets over multi-decadal time scales. The black lines show nominal fishing effort, the gigawatt days put into fishing by the fishing vessels. Red lines are estimates of the effective power of this nominal effort, after accounting for the creeping increase in catching power brought about by innovations in gears, navigation, fish finding techniques etc. Here, it is assumed that the rate of this technological progress is 2.6% yr⁻¹. Dashed and dotted lines reflect artisanal and industrial fleets respectively.

Technological progress also has a great impact on labor (Debertin et al., 1990; Hayami and Ruttan, 1970; Lianos, 1971), a key human dimension in fisheries (see section 3.6). Machines and engines now propel the fishing vessels, search for fish, haul the nets and perform the handling of the catch. This aspect of technology can drive major reductions in fisheries labor (Garcia and Rosenberg, 2010; Hannesson et al., 2010; Heen, 1988), and is the focus of Chapter 4 of this thesis.

Finally, technological progress drives indirect, and often unwanted, changes in marine ecosystems. Marine pollution by plastic debris or fertilizers are conspicuous byproducts of technology, but industrialization has also been accompanied by emissions of greenhouse gases to the atmosphere. The climatic changes caused by these emissions have major implications for the world's fisheries (section 3.3). Global warming alters water temperatures, ocean circulation and primary productivity (IPCC 2019), thus altering the environmental factors that determine the growth of fish populations (Chassot et al., 2010; Friedland et al., 2012). And at the extreme end, technological and scientific advances in the fields of geoengineering and nuclear warfare (section 3.4) have made humanity theoretically capable to substantially alter the Earth's climate within years or months (Matthews and Caldeira, 2007; Toon et al., 2019; Trisos et al., 2018; Turco et al., 1983). Indirect climatic impacts on fisheries are investigated in Chapters 2 and 3 of this thesis.

3.3 Climatic impacts on fisheries

In recent years, much research has focused on quantifying the impact of climate change on marine ecosystems and fisheries. The long-term implications of warming on fisheries is treated in Chapter 2, and the short-term response to cooling in Chapter 3. Climate change has multiple impacts at different levels, from the cellular and individual to the population and community level (Pinsky et al., 2020). Consequently, many different kinds of models that can estimate climate impacts have been developed (Koenigstein et al., 2016). For example, biogeographic approaches use knowledge of the preferred climate niche of organisms to project the shifts in the distribution of species (Jones and Cheung, 2015), while physiological

approaches use the metabolic temperature response of organisms to project changes in the growth and biomass of whole fish communities (Lefort et al., 2015; Pörtner and Gutt, 2016). The appropriate approach depends on the questions asked. However, across fields, most models use the projected changes in climatic parameters modeled by ESMs as input to create future projections for the marine ecosystems under climate change.

Multiple mechanisms by which climate change influences fisheries have been proposed. Changes in water temperature, nutrient circulation, oxygen levels and pH have direct physiological impacts on marine organisms, and by affecting organisms differently, these changes alter community composition and function (Doney et al., 2012; Pinsky et al., 2020). The direct impacts on a specific species may be relatively well understood, but the consequences for the functioning of the whole ecosystem can be difficult to predict since species interact with and replace each other (Kordas et al., 2011; Lord et al., 2017). At the macroscale, we are often interested in knowing if ecosystems altered by climate change will maintain different amounts of fish, if their fish populations will grow faster or if they will respond differently to fishing pressure. Such general questions can be investigated by macroecological, size-based frameworks (Blanchard et al., 2017; Jennings et al., 2008). In macroecological applications for the ocean, the focus so far lies on the effects of temperature and net primary production. Since NPP is a product of both water chemistry, circulation and temperature, it integrates multiple climate change effects.

Temperature and NPP put large-scale constraints on the productivity of marine ecosystems. NPP, in the forms of micro and macroalgae, makes up the basal food source for all other marine organisms. Thus, NPP limits the total amount of energy available for the upper trophic level organisms that are targeted by fisheries (Chassot et al., 2010; Stock et al., 2017). Further, the majority of marine organisms are ectothermic, with a body temperature similar to the surrounding water. Therefore, sea surface temperature impacts the vital rates of marine organisms, which in turn influences the transfer of the energy available from NPP up the trophic food chain (Allen and Gillooly, 2007).

3.4 *Nuclear war as an extreme climatic and socioeconomic perturbation*

“Now I am become death, the destroyer of worlds”

J.R. Oppenheimer, 1904-1967

While the past decades have been ones with relative peace and food system stability, our provision of food both from land and ocean could be jeopardized by large-scale socioeconomic and climatic shocks. One of the most chilling potential causes of such a shock is nuclear conflict. The quote from the Hindu scripture "the Bhagavad-Gita" went through the mind of J.R. Oppenheimer, one of the creators of the nuclear bomb, as he witnessed the first nuclear explosion on 16 July 1945 (Hijiya, 2000). Being an ultimate and terrifying example of humanity's technological ingenuity, nuclear weapons have since then multiplied both in numbers and destructive power. Research suggests that these weapons truly have the potential to destroy worlds, even beyond the vast direct destruction and fatalities (Toon et al., 2019). A nuclear war could have global and almost instantaneous impacts on both the climate system, the ecosystems and our socioeconomic systems (Crutzen and Birks, 1982; Harwell and Hutchinson, 1986). The effects of a nuclear war could likely resemble those of major volcanic eruptions, which have caused historical famines and epidemics (Stothers, 1999).

There are several reasons to take the risks associated with nuclear war very seriously. The existence of about 14,000 nuclear warheads globally, with about 9,500 in military service (Arms Control Association, 2020), makes the catastrophic consequences of a nuclear war a real concern. More countries are acquiring nuclear weapons, including India and Pakistan, which have fought three major wars since their declared independence in 1947, and most recently North Korea (Kristensen, 2019; Kristensen and Norris, 2013). If a war were to break out, whether intentionally or triggered by human error (Baum et al., 2018), the consequences would be disastrous. Beyond the immediate fatalities and destruction, the fires ignited by the detonations in a war could emit enough soot into the atmosphere to reduce incoming solar radiation and cool the planet (Robock et al., 2007; Turco et al., 1983). The most recent simulations suggest that in this way, even a limited regional conflict between India and

Pakistan, using less than 1% of the world’s nuclear weapons, could cause an 11 % fall in the global production of major cereal crops lasting for five years (Figure 4; Jägermeyr et al., 2020). Such adverse consequences for global food security would be unmatched in modern history.

New simulations of the climatic effects of nuclear war have recently been performed with a state-of-the-art ESM (Coupe et al., 2019; Toon et al., 2019), allowing more in-depth analysis of the effects of nuclear war on marine ecosystems and fisheries. Simulated changes oceanic net primary production and sea surface temperature can be used as input to global fisheries models, which in turn simulate the climatic impacts of nuclear war on the world’s fisheries. Further, nuclear war is expected to cause major socioeconomic changes in for example food demand and fuel availability that would likely have large impacts on fisheries. Investigating these combined climatic and socioeconomic effects can bring many new insights about the dynamics of global fisheries. This is the aim of Chapter 3 in this thesis.

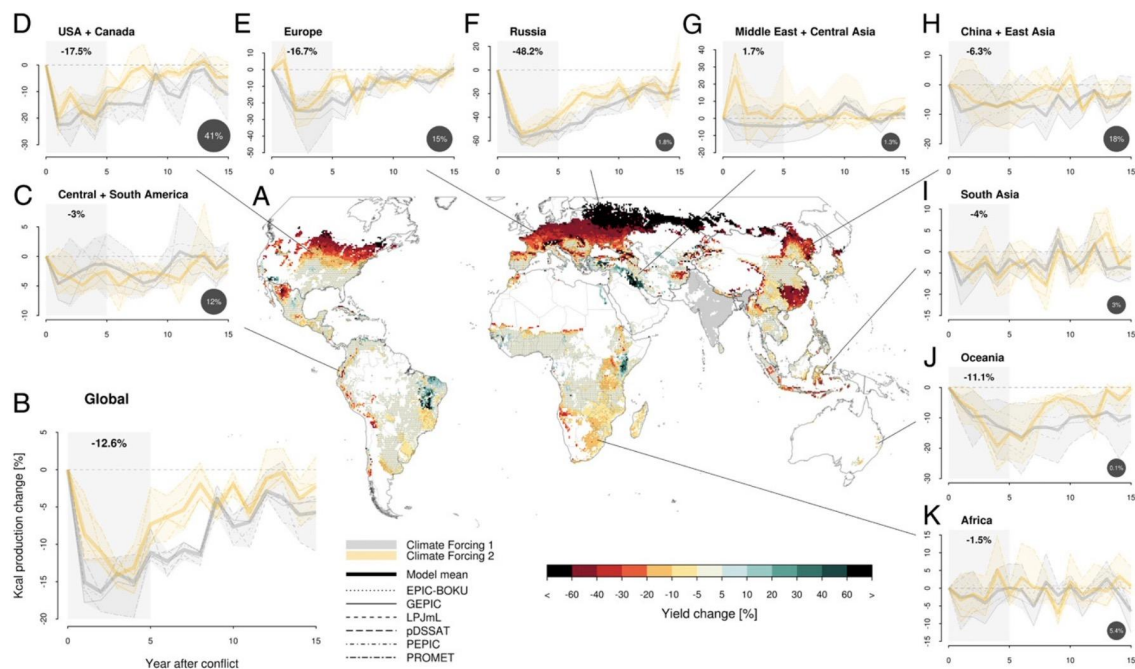


Figure 4. The impact of a regional nuclear conflict between India and Pakistan on global agriculture production of the world’s major crops, from Jägermeyr et al., (2020; licensed under CC BY-NC-ND 4.0). The climatic perturbation following the war would have different impacts on different crops and regions, and cause major losses in the world’s breadbasket

regions (Russia, North America, Europe). The total global decline, $\sim 12\%$, is four times larger than the largest historical variation in crop yield. Chapter 3 of this thesis explores the effects of these kinds of climate perturbations and the accompanying global food emergency on global fisheries.

3.5 *Labour – a key human dimension in fisheries*

The aim of this thesis is to advance the representation of humans and their activities in a global modelling framework. Fishing effort, catch and climatic change constitute key links between humans and the marine ecosystems, but one of the most fundamental human dimensions of fisheries is the actual time that humans spend fishing, i.e. fishery employment or labor. Yet while labor in fisheries is tightly linked to a range of socio-cultural well-being aspects, both positive and negative (Acheson, 1981; FAO, 2020b; Pollnac and Poggie, 1988; Seara et al., 2017; Woodhead et al., 2018), large-scale analyses are often limited to the importance of catch and profit (e.g. Costello et al., 2016; Gaines et al., 2018; Galbraith et al., 2017). The many socio-economic and well-being aspects make it important to better understand the long-term development of employment in global capture fisheries. Further, this understanding is necessary in order to explicitly include human labor in a global fisheries model framework. Therefore, the work presented in Chapter 4 of this dissertation investigates the historical development of labor in fisheries.

3.6 *Global fisheries models and their use*

This thesis work is centered around a global fisheries model, the so-called BiOeconomic mArine Trophic Size-spectrum (BOATS) model (Carozza et al., 2017, 2016). A great number of models for fisheries exist, but the number of *global* models is limited, with six models currently included in the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP; Lotze et al., 2019). These global models are generally used to project changes in global catch potential, species distributions or biomass through input of gridded and temporally changing key variables such as water temperature and net primary production

(Blanchard et al., 2012; Cheung et al., 2016; Christensen et al., 2015.; Galbraith et al., 2017; Lefort et al., 2015).

Model projection is a widespread tool in climate science and economics, used to assess how a system would evolve under certain hypothetical developments. Scenarios for future carbon emissions are used as inputs to ESMs, which simulate not only the ocean's circulation, temperature and chemistry, but also its biogeochemical cycles. The generated spatiotemporal evolution of variables such as water temperature, primary production and oxygen can in turn be used as inputs in global fisheries models, affecting fish growth in various ways (Section 6.4). While most of the global model applications have focused on projecting climate impacts on marine ecosystems and fisheries (e.g. Lotze et al., 2019), other socioeconomic projections for technology, regulation and other human dimensions have received relatively little attention (but see e.g. Dueri et al., 2016; Galbraith et al., 2017; Maury et al., 2017).

However, formal mathematical models like BOATS have multiple benefits and purposes beyond projection (Epstein 2008). The process of constructing models often helps us identify knowledge or data gaps, and the use of a model can help explain phenomena, suggest new hypotheses, identify key drivers of change or bound the plausible ranges of future projections. The BOATS model used and further developed in this thesis has demonstrated the dominant role of technological progress in shaping the historical development of global fish catches (Figure 2; Galbraith et al., 2017); showed that ecological factors can explain a substantial part of the different temporal developments of fish catches in different regions (Güet et al., 2020); and suggested that iron limitation of fish may explain the low fishing activity seen in several iron-poor domains of the ocean (Galbraith et al., 2019). This illustrates that a global model can help advance the understanding of key mechanisms in the global fishery.

Among the global fisheries models, BOATS is one of the few that dynamically models the spatio-temporal evolution of fishing effort (Figure 5; Tittensor et al., 2018). The complexity and perceived unpredictability of human behaviors in fisheries (Fulton et al., 2011), especially when compared with the behaviors of fish or plankton, and when considering the great diversity of fisheries worldwide, may be some of the factors that hinder the development of

mechanistic fishing modules in global models. Yet, human behavior is the very cause of the phenomena investigated by the global models (e.g. overfishing or climate change). Further advancing the representation of humans and their behaviors as an integrated factor in global fisheries models is therefore an important research task (Galbraith, 2020; Österblom et al., 2017), and a key focus of this thesis.

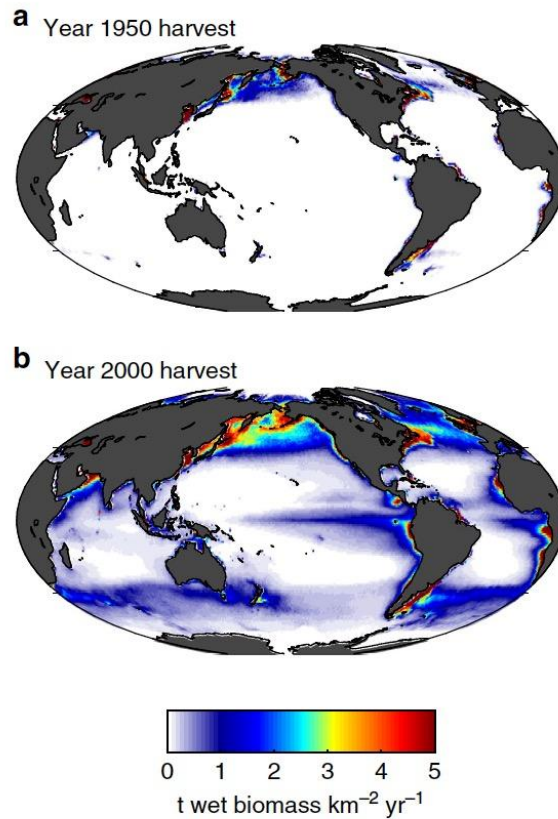


Figure 5. Spatial distribution and temporal development of fish catch (harvest) hindcast in the BOATS model (Galbraith et al., 2017; licensed under CC BY 4.0). The BOATS model represents a class of spatially explicit global fisheries models that use either gridded datasets of variables such as temperature, net primary production or the corresponding output from Earth system models as input. The fishing effort evolves dynamically based on the modelled fish abundance and key socioeconomic variables.

3.7 *The BOATS model – an overview*

In this section, I provide a brief description of the BOATS model. The key features of BOATS are described using a modified excerpt from the supplemental material of (Scherrer and Galbraith, 2020), in order to provide a general methodological background for Chapters 2 and 3.

BOATS is a mechanistic macroecological size-spectrum model that dynamically simulates the biomass of fish of different sizes on a 1-by-1 degree grid of the global ocean (Figure 6; Carozza et al., 2016). The model also includes a coupled fishing module that simulates dynamic and spatially resolved fishing effort (Carozza et al., 2017). Biomass size-spectra of “fish”, here including all commercially-caught marine organisms, grow according to empirical limits of trophic transfer of energy from NPP (Andersen et al., 2015; Jennings et al., 2008; Sprules and Barth, 2015) and organism-level bio-energetics (Bertalanffy, 1949; Brown et al., 2004; Kooijman, 2008). The model’s ecological parameters are rigorously calibrated to optimize the agreement with Large Marine Ecosystem (LME) catch peaks according to the Sea Around Us Project (SAUP; Pauly and Zeller, 2016), and to lie within the ecosystem-level catch:biomass ranges found in stock assessments in the RAM Legacy database (Ricard et al., 2012). Essential life cycle processes such as maturation, reproduction, recruitment and mortality are resolved using size-based relationships and depend empirically on water temperature and NPP where relevant (Andersen and Beyer, 2015; Charnov et al., 2013; Gislason et al., 2010; Hartvig et al., 2011). Although this kind of macroecological marine ecosystem modeling approach is unsuitable to make detailed analyses of specific stocks and species, it allows predicting the whole-ecosystem, size-resolved fish biomass directly from environmental variables (NPP and SST), globally, using relatively few model parameters. Equations for the ecological model are available in Carozza et al., (2016).

The model developments performed in Papers 1 and 4 in this thesis work build on the original model presented in Carozza et al. (2017). Therefore, I here provide an overview of the original equations that describe the evolution of fishing effort. BOATS uses a Gordon-Schaefer bio-economic model for an open access (OA) fishery (Gordon, 1954; Schaefer, 1954) to simulate the first-order fleet dynamics. This means that the fishing effort on each fish

biomass spectrum f_k , E_k , evolves over time in each cell on the global grid as a function of the average profit (i.e. revenue minus cost; eq 1). E_k is defined as the total energy inputs (W m^{-2}) used in fishing, a measure of nominal effort, which does not include the influence of fishing technology on the ability to catch available fish. All effects of technology are encapsulated in a catchability parameter, q_k , which represents the yield of fish from the available biomass, per unit effort, per unit time. A sigmoidal selectivity function for each group, σ_k , links effort to catch (Hartvig et al., 2011), and generates a catch spectrum,

$$h_k dt dm = q_k \sigma_k E_k f_k dt dm \quad (1)$$

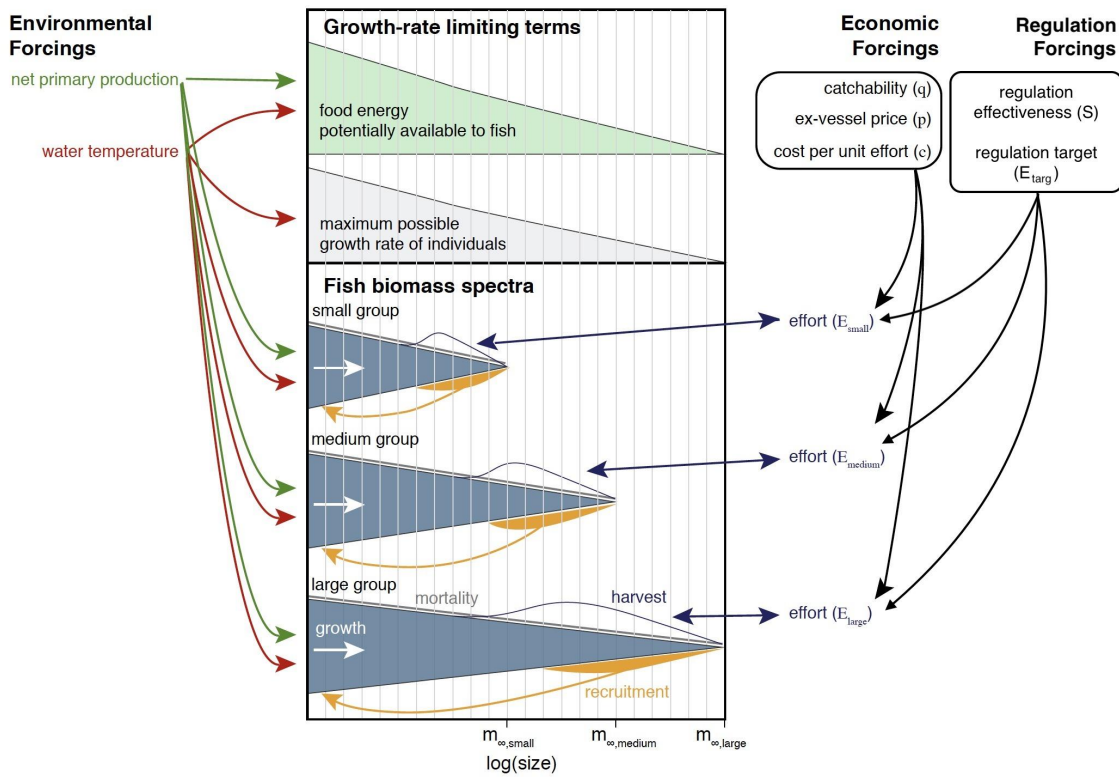


Figure 6. Schematic overview of the BOATS model modified with permission from Carozza et al. (2017) to include the additional drivers from Chapter 2. Global grids of net primary production (NPP) and water temperature determine the growth of three size-structured fish populations (blue area) in each grid cell. Growth is limited by the temperature dependent physiological maximum possible growth rates of individuals (grey area) and the food energy potentially available to a fish of a given size (green area). Red and green arrows indicate influence of temperature and NPP respectively. Fish in each population begin to reproduce at a given size and produce new biomass in the smallest size class (yellow area). Three

economic and two regulation forcings, together with the biomass of available fish, determine the fishing effort E , which results in harvest of the larger fish in each population (blue curve).

Revenue is the product of catch and the ex-vessel price of fish, p_k , and is hence calculated from the catch spectrum by integrating over mass (eq 2, where m_0 is the recruit size and $m_{\infty,k}$ the asymptotic mass of group k). Effort thus ultimately depends on the spectrum of available biomass, f_k , the catchability q_k , the cost of fishing per unit effort, c_k , and p_k . The fleet dynamics parameter K_e ($W^2 m^{-2} \$^{-1}$) determines the rate of change under a given average profit (Seijo et al., 1998).

$$\frac{dE_k}{dt} = K_e \frac{\text{revenue}_k - \text{cost}_k}{E_k} = K_e \frac{q_k E_k dt \int_{m_0}^{m_{\infty,k}} p_k \sigma_k f_k dm - c_k E_k dt}{E_k} \quad (2)$$

BOATS is forced with time-varying 2-dimensional inputs of SST and NPP at a 1-degree spatial resolution, while the coupled bio-economic module requires specifying c_k , p_k , q_k , S and E_{larg} , each of which can be spatio-temporally varying or constant (see Chapter 2). Given a set of external forcings, the model dynamically calculates size-resolved fish biomasses and trajectories of the fishing effort in each grid cell of the model, as well as the ensuing catch and profit. Using historical estimates of the bio-economic forcings, the model reproduces the first-order features of the historical development of fisheries worldwide (Galbraith et al., 2017).

To keep the model computationally efficient, while still relevant for large-scale processes, BOATS is run independently in each cell (i.e. not attempting to predict movement of fish or fleets between grid cells). The biomass spectra of the k size groups in each cell are fished independently. These assumptions mean that spatial differences in the timing, magnitude and dynamics of the state variables emerge from the spatial differences in vital rates as determined by NPP and SST. The model is usually set up with three fish groups ($k = 3$), each of which is resolved by a size spectrum with up to fifty mass classes, with asymptotic masses of 0.3, 8.5 and 100 kg (Carozza et al., 2016). These asymptotic sizes roughly correspond with the length classifications in the SAUP database (Pauly and Zeller, 2016).

To capture uncertainty in the ecosystem model parameters, simulations with BOATS are repeated with different sets of parameter combinations. These sets (the parameter ensemble

members) were chosen from a 10000-member Monte Carlo simulation, using calibration criteria based on global fisheries data, as thoroughly documented by Carozza et al. (2017). Generally, the five ensemble members chosen by Galbraith et al. (2017) are used in order to span a large range of the likely parameter values suggested by the literature, whilst still producing realistic catches and biomasses.

Chapter 2


Regulation strength and technology creep play key roles in global long-term projections of wild capture fisheries

Kim J.N. Scherrer, and Eric D. Galbraith

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Regulation strength and technology creep play key roles in global long-term projections of wild capture fisheries

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Many studies have shown that the global fish catch can only be sustained with effective regulation that restrains overfishing. However, the persistence of weak or ineffective regulation in many parts of the world, coupled with changing technologies and additional stressors like climate change, renders the future of global catches uncertain. Here, we use a spatially resolved, bio-economic size-spectrum model to shed light on the interactive impacts of three globally important drivers over multidecadal timescales: imperfect regulation, technology-driven catchability increase, and climate change. We implement regulation as the adjustment of fishing towards a target level with some degree of effectiveness and project a range of possible trajectories for global fisheries. We find that if technological progress continues apace, increasingly effective regulation is required to prevent overfishing, akin to a Red Queen race. Climate change reduces the possible upper bound for global catches, but its economic impacts can be offset by strong regulation. Ominously, technological progress under weak regulation masks a progressive erosion of fish biomass by boosting profits and generating a temporary stabilization of global catches. Our study illustrates the large degree to which the long-term outlook of global fisheries can be improved by continually strengthening fisheries regulation, despite the negative impacts of climate change.

Keywords: catchability, climate change, collective action, fisheries management, future fisheries, management effectiveness, marine ecosystem modelling

Introduction

The world's annual marine fish catches have stagnated since the 1990s, after more than a century of astonishing growth (FAO, 2018; Watson and Tidd, 2018). The subsequent significant decline in the global catch rate, indicated by data reconstructions, has occurred despite a continued rise of the effective fishing effort (Pauly and Zeller, 2016; Rousseau *et al.*, 2019). Syntheses have suggested that for the world's assessed fish stocks, the median fishery is unsustainably fished (Costello *et al.*, 2016), and data to assess biomass and catch trends are lacking for at least half of the global catch (Hilborn *et al.*, 2020). Together, these

observations raise concerns for the future trajectory of global catches.

The future of global catches, which determines the sustained provision of nutrition and source of income for millions of people worldwide (Teh and Sumaila, 2013; Golden *et al.*, 2016), now depends on multiple interacting forces at play within human societies, including fisheries regulation and governance, technological and economic progress, and the capacity to mitigate climate change (Worm and Branch, 2012; Costello *et al.*, 2016; Galbraith *et al.*, 2017; Österblom *et al.*, 2017; Gaines *et al.*, 2018; Free *et al.*, 2019; Lotze *et al.*, 2019). The complexity of these interacting

factors and their multidecadal time horizons call for an improved mechanistic and quantitative understanding of the drivers that determine long-term outcomes for global fisheries.

The understanding of large and complex socio-ecological systems, such as the global fishery, agricultural, or climate system, has recently been greatly advanced through the development of process-based numerical models. For fisheries, global ecosystem models that allow long-term projections under both climatic and socio-economic change are providing new insights (Lotze *et al.*, 2019) and have the potential to evaluate the outcomes of multiple interacting drivers on marine fisheries (Dueri *et al.*, 2016; Galbraith *et al.*, 2017). While the coarse spatial resolution of these global approaches gives them limited accuracy for any given fishing region, they make it possible to perform mechanistically founded long-term projections that help us understand what the future of global fisheries might hold.

Arguably, the main cause for the detrimental overdevelopment of many fisheries (Hilborn *et al.*, 2005; Branch *et al.* 2006), and the key reason why fisheries need to be effectively regulated (Smith and Sissenwine, 2001), is the problem of open access (OA) (Gordon, 1954; Hardin, 1968). The OA problem can be effectively overcome through a great variety of regulatory systems, as has been demonstrated in diverse fisheries, from indigenous to industrial, throughout history (Ostrom, 1990; Berkes *et al.*, 2000; Caddy and Cochrane, 2001; Hilborn *et al.*, 2005). Today, regulation measures are improving the status (i.e. increasing the fish biomass and lowering the fishing mortality rate) of the majority of the scientifically assessed fish stocks worldwide (Hilborn *et al.*, 2020), moving beyond the earlier, more regionally limited examples of management successes in places like Alaska, Australia or New Zealand (Hilborn *et al.*, 2005). This development encourages optimism about the recovery of global fisheries (Duarte *et al.*, 2020).

However, despite this progress, substantial challenges for fisheries management still lie ahead. The scientifically assessed fish stocks make up only about 50% of the global reported fish catches, or 40% when considering global catch reconstructions (Pauly and Zeller, 2016; FAO, 2018; Hilborn *et al.*, 2020). The remaining unassessed stocks are believed to be in substantially worse states than the assessed stocks, with low biomass and high exploitation rates (Costello *et al.*, 2012; Hilborn *et al.*, 2020). Supporting this notion, global assessments of management effectiveness indicate that inefficient regulation is widespread (Mora *et al.*, 2009; Pitcher *et al.*, 2009; Coll *et al.*, 2013), with lax limits and an inability to enforce compliance with the limits both being key challenges (Bundy *et al.*, 2017; Melnychuk *et al.*, 2017; Ye and Gutiérrez, 2017). This overall inefficiency in keeping fishing pressure at sustainable levels makes it important to investigate the long-term implications of imperfect regulation.

Technological progress, or creep, in catch efficiency (Eigaard *et al.*, 2014; Palomares and Pauly, 2019), has played a tremendously important role in the history of fisheries (Squires and Vestergaard, 2013b) but may also pose a major future sustainability challenge. The great increase in global catches seen over the industrialization of fisheries in the 20th century, and the associated nutritional and economic gains, would not have been possible without development of better fishing gears, vessels, navigation systems and fish-finding methods (Finley, 2016). Recent modelling work suggests that technology-driven catchability increases explain the first-order historical development of global catch (Galbraith *et al.*, 2017). However, while being a large potential source of increased efficiency, technological creep exacerbates

overfishing in poorly regulated fisheries by allowing fishers to obtain profits at progressively lower fish abundance, and shifts the fish biomass at the theoretical OA equilibrium to lower and lower levels (Smith and Krutilla, 1982; Whitmarsh, 1990; Squires and Vestergaard, 2013a, 2015). Thus, if the productivity limits of ecosystems are exceeded, technology-driven catchability increase transitions from a source of increasing catches into a cause for catch decline.

At the same time, the impact of climate change on marine ecosystems is intensifying. In addition to the conspicuous species range shifts and ecosystem restructuring (Perry *et al.*, 2005; Poloczanska *et al.*, 2013), climate change appears to be decreasing the overall ecosystem productivity and thus the global fisheries potential (Lotze *et al.*, 2019; Free *et al.*, 2019). Climate change effects are likely to include a net decrease in marine net primary production (NPP) due to increased stratification (Bopp *et al.*, 2013; Kwiatkowski *et al.*, 2019) while warmer waters will accelerate the metabolic rates of marine ectotherms, resulting in more rapid dissipation of energy and therefore a smaller biomass of upper trophic-level organisms (Carozza *et al.*, 2019; Heneghan *et al.*, 2019). Given that climate change is acting on ecosystems that have already been heavily overfished in many regions, it has recently been suggested that the future effects of climate change can be mitigated by improving fisheries regulation (Galbraith *et al.*, 2017; Gaines *et al.*, 2018).

Many recent analyses have highlighted the potential benefits of reducing human pressures on marine ecosystems (e.g. Blanchard *et al.*, 2014; Dueri *et al.*, 2016; Fulton *et al.*, 2019), but few global studies have assessed the dynamics of fisheries regulation in combination with other human drivers of change. Studies performing long-term global projections based on available stock assessments (Costello *et al.*, 2016; Gaines *et al.*, 2018) are well-grounded in observations where assessments have been made but do not include energetic constraints at the ecosystem level or physiological representations of temperature response. Moreover, although realistic long-term simulations should include technological progress (Galbraith *et al.*, 2017; Palomares and Pauly, 2019), this has generally been lacking in previous global projections (Costello *et al.*, 2016; Gaines *et al.*, 2018). Thus, there is a need for complementary investigations of how imperfect regulation and continuous technological progress affect long-term global fisheries dynamics.

Here, we perform the first whole-ecosystem simulations of global fisheries that simultaneously include a variable effectiveness of fisheries regulation, the possibility of future technological progress, and the bio-energetic impacts of climate change. We describe a new generalized regulation component for the dynamical, spatially resolved BiOeconomic mArine Trophic Size-spectrum model, BOATS (Carozza *et al.*, 2016, 2017) that reflects the tension between the individual profit motivations and a common, socially defined fishing target. We use the model to evaluate the theoretical importance of fisheries regulation and its effectiveness in the face of technological and climatic change and compare the results with observed global catches, with the aim to better understand the mechanisms that will determine long-term sustainability in the global fishery.

Existing model

BOATS is a global, ecosystem-scale model of fish size distributions, coupled with an economic model of profit-driven fishing activity. As inputs, the model uses global time-varying grids of sea surface temperature (SST) and NPP at 1° spatial resolution,

and three economic forcings (the cost of fishing per unit effort c , the ex-vessel price of fish p , and the catchability parameter q), each of which can be spatio-temporally varying or constant (see Model simulations for forcing specifications). The reader is referred to [Carozza et al. \(2016, 2017\)](#) for a thorough description of the original model, which we briefly summarize in the [Supplementary Material](#). The version of the model used here differs only in its inclusion of the new regulation component.

New fisheries regulation component

Main features of regulation

To model the regulation of capture fisheries on a global scale and over long time periods, we must boil the process of regulation down to the most significant features that are common through time and across fisheries types. Fisheries regulation can be seen as a manifestation of collective action, “the action taken by a group (either directly or on its behalf through an organization) in pursuit of members’ perceived shared interests” ([Marshall, 1998](#)), to overcome the OA problem ([Gordon 1954](#); [Hardin, 1968](#)). In a renewable resource system, the shared interest is often to maintain the extraction rate at an optimal level given the group’s values and interests, which could be to maximize food production for a society, or to maximize profit for a fishing collective. Achieving the desired optimum generally requires creating rules and enforcement mechanisms that incentivize (through rewards and/or punishments) individual behaviour in line with the shared interest ([Oliver, 2013](#)).

In many aspects, modern fisheries regulation systems can be considered fundamentally similar to the traditional ones ([Lertzman, 2009](#)) and often apply similar regulation practices ([Gadgil and Berkes, 1991](#)). The same universal components of regulation can be identified in subsistence, small-scale, and industrial fisheries: target setting, rule design, and enforcement ([Table 1](#)). The target may be based on different knowledge systems (e.g. scientific vs. traditional knowledge), and enforcement methods range from traditions and religious beliefs ([Johannes, 1978](#); [Gadgil and Berkes, 1991](#); [Berkes et al., 2000](#)) to fines and criminal sanctions ([Caddy, 1999](#); [Caddy and Cochrane, 2001](#); [Cacaud et al., 2003](#)) depending on the context. However, the basic types of rules tend to be similar across fisheries: generally, they control access to the fishery, protect vulnerable life stages, and limit the allowed catch ([Johannes 1978](#); [Acheson, 1997](#); [Gullestad et al., 2017](#)).

Thus, despite great diversity, the regulation measures applied in fisheries have a universal aim to align fisher behaviour to maintain a broadly desired state of the fish resource. At the same time, the degree to which regulations succeed varies widely ([Melnychuk et al., 2017](#)). We use these fundamental features to create a generalized model of regulated fisheries.

Mathematical representation

Our generalized regulation model contains two key elements: (i) societal determination of a fishing target and (ii) adjustment of fishing effort towards the target by societal enforcement mechanisms. Undesired behavioural responses to regulations, which render management ineffective, is a pervasive problem in fisheries ([Fulton et al., 2011](#)), which we represent explicitly with a societal enforcement strength parameter, S . Since the individual incentive to overfish under OA is the essence of the regulation challenge, we define S as the extent to which OA is eliminated. Fisheries are then modelled on a simple continuum between pure OA behaviour and behaviour perfectly in line with the shared societal interest.

The new component is implemented by modifying equation ([Supplementary S2](#)) so that the fishing effort exerted on a fish size group k , E_k ($W m^{-2}$), evolves over time as

$$\frac{dE_k}{dt} = K_e \frac{\text{revenue}_k - \text{cost}_k}{E_k} e^{-S} + (1 - e^{-S}) K_s (E_{\text{targ},k} - E_k), \quad (1)$$

where $E_{\text{targ},k}$ ($W m^{-2}$) is the societal target for fishing effort, S (dimensionless) is the societal enforcement strength ($S \geq 0$), K_e is the fleet dynamics parameter ($W^2 m^{-2} \$^{-1}$), and K_s ($m^2 s^{-1}$) is the regulation response parameter. Simplified, $\text{revenue}_k = p_k q_k E_k B_k$, where p_k is the ex-vessel price of fish, q_k is the catchability parameter and B_k is the selectable biomass of size group k , while $\text{cost}_k = c_k E_k$, where c_k is the cost of fishing per unit effort (see [Supplementary Material](#) for details). The first term in (1), weighted by the exponential function e^{-S} , thus represents the influence of individual, immediate profit incentives in a population of fishers. The second term, weighted by $1 - e^{-S}$, represents the influence of regulation; it will be negative if $E_k > E_{\text{targ},k}$ and positive if $E_k < E_{\text{targ},k}$.

In real-world fisheries, defining a target in terms of effort (input regulation) rather than catch (output regulation) means that $E_{\text{targ},k}$ must be adjusted to account for technological progress in catchability, known as technological creep ([Walters and Martell, 2004](#)). This problem is addressed in the model by calculating the nominal effort target $E_{\text{targ},k}$ every year depending on a fishing mortality target for fish group k , $F_{\text{targ},k}$ (s^{-1}), and the current catchability, q_k , according to

$$E_{\text{targ},k}(t) = \frac{F_{\text{targ},k}}{q_k(t)}, \quad (2)$$

so that $E_{\text{targ},k}$ varies inversely with q_k to maintain a constant fishing mortality. Thus, although nominal effort is the regulated

Table 1. Examples of universal components of regulation systems in three diverse fisheries.

Fishery	Type	Basis for target	Rules	Enforcement	Source
Maine lobster	Small-scale	Fisher experience and interests	Limited access, seasonal and spatial closures, protection of vulnerable life stages	Social sanctions, moral obligations	Acheson (1997)
Norwegian fisheries	Large-scale	Scientific model	Catch limits, limited access, spatial closures, gear restrictions, protection of vulnerable life stages	Fines, criminal sanctions	Gullestad et al. (2017)
Oceania island	Subsistence	Traditional ecological knowledge	Limited access, seasonal and spatial closures, escapement, protection of vulnerable life stages	Taboos, religion	Johannes (1978)

variable in our model, the real target is actually $F_{\text{targ},k}$ which makes it equally applicable to output targets (e.g. quotas) or well-designed adaptive input targets (e.g. access, fishing time, or engine size restrictions). In reality, insufficient knowledge and ecosystem variability may prevent accurate estimation of a fishing target (Mace, 2001), and strong trade-offs between objectives may result in biologically unsustainable targets (Pascoe *et al.*, 2017). The impact of such uncertainty in target setting could be explored in our model framework, but we do not model this aspect of imperfect regulation here (as explained in Regulation target).

The diverse mechanisms by which regulation is enacted (e.g. those listed in Table 1) cannot feasibly be explicitly modelled at the global scale. Thus, we treat regulation systems implicitly, meaning that we consider only the extent to which OA is eliminated and not the mechanisms by which this is achieved (whether it is through quotas, seasonal closures, or licensing). The fact that some structures are more effective than others (e.g. Hilborn *et al.*, 2005; Ostrom, 2009; Fulton *et al.*, 2011) is captured by variations in S , which could reflect the effect of diverse enforcement mechanisms, like local, governmental, satellite, or divine surveillance, or social, monetary, or religious sanctions, that promote compliance (Table 1). We do not treat these factors implicitly because they are unimportant or uninteresting, but rather as a useful simplification to generate tractable global models of regulation.

Behavioural change is often hindered by structural and psychological barriers (Amel *et al.*, 2017). In fisheries, uncertainty and conflicting values contribute to making regulation reactive rather than proactive (Rosenberg, 2003). Therefore, we assume that regulation will not begin before a substantial decline in catch of a given fish size group occurs at a given location. We define the time of regulation onset for a size group, $t_{\text{ro},k}$ as the time when catch declines below a certain fraction, θ_{ro} , of the observed maximum historical catch, $H_{\text{max},k}$. We here use $\theta_{\text{ro}} = 0.75$, reflecting a relatively rapid reaction to declining catch. As long as the fishing mortality ($q_k E_k$) is larger than $F_{\text{targ},k}$ regulation is initiated at

time $t_{\text{ro},k}$. This guarantees that regulation is only initiated after local overfishing has occurred:

$$\text{Initiate regulation if } \begin{cases} H_k(t) < \theta_{\text{ro}} H_{\text{max},k} \\ q(t) E_k(t) > F_{\text{targ},k} \end{cases}. \quad (5)$$

Once initiated, regulation forces the nominal effort towards $E_{\text{targ},k}$. The value of K_s determines the rate of effort change due to regulations. For example, the abrupt establishment of well-enforced marine protected areas and fishing moratoria can result in rapid and substantial effort decreases for individual stocks or whole ecosystems over short time periods, as would be represented by a large value of K_s . We here choose a value ($K_s = 4 \times 10^8$) that allows the nominal effort to respond on a timescale of a few years, so that the model can stabilize at the fishing target when S is high in our scenarios.

Model simulations

We explore the emergent dynamics of the new global regulation model through a suite of hindcasts and future scenarios that focus on the interactions with technological progress and climate change. Following Galbraith *et al.* (2017), the simulations are performed by forcing the model with constant c (1.8×10^{-4} \$ kW⁻¹) and constant p (1.1 \$ kg⁻¹) for all grid cells and size groups, reflecting global average values. The possible effects of future changes in average fish prices or fishing costs are discussed in Additional economic drivers. The scenarios for regulation, technological progress, and climate change are described below and summarized in Table 2. We also describe a simulation protocol for comparing the model with observed fisheries in Alaska.

Regulation target

We here use the maximum sustainable yield (MSY) as an illustrative target for regulation. We define the target as $F_{\text{MSY},k}$ (2), the fishing mortality associated with maximum catch from a long-term simulation in which catchability increases very slowly,

Table 2. Overview of model forcing variables used in scenarios.

	Forcing variable	Meaning	Values applied	Motivation	Domain
Technology	q	Embodied and disembodied fishing technology and skill	I. 5% increase year ⁻¹ 1950–2100 II. 5% increase year ⁻¹ until 2020, then stable	I. Exogenous technology adoption, economic incentives II. Exogenous technology stagnation, no incentives in fisheries	Equal for all grid cells and fish size groups
Regulation	F_{targ}	Fishing mortality target for regulation	I. F_{MSY} II. $0.3 \times F_{\text{MSY}}$	I. Maximized food production, SDG 13 II. Precautionary target	Specific for each cell and fish size group
	S	Regulation strength	I. $S = 0$ II. $S = 3$ III. $S = 10$	I. Open access fishing II. Weak regulation III. Strong regulation	Equal for all grid cells and fish size groups
Climate	NPP	Net primary production, upper 75 m	I. Time varying (1950–2100) according to IPSL RCP 8.5 II. Stabilizing at 2015–2020 levels according to IPSL	I. Upper range of projected climate change impact II. Comparison scenario with no further climate change	Specific for each grid cell
	SST	Average sea surface temperature, upper 75 m	I. Time varying (1950–2100) according to IPSL RCP 8.5 II. Stabilizing at 2015–2020 levels according to IPSL	I. Upper range of projected climate change impact II. Comparison scenario with no further climate change	Specific for each grid cell

approximating steady state (see Galbraith *et al.*, 2017). Experiments were run using the $F_{MSY,k}$ at each simulation year for each fish size group, corresponding to the respective temperature and NPP conditions given by the Institute Pierre Simon Laplace (IPSL) Earth System Model. Since there are no explicit interactions between the three size groups (only within each of the three size spectra), the MSY represents a size group maximum in an idealized ecosystem where small, medium, and large fish occupy independent niches. We emphasize that, although our main simulations use an MSY target for illustration, a more precautionary target than MSY is generally recommended given real-world uncertainties (Mace, 2001; UN General Assembly, 2015).

Societal enforcement strength scenarios

S represents the strength with which the effort dynamics of a pure OA fishery are opposed. While this definition is theoretically useful, S lacks a directly measurable counterpart. For illustration, we use three values to represent no regulation ($S=0$, OA), weak regulation ($S=3$), and strong regulation ($S=10$). To better interpret the meaning of these S values, we also compare the model's performance with some well-regulated stocks (see Model comparison with observed Alaskan fisheries). Although it should be feasible to use global proxies to estimate the variations in enforcement strength between jurisdictions and over time, such as the World Governance Index or estimates of fisheries management effectiveness (Mora *et al.*, 2009; Pitcher *et al.*, 2009; Melnychuk *et al.*, 2017), these qualitative estimates are not directly translatable to numerical values of S . Thus, as a simple first step, we here simulate global catches under spatially and temporally constant S .

Technology scenarios

Technological improvements that increase catch efficiency can be modelled by increasing the catchability parameter, q (1 and Supplementary S1), reflecting both embodied and disembodied aspects of technology (Pauly and Palomares, 2010; Squires and Vestergaard, 2013b). Empirical studies have estimated an average rate of increase of 2–8% year⁻¹ in diverse fisheries and time periods (Wilberg *et al.*, 2009; Pauly and Palomares, 2010; Squires and Vestergaard, 2013b; Eigaard *et al.*, 2014; Palomares and Pauly, 2019). Most of these estimates consider only a subset of technological aspects and therefore would be expected to underestimate the overall rate of catchability increase (Scherrer and Galbraith, 2020). Consistent with this expectation, the rate of q increase in BOATS that best reproduces the observed global catches is a relatively high value of 5% year⁻¹ (see Galbraith *et al.*, 2017 for model sensitivity to different rates).

Technological progress often undergoes local hiatuses, and its future rate will undoubtedly vary, but the underlying mechanisms are difficult to untangle, making predictions highly uncertain (Nagy *et al.*, 2013). We therefore choose two simple model scenarios that bracket the likely range: one with a continued constant catchability growth rate of 5% year⁻¹ throughout the 21st century and the other stagnating, with catchability increasing only until the year 2020 value after which it is held constant. We impose the change in catchability homogeneously across all grid cells.

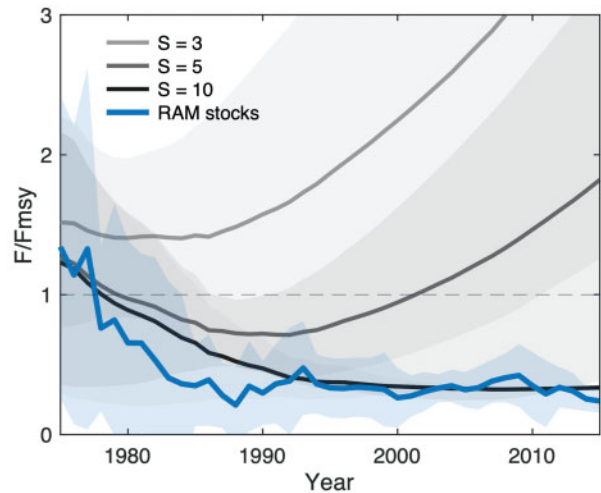


Figure 1. Modelled and empirical fisheries reference points in a well managed fishery. Lines show stock assessments (blue) and corresponding modelled fish populations in BOATS under different regulation effectiveness (grey) in US Alaska. If $S \geq 10$, the F is maintained at 30% of F_{MSY} over the historical period like in observations. For lower, constant S , technological creep in the model makes F diverge from the target level. Shaded areas show uncertainty ranges: 1 SD among stock assessments, and model ensemble members.

Climate change scenarios

To investigate global fisheries dynamics under climate change, we used gridded monthly NPP and SST output from the IPSL Earth System Model as input for BOATS. We use Representative Concentration Pathway (RCP) 8.5 for the upper-range baseline scenario with no climate mitigation and provide a comparison simulation where the average present day (2015–2020) greenhouse gas levels are kept constant into the future. These two idealized scenarios span a wide range of possible futures in a way that is consistent with the scenarios for technology. Separate simulations were performed using monthly climatological fields of empirical NPP and SST [as in Carozza *et al.* (2016)], and are used in Different global catch trajectories.

Model comparison with observed Alaskan fisheries

To provide a real-world example, we compare the model output to stock assessments in Alaskan fisheries, which have a long history of effective regulation (Hilborn and Ovando, 2014), mainly through strict quota systems (Worm *et al.*, 2009). Technological progress (for example improvements in fish finding, navigation and processing) has undoubtedly raised the catchability of the Alaskan fleet during the past decades. Yet, a survey of all the stocks in the “US Alaska” region in the RAM legacy database (version 4.4) shows that the average biomass weighted fishing mortality (F) has been maintained near 30% of the fishing mortality corresponding to MSY (F_{MSY}) since the late 1980s (Figure 1), testament to the high degree of regulation effectiveness.

We applied a similar precautionary target of 30% of F_{MSY} , assumed a 5% year⁻¹ catchability increase with the RCP 8.5 climate scenario, and tested multiple values for S ($=3, 5, 10$) to investigate which level of enforcement strength would best recreate the historical trends in Alaskan stocks. The RAM legacy data show that about 80% of the total catch during 1980–2014 was from fish

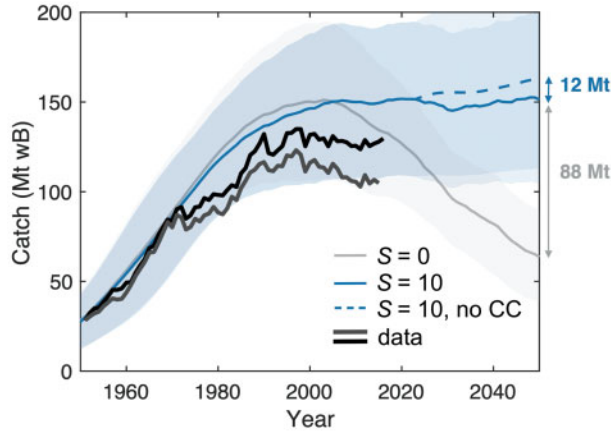


Figure 2. Simulated and empirical global catch (1950–2050). Two end-member scenarios with continued technological progress and either open access ($S = 0$, light grey) or strong regulation ($S = 10$, blue) are compared with historical catch data (1950–2014) from the SAUP (dark grey) and Watson and Tidd (black; 2018). Solid and dashed blue lines show results with (RCP 8.5) and without future climate change effects (no CC), respectively. Shaded areas show uncertainty ranges (1 SD among model ensemble members) of simulated catches. With technological progress of $5\% \text{ year}^{-1}$, regulation plays a larger role than climate, indicated by the grey and blue arrows, respectively.

stocks with an asymptotic size corresponding to that of the large fish size group modelled here ($<8.5 \text{ kg}$ or 90 cm ; Carozza *et al.*, 2016; Pauly and Zeller, 2016; FishBase, 2020), while vessel tracking indicates that fishing mainly takes place in highly productive waters surrounding Alaska (Kroodsmas *et al.*, 2018). We therefore show BOATS results for the large fish group, averaged over all grid cells of the Bering Sea and Gulf of Alaska large marine ecosystems that have higher NPP than the regional average.

Results

Comparison with observed Alaskan fisheries

Figure 1 compares the simulated BOATS historical trajectories of fishing mortality in the US Alaskan fisheries with different levels of S with the historical fishing mortality obtained from stock assessments. The modelled trajectory of F/F_{MSY} for this subset of fish populations in BOATS coincided with the observations when S approached 10 (Figure 1). We therefore take a value of $S=10$ as representing highly effective, yet achievable, regulation.

Range of possible future catches

Figure 2 compares historical global catch estimates to the range of model ensemble trajectories, including technological progress, two levels of regulation, and two climate projections (Table 2). The empirical estimates suggest that global catches have either declined (Pauly and Zeller, 2016) or reached a plateau (Watson and Tidd, 2018) over the past decades (Figure 2). Neither of the estimates are consistent with the short peak and rapid global catch decline that the model simulates under global OA, but the estimate by Pauly and Zeller (2016) is clearly inconsistent with the stable plateau of globally strong regulation.

In contrast to the agreement between the two simulated historical regulation trajectories, the future regulation scenarios diverge dramatically if technological progress continues apace. Under

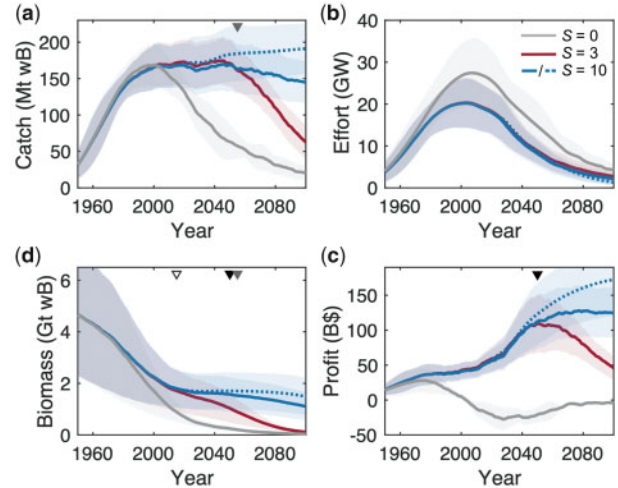


Figure 3. Simulated fisheries trajectories under continued technological progress. Aggregated global (a) catch, (b) effort, (c) profit (in year 2000 US\$), and (d) biomass under no ($S = 0$, dark grey), weak ($S = 3$, red), or strong ($S = 10$, blue) regulation. Weak regulation prolongs the period of high catch and profit and slows down biomass loss, but to achieve perpetual sustainability, open access must be strongly offset ($S > 10$). The dashed blue line shows the development without future climate change. Triangles mark the start of divergence between the weak and strong regulation scenarios.

globally strong enforcement ($S=10$, solid blue line), the catch plateaus at $150 \pm 50 \text{ Mt wB year}^{-1}$ by year 2050 under climate change scenario RCP 8.5, with potential for an 8% increase in catches if the climate was stabilized. On the other end of the spectrum, pure OA fishing ($S=0$) with climate change results in a 60% catch decrease by the middle of the century relative to the peak catch in the early 2000s, a loss of about 90 Mt year^{-1} compared to the strongly regulated case.

Global outcomes of variable regulation strength

Figure 3 shows global trajectories of four key fisheries variables under three different regulation strengths and continued technological progress. The catch projections in Figure 3a carry on from those shown in Figure 2, with the addition of a scenario with weak regulation ($S=3$). For the latter, global catches remain high and close to the strong regulation case until mid-century but then decline to $50 \pm 20 \text{ Mt year}^{-1}$ in 2100 (Figure 3a). This result is qualitatively robust to the choice of regulation target; a long-term catch decline under weak regulation also occurs when the target is 30% of $F_{\text{MSY},k}$ (Supplementary Figure S1).

Regulation places a limit on the nominal fishing effort, reducing it relative to OA by about 30% in 2020 and by 35–70% in 2100 depending on the scenario (Figure 3b). If the fishery is unregulated, the simulated effort continues to increase after the catch peak despite stagnating catches, as is the case in effort reconstructions (Rousseau *et al.*, 2019). The reduction in effort achieved by regulation greatly improves the projected global profit (Figure 3c), with the strongly regulated fishery yielding a continuously increasing profit over time thanks to the technology-driven increase in catch efficiency. Under weak regulation, profit remains high in the short term and is continually positive throughout the rest of the century.

While weak regulation significantly increases profits compared to the corresponding OA scenarios, it does relatively little to mitigate the loss of fish biomass (Figure 3d). Although $S = 3$ slows the decline in global biomass in the near future, biomass diverges from the strong regulation scenarios early in the 21st century (marked by the empty triangle in Figure 3d). In the long term, weak regulation fails to fulfil conservation objectives; by simulation year 2100, the global biomass has been fished down to $<3\%$ of the pristine biomass (5 ± 2 Gt), and profit also dwindles. Under strong regulation, the global biomass initially stabilizes at about 30% of the pristine biomass, the model estimate of biomass associated with global average MSY (B_{MSY}). However, in the final decades, biomass begins to decline even under $S = 10$ (Figure 3d).

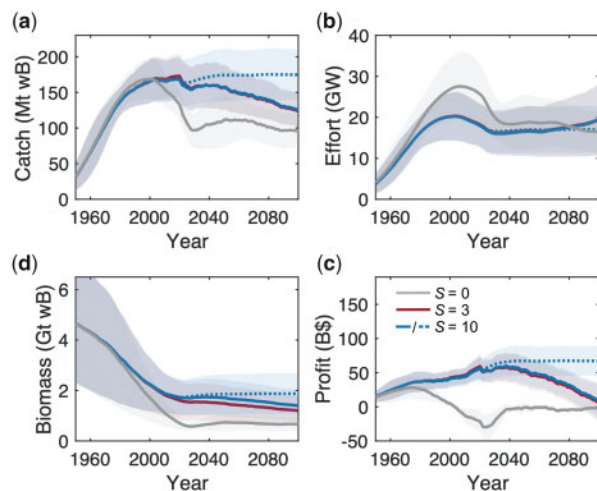


Figure 4. Simulated fisheries trajectories under stabilizing technology. Aggregated global (a) catch, (b) effort, (c) profit (in year 2000 US\$), and (d) biomass under no ($S = 0$, dark grey), weak ($S = 3$, red), or strong ($S = 10$, blue) regulation. The importance of regulation strength is greatly diminished if technology stabilizes and the race between catchability and regulation strength ceases. Still, regulated fisheries yield substantially higher benefits. The dashed blue line shows the development without future climate change.

Abrupt technological stagnation

The importance of regulation strength is greatly diminished in the scenarios where catchability abruptly stops increasing at the year 2020 level (Figure 4). In this case, the largest gains that can be achieved through stronger regulation are about 30% more catch than OA by end-of-century if climate change continues, with roughly twice as much global fish biomass, and the difference between strong and weak regulation is small (Figure 4a and d). Moreover, without technologically driven improvements in catch efficiency, the decreasing catch per unit effort under climate change results in a long-term decrease in global profits. In contrast, a stabilizing climate in this case leads to completely stabilizing biomass, catch, and profit, which means that these three factors are considerably higher than under scenarios with climate change by the end of the century.

Discussion

Different global catch trajectories

We find that under continued technological progress, different levels of regulation strength generate qualitatively different global catch curves with very different implications. In the absence of regulation (Figure 5a), the global catch curve increases, peaks, and declines, reflecting the sum of catch trajectories in individual regions throughout the world (grey lines). Under weak regulation, the global catch passes through a temporary plateau (Figure 5b), as regulation slows down the post-peak catch decline in each region, until technological progress overcomes the societal enforcement strength. If strong regulation pushes all regional catches to approach their local MSY targets (Figure 5c), rebuilding efforts and new exploitations lead to a global increase prior to stabilization at the global MSY (which in this illustration is unaffected by climate change).

A “Red Queen race” in regulated fisheries

Our simulations illustrate a persistent challenge that arises under imperfect regulation. Increasing catchability ultimately leads to higher instantaneous individual profit, strengthening the profit incentive even as stocks are depleted and yields fall. From (1), it can be inferred that if S is constant, this applies regardless of the exact rate of technological progress. Thus, although the time

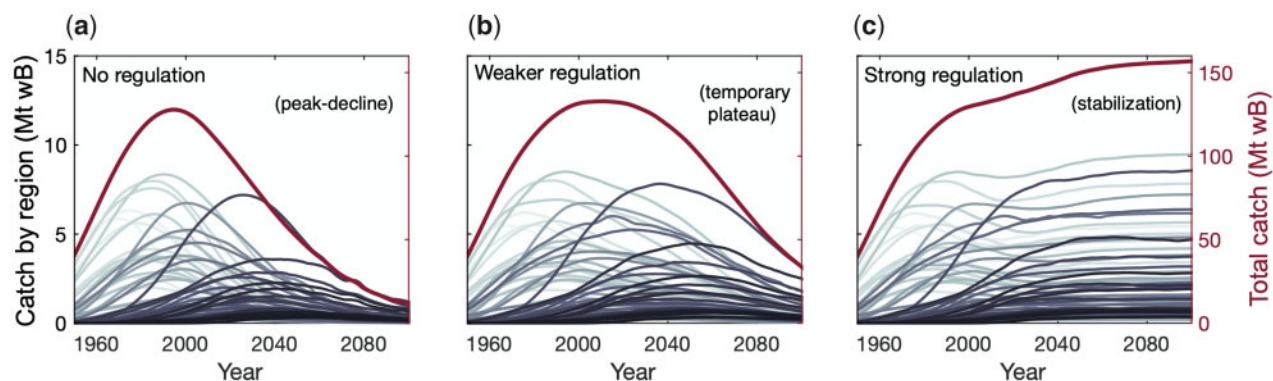


Figure 5. Illustration of the impact of regulation strength. Three types of global catch curves (thick red line) arise under different regulation strengths and continued catchability increase ($5\% \text{ year}^{-1}$). Grey lines show underlying catches in each of the world’s large marine ecosystems, and shade of grey indicates the timing of the catch peak. In contrast with the unregulated case, $S = 0$ (a), weaker regulation, $S = 1.2$ (b) results in a temporary global catch plateau, while strong regulation, $S = 10$ (c) results in growing and stabilizing global catches. Illustrations are representative of a stable climate.

horizon depends on S and q , long-term sustainability eventually depends on a race between improving catchability and improving regulation—in line with the arguments of Whitmarsh (1990). We call this the “Red Queen race” of fisheries regulation, analogous to the ecological Red Queen hypothesis that organisms must continuously evolve to keep up with the evolution of competitors and predators. This Red Queen race occurs even though we here assume that the effort target is perfectly adjusted for technological creep [by continuously adjusting the nominal effort target according to (2)], a correction that can be very difficult to make in input-regulated fisheries (Branch *et al.*, 2006; Eigaard *et al.*, 2014).

The role of technological creep is here shown using a model in which regulation reduces OA behaviour in favour of a societal target, but similar dynamics should arise under alternative formalizations of fisheries regulation. In models of compliance, regulation can be represented as additional costs of fishing, either monetary (fines/taxes) or non-monetary (social/moral) (see Sutinen and Kuperan, 1999; Nøstbakken, 2008). Adding regulatory costs in the original effort equation (Supplementary S2) would also give rise to a Red Queen race; as increasing q increases potential revenues, the costs (i.e. fines, taxes, or fear of sanctions) would have to increase continuously at a rate that counteracts catchability increases, if catches are to be sustainable.

The realized impact of the Red Queen race will depend on the rate of continued technological progress, as illustrated by the two contrasting scenarios (Figures 3 and 4). Predicting how future technology will progress is difficult, but fisheries technologies generally originate from exogenous fields (e.g. echo location, positioning systems, material development, robotics, ocean modelling, or artificial intelligence), while also responding to economic incentives (Hilborn *et al.*, 2005; Squires and Vestergaard, 2013b). This suggests that continued technological progress in fisheries is likely as long as the overall global rate of technological progress does not stagnate. We underline, however, that the future technology scenarios used here are exploratory, intended to help illustrate mechanisms.

Hidden losses

Our simulations show that, under weak regulation, technological progress helps to maintain a relatively high global profit and extends the period of relatively stable catches, hiding a steadily declining biomass (Figure 6). These hidden losses are in line with theoretical work on economic optimality under technological progress in fisheries (Squires and Vestergaard, 2015). Because catch and profit are easier to measure than biomass, technological progress could thus give a false sense of security, especially by creating a temporary plateau in total catches (Figure 5c). These hidden losses would be expected to render fish conservation particularly difficult and would become more severe if ex-vessel prices increase in future (rather than staying constant as in our simulations).

Additional economic drivers

The effects of many additional economic factors and developments, not explicitly included in our scenarios, can be discerned from the effort equation (1). For example, the FAO projects that the global demand for fish will rise faster than the supply in the upcoming decade due to the growth of both the human population and their incomes, and the expected slowdown of

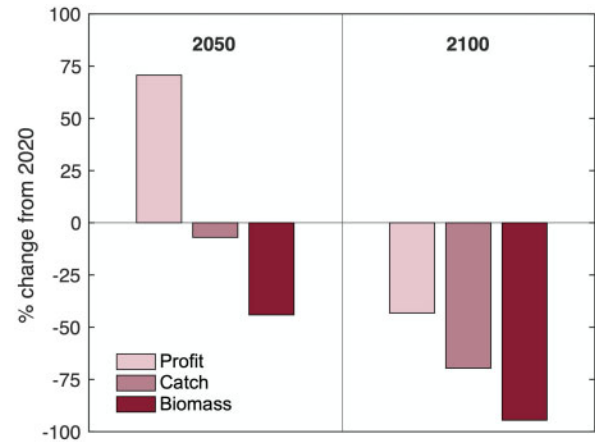


Figure 6. Hidden losses under weak regulation. The percent change in ensemble average global profit, catch, and biomass is shown for 2050 and 2100 relative to year 2020, for the simulation with weak regulation ($S = 3$), continued technological progress, and climate change. In year 2050, weak regulations uphold relatively high profit and stable catch, masking a substantial biomass decline that ultimately leads to a large decline of catch and profit by 2100.

aquaculture growth (which also requires feed from capture fisheries; FAO, 2018). If such a development was to drive up real ex-vessel prices of wild-caught fish, profitability would be increased, enhancing the profit incentive and weakening the effect of regulation, all else being equal (as shown under OA conditions in Galbraith *et al.*, 2017). Thus, rising prices would have a dynamical impact similar to that of technological progress. Similarly, subsidies that reduce the cost of fishing, or encourage technology uptake (Sumaila *et al.*, 2016), would also exacerbate biomass depletion and catch losses. Conversely, higher cost per unit effort, e.g. due to rising oil prices in response to carbon pricing, would abate the profit incentive, making a given strength of regulation more effective. However, explicitly modelling price dynamics would be a possible avenue for future work.

Real-world variability in regulation

Since this study focused on mechanistic understanding and since variability in regulation effectiveness is difficult to quantify globally, S was held spatially homogeneous and constant in our scenarios. In reality, regulation effectiveness varies between regions, countries, or even individual fish stocks, as it depends on complex interactions between socio-economic and ecological factors (Hilborn *et al.*, 2005; Ostrom 2009; Fulton *et al.* 2011). Different management solutions, tailored to the local context, are therefore required to achieve effective regulation for different target species, fishing techniques, and socio-economic circumstances (Duarte *et al.*, 2020). Although all these nuances are unfeasible to include into a global model, some general patterns of regulation effectiveness are suggested by global studies. Generally, developed and high-latitude regions have higher regulation effectiveness, likely due to their higher capacity to assess fish stocks and enforce regulations (Ye and Gutiérrez, 2017; Melnychuk *et al.* 2017; Hilborn *et al.*, 2020). To provide more detailed projections, future work could find ways to translate such knowledge into regionally varying values for S .

Potential future benefits from the global fishery

The results from our global, whole-ecosystem modelling approach strongly corroborate stock-assessment-based estimates in predicting large benefits of strong regulation and fishery rebuilding (Worm *et al.*, 2009; Costello *et al.*, 2016). The analysis by Costello *et al.* (2016) projected biomass, catch, and profit to be about 0.8 Gt, 70 Mt year⁻¹, and 50 B\$ year⁻¹, respectively, in 2050 for a subset of global stocks under a perfectly implemented global MSY strategy. Our mean estimates in 2050 under $S = 10$ and no future climate change are consistently about twofold for all three measures (1.7 Gt, 160 Mt year⁻¹, and 120 B\$ year⁻¹; Figure 3). The higher values arise because BOATS is designed to simulate all global catch, including an estimate of unreported catches (Pauly and Zeller, 2016), as well as possible future expansions in targeted fish, such as a greater exploitation of small fish in the deep sea (Carozza *et al.*, 2017). Given the fact that our approach models the flow of energy through the whole ecosystem, while that of Costello *et al.* (2016) uses logistic growth models for individual fish stocks, we find the remarkably strong agreement of the relative impacts on biomass, catch, and profit arrived at by the two approaches to be very encouraging. The finding that strong regulation can more than offset climate-driven productivity declines is also in line with perfectly regulated simulations with the same model (Galbraith *et al.*, 2017) as well as with a thermal-niche-based approach (Gaines *et al.*, 2018).

The model suggests that the maximum possible global catch is larger than the observed historical maximum. If effort was strongly regulated to achieve MSY and if the climate was stabilized, simulated catches and profits continue to increase towards 180 ± 40 Mt year⁻¹ and 170 ± 50 B\$ year⁻¹ throughout the 21st century. However, in line with previous work, unmitigated climate change decreases the MSY by almost 30% by 2100 (the difference between the blue dashed and solid lines in Figure 4a). Thus, the sustainable future catch may yield somewhat less fish than at the historical peak, though it could be far more profitable. Furthermore, the results imply that a gradual catch decline following global peak [as found by Pauly and Zeller (2016)] is consistent with globally weak fisheries regulation, potentially exacerbated by climate change effects.

Finally, we underline that mesopelagic fish are not well represented by our model since they have not been targeted by fisheries and therefore were not included in the model tuning (Carozza *et al.*, 2017). If the mesopelagic fish biomass is as large as recently suggested (Proud *et al.*, 2019), and if future technological progress enables efficient catch methods, they may support large additional catches beyond those estimated here. This would however not alter our results for currently exploited species, and mesopelagic fisheries would also be subject to the Red Queen race of regulation.

Conclusion

Fisheries regulation includes a diverse array of collective actions that counteract detrimental OA fishing, all of which define a fishing target and implement practices to achieve it. We have described a new, simple mathematical formulation to represent these universal features in a global bio-economic model, and used it to explore how variable regulation effectiveness, technological progress, and climate change may shape the future of global fisheries.

Our model scenarios suggest that, under continued technological progress, weak fisheries regulation results in hidden biomass losses and fails to ensure long-term sustainability due to what we term the “Red Queen race” of fisheries regulation. Rising demand for fish would further exacerbate this race. As a result, regulation effectiveness must be continually improved to sustain the global fishery. Optimally, under strong regulation and technological progress, simulated global catches, biomass, and profit approach 180 ± 40 Mt year⁻¹, 1.7 ± 0.7 Gt, and 170 ± 50 B\$ year⁻¹, respectively. Unmitigated climate change is likely to decrease the maximum catch potential (MSY) and fish biomass, but global catches can largely be maintained at present levels throughout the 21st century if regulations are effective and technological progress continues.

The dynamics that arise in our regulated fisheries model outline key long-term challenges for global fisheries. We find that global fisheries regulations must continue to be strengthened as long as catchability in the fishery continues to increase. This reinforces the great importance of initiatives that strengthen regulations, from the revitalization of traditional community-based management (Johannes 2002; Ostrom, 2009), improved leadership and community cohesion (Gutiérrez *et al.*, 2011), and implementation of catch share systems (Costello *et al.*, 2008), to technologically aided monitoring, control, and surveillance (Caddy, 1999; McCauley *et al.*, 2016; Bradley *et al.*, 2019). The degree to which technological improvements can empower regulation may play a critical role in determining the outcome of the Red Queen race of fisheries regulation. If successful, such regulatory advances might prevent a dramatic decline in global biomass and catches over the 21st century and ensure an indefinite supply of wild-caught fish to support human nutrition and well-being.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Data availability statement

The model code and output supporting the findings of this study are available from the corresponding author on request.

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Chapter 3

Marine wild-capture fisheries after nuclear war

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Marine wild-capture fisheries after nuclear war

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Nuclear war, beyond its devastating direct impacts, is expected to cause global climatic perturbations through injections of soot into the upper atmosphere. Reduced temperature and sunlight could drive unprecedented reductions in agricultural production, endangering global food security. However, the effects of nuclear war on marine wild-capture fisheries, which significantly contribute to the global animal protein and micronutrient supply, remain unexplored. We simulate the climatic effects of six war scenarios on fish biomass and catch globally, using a state-of-the-art Earth system model and global process-based fisheries model. We also simulate how either rapidly increased fish demand (driven by food shortages) or decreased ability to fish (due to infrastructure disruptions), would affect global catches, and test the benefits of strong prewar fisheries management. We find a decade-long negative climatic impact that intensifies with soot emissions, with global biomass and catch falling by up to $18 \pm 3\%$ and $29 \pm 7\%$ after a US–Russia war under business-as-usual fishing—similar in magnitude to the end-of-century declines under unmitigated global warming. When war occurs in an overfished state, increasing demand increases short-term (1 to 2 y) catch by at most $\sim 30\%$ followed by precipitous declines of up to $\sim 70\%$, thus offsetting only a minor fraction of agricultural losses. However, effective prewar management that rebuilds fish biomass could ensure a short-term catch buffer large enough to replace $\sim 43 \pm 35\%$ of today's global animal protein production. This buffering function in the event of a global food emergency adds to the many previously known economic and ecological benefits of effective and precautionary fisheries management.

food from the ocean | fisheries management | abrupt climate change | nuclear winter | global food security

Nuclear weapons continue to pose a threat to humanity. Although global nuclear weapons stockpiles are lower today than at their peak in 1986, arsenals are growing in India, Pakistan, and North Korea, adding to those already maintained by the United States, Russia, China, France, the United Kingdom, and Israel (1–4). The United States and Russia are both undertaking extensive modernization programs for warheads and delivery systems (5, 6), and increased tension in South Asia and recent failures to renew arms control treaties have intensified concerns about the prospect of imminent nuclear war (7, 8). Beyond the devastating direct impacts, the soot inputs from fires ignited by nuclear air bursts are likely to cause global cooling and reductions in sunlight (9–13), similar to historical volcanic eruptions (Table 1) (3, 14–23). Nuclear-war–driven climate perturbations are expected to disrupt global primary productivity, with a potential threat to human lives through crop failure in breadbasket regions and subsequent food shortages worldwide (24–28).

Modeling approaches make it possible to evaluate the effects of nuclear war of varying magnitudes, with the model simulations used here (3, 15) agreeing well with earlier simulations in terms of climate response (12, 16, 17, 29). Process-based crop modeling frameworks have recently made it possible to further investigate potential implications of a nuclear conflict for global food security. Jägermeyr et al. (28) found that even a limited regional nuclear conflict between India and Pakistan, using less than 1% of the world's nuclear weapons (5-Tg soot), is likely to decrease global caloric crop production by 11% for 5 y. This decrease would be four times larger than the highest observed historical anomalies. The high-latitude production shock would propagate globally through food trade dependencies. These alarming findings make it important to investigate how other parts of the global food production system may be affected by a nuclear war, in particular global fisheries, on which many societies depend (30, 31).

The responses of global marine ecosystems and fisheries to both volcanic and nuclear-war–driven abrupt climate perturbations are largely unknown. Here, we explore the impacts of

Significance

Nuclear conflict poses the chilling prospect of triggering abrupt global cooling, and consequently, severely reduced crop production. However, the impacts on marine fisheries are unknown. If agricultural yields fall on land, could we turn to the sea instead? Here, we show that agricultural losses could not be offset by the world's fisheries, especially given widespread overfishing. Cold temperatures and reduced sunlight would decrease the growth of fish biomass, at worst as much as under unmitigated climate change. Although intensified postwar fishing could yield a small catch increase, dramatic declines would ensue due to overharvesting. However, effective prewar fisheries management would create a substantial buffer of fish in the ocean, greatly increasing the oceans' potential contribution during a global food emergency.

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Table 1. Overview of nuclear-war-driven climatic perturbations

	Soot load	Warring nations	Δ Radiative forcing, $W \cdot m^{-2}$	Δ SST, $^{\circ}C$	Δ NPP, %	Anomaly duration, y	Description
War simulations used in this study	5 Tg	India and Pakistan	-10.9	-0.5	-3	~10	Lower-end regional conflict; 100 15-kt weapons
	16 Tg	India and Pakistan	-31.1	-1.4	-7	~10	Intermediate regional conflict; 250 15-kt weapons
	27 Tg	India and Pakistan	-46.9	-2.3	-10	~10	Intermediate regional conflict; 250 50-kt weapons
	36 Tg	India and Pakistan	-57.8	-2.9	-12	~10	Higher-end regional conflict; 250 100-kt weapons
	47 Tg	India and Pakistan	-68.7	-3.5	-16	~10	Upper-limit regional conflict; 500 100-kt weapons
Previous war simulations	150 Tg	Russia and United States	-115.3	-6.4	-37	~10	Nuclear superpower conflict; ~4,400 100-kt weapons
	5 Tg	India and Pakistan	~ -10	-0.8	NA	~10	From ref. 16
	5 Tg	India and Pakistan	-8.2 to -10	-0.1 to -0.6	NA	~10	From ref. 17, range depends on war duration
Other climatic perturbations	150 Tg	Russia and United States	-84.7	NA	NA	~10	From ref. 18
	Perturbation						
		Pinatubo eruption (1991 CE)	-6.5 \pm 2.7	~ -0.1	NA	~2	Refs. 19–21
		Tambora eruption (1815 CE)	-17.2 \pm 4.9	~ -1	NA	~2	Refs. 19–21
		Samalas eruption (1257 CE)	-32.8 \pm 9.6	~ -1 to -2	NA	~2	Refs. 19–21
		RCP 2.6 global warming (2100 CE)	+2.6	0 to +1	-2 to +1	—	Refs. 22 and 23
	RCP 8.5 global warming (2100 CE)	+8.5	+2 to +4	-11 to -4	—	Ref. 22	

Radiative forcing, sea surface temperature (SST), and oceanic net primary productivity (NPP) anomalies are the maximum annual global means. Anomaly duration is the atmospheric residence time of aerosols. Details for India–Pakistan scenarios are in ref. 3, and for United States–Russia in ref. 15. Previous nuclear war simulations, historical volcanic anomalies, and projected global warming anomalies are given for comparison. NPP has not been reported for previous simulations of nuclear war or volcanic eruptions, indicated by not available (NA).

nuclear war scenarios on wild-capture fisheries. Fish and other seafood provide almost 20% of the animal protein consumed by the global human population, out of which wild-caught seafood—the focus of the present study—make up approximately one-half (~80 to 120 Mt·y⁻¹) (32, 33). Furthermore, wild-caught seafood (herein simply “fish”) is a particularly important source of essential micronutrients in developing countries, with almost 1 billion people at risk to become micronutrient deficient if global fish catches fall (31). Concerningly, global catches have been stagnant or slightly declining since the 1990s (Fig. 1) (32, 33), and in a majority of the world’s fisheries, biomass is depleted below the level that generates the maximum sustainable yield (B_{MSY}) (34). This indicates that present-day catches exceed the limits of productivity in many regions, and effective management measures, which are crucial to remedy this situation (35), have been projected to increase global fish biomass by 200 to 800 Mt (34). A closer investigation into the response and potential of the global fishery under an abrupt global food emergency is therefore warranted.

While fishing pressure has a major impact on fish populations and their ability to reproduce, the production of fish biomass also depends on environmental characteristics, most importantly net primary production (NPP) and water temperature (36, 37). Since a nuclear war is expected to cause global cooling and decrease oceanic NPP (3, 15, 38), it is likely to have a significant impact on global fish catch. However, it is unknown how these global-scale shifts in NPP and temperature could combine to affect marine ecosystems and marine food productivity, and

whether these effects would worsen or mitigate the predicted losses in agricultural food production.

Beyond direct climatic perturbations, a nuclear conflict is also likely to cause socioeconomic perturbations that change global fishing behavior. Altered climate conditions leading to decreased crop production on land (24, 25, 27, 28) could cause a general decrease in caloric supply and limit aquaculture and livestock production due to their dependence on feed (39, 40). This would

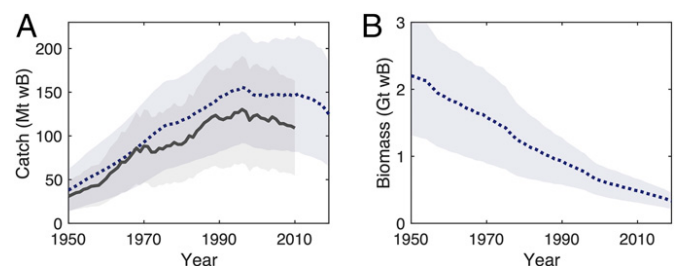


Fig. 1. Prewar trajectories of global fisheries. Simulated (A) annual wild fish catch (megatons wet biomass) and (B) total wild commercially targeted fish biomass (gigatons wet biomass) over 1950 to 2019 from the prewar fisheries baseline using the BOATS model with no fisheries regulation. Shaded areas show the SD for the five parameter ensemble runs, and the dotted lines show the ensemble mean. The fishery and ecosystem state in 2019 are used as initial conditions for the nuclear war scenarios. In A, the gray solid line shows empirical global catches from ref. 33, with uncertainty indicated by the shaded area.

likely raise the demand for wild-capture fish as a source of animal protein, leading to an increase in price and intensified fishing. For example, the Tambora volcanic eruption in 1815 and the associated crop failures triggered a hundredfold increase in the exported catch of marine pelagic fish in the Gulf of Maine (41). On the other hand, substantial damage to fisheries infrastructure (e.g., ships, harbors, fuel supply, processing facilities) along with supply chain disruptions could lead to reduced fishing effort, as would unsafe ocean travel due to geopolitical instability (42). Although difficult to predict, such socioeconomic changes may greatly influence fisheries outcomes after a nuclear war.

This study explores the effects of six nuclear war scenarios (Table 1) on the global biomass and catch of fish: five India–Pakistan scenarios of increasing intensity with black carbon (soot) loads of 5 to 47 Tg (details in ref. 3) and one substantially larger US–Russia war injecting 150 Tg of soot (details in ref. 15). All war scenarios are generated by a state-of-the-art Earth system model (Community Earth System Model–Whole Atmosphere Community Climate Model [CESM-WACCM]; *Materials and Methods*). Output from CESM-WACCM is used as input to the Bioeconomic Marine Trophic Size-Spectrum (BOATS) model, a process-based ocean ecosystem model with dynamic fishing that has been used in a number of future climate applications (23, 43–46). With an unregulated prewar fisheries baseline simulation as the starting point (Fig. 1 and *Materials and Methods*), we use BOATS to model the impact of nuclear war on global fisheries. Bracketing a range of possible changes in fishing behavior due to the war, we explicitly model five simplistic socioeconomic responses: business-as-usual (BAU) fishing and a large or very large increase (F+, F++) or decrease (F–, F––) in fishing intensity (Table 2 and *Materials and Methods*). We also investigate how strong prewar fisheries management improves the ocean’s capacity to alleviate food losses (*SI Appendix, Fig. S8* and *Materials and Methods*). Beyond quantifying the effects of nuclear war, these simulations illustrate the potential effects of large volcanic eruptions or of socioeconomic shocks on global marine capture fisheries.

Results

Below, we present the impacts of both nuclear-war–driven climatic perturbations (soot inputs, Table 1) and socioeconomic fishing responses possibly triggered by the global crisis (Table 2). For clarity, we hereon define a scenario as a specific combination of soot input and socioeconomic response. First, we present an overview of the impacts in year 2 postconflict, pinpointing the initial, transitory effects of altered fishing behavior. We then describe the longer-term (15-y) fisheries trajectories for all scenarios, illustrating the duration and rate of recovery. Then, we investigate the spatial patterns of change and link these to national-level seafood dependence for the 5-Tg case. Finally, we show how strong fisheries regulation increases the potential for higher global catches postwar. Unless otherwise stated, presented relative

changes are anomalies from the BAU-control scenario, which has no war and BAU fishing behavior (*Materials and Methods*). In the text, we generally present numbers for the end-member cases of 5- and 150-Tg soot inputs.

Initial Impacts on Catch and Biomass. Nuclear-war–driven climate perturbations (Table 1) generally lead to significant short-term losses in global fish catch and biomass in year 2 postwar (Fig. 2 and *SI Appendix, Fig. S1*). Larger soot input exacerbates losses, and the effect is linear with the associated reduction in photosynthetically active radiation (PAR) (*SI Appendix, Tables S1–S4* and *Materials and Methods*), which presumably drives the net reduction in global NPP (*SI Appendix, Fig. S6*). On average for all socioeconomic fishing responses, catch and biomass decrease by ~2% and ~1%, respectively, for every 1 Tg of soot (~4% and ~3%, respectively, for every 10% decrease in PAR).

Under BAU fishing, global biomass decreases by 1.6% ($\pm 0.7\%$, SD of the five BOATS ensemble runs; *Materials and Methods*) in the scenario with a 5-Tg soot input, and up to 18 ($\pm 3.5\%$) in the 150-Tg scenario (Fig. 2A and *SI Appendix, Fig. S1A* and *Tables S1* and *S3*). Since this biomass decrease also leads to a decrease in the global fishing effort (Eq. 1), catches fall more than biomass: by 2.4 ($\pm 0.8\%$) under 5 Tg, and up to 29 ($\pm 7\%$) in the 150-Tg case (Fig. 2B and *SI Appendix, Fig. S1B* and *Tables S2* and *S4*).

If the conflict is followed by intensified fishing due to increased demand (F+, F++; Table 2), catch initially increases at the expense of biomass. Under the 5-Tg soot input, where the climatic effect is relatively small, F+ and F++ generate catch increases of 13% ($\pm 17\%$) and 17% ($\pm 14\%$), respectively, in year 2 postwar (Fig. 2B). At the same time, F+ and F++ cause a 10% ($\pm 4\%$) and 23% ($\pm 9\%$) global biomass decline (Fig. 2A). Larger climate perturbations cause more rapid biomass collapse and can preclude a net increase in catch. In the 150-Tg case, representing the strongest perturbation, even the greatly intensified fishing effort in F++ fails to compensate for the large negative climate impact, as global catches still fall by 14% ($\pm 20\%$) (Fig. 2B).

Conversely, decreased fishing intensity due to decreased ability to fish (F–; F––) decreases catch but creates a net increase in biomass despite the climate-driven losses for almost all soot inputs (Fig. 2). Under the 5-Tg soot input, F– and F–– result in substantial falls in global catch of 23% ($\pm 19\%$) and 52% ($\pm 24\%$), respectively. This increases global biomass by 7% ($\pm 4\%$) and 26% ($\pm 7\%$), respectively. Larger soot inputs both exacerbate the falls in catch and diminish the biomass recovery that is enabled by the lowered fishing pressure. Again, the climatic effect is linear with PAR (Fig. 2 and *SI Appendix, Tables S1* and *S2*).

Decadal Fishery Response. Longer-term global fisheries trajectories under BAU fishing (Fig. 3A–C) show the general decrease

Table 2. Overview of modeled socioeconomic responses

Socioeconomic response	Code	Drivers	Implementation
Business-as-usual	BAU	Socioeconomic parameters unaffected by war	Unchanged fish price (p) and fishing cost (c)
Intensified fishing	F+	Crop failure, food system collapse, increased fish demand	Twofold increase in p
Greatly intensified fishing	F++	Severe crop failure, food system collapse, greatly increased demand	Fivefold increase in p
Decreased fishing ability	F–	Fuel scarcity, infrastructure destruction, security concerns	Twofold increase in c
Greatly decreased fishing ability	F––	Severe fuel scarcity, infrastructure destruction, security concerns	Fivefold increase in c

Price and cost changes are implemented instantaneously (step change) in the year of the war. Each socioeconomic response combined with a war-driven climatic perturbation (Table 1) makes up a model scenario. Details are in Socioeconomic Responses.

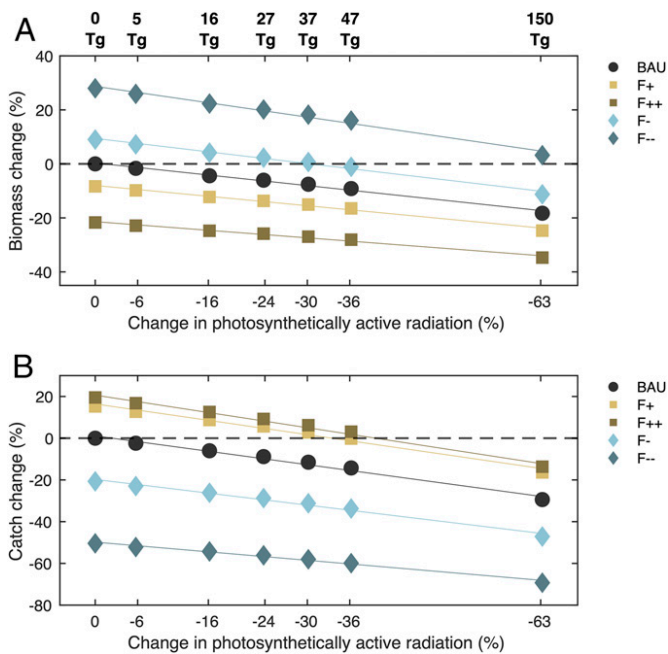


Fig. 2. Short-term impacts of nuclear war on global fisheries. Panels show the average percent difference in (A) biomass and (B) catch between the business-as-usual (BAU) control simulation (no war) and different nuclear war simulations (5 to 150 Tg), in year 2 postconflict. Each value is plotted against the war scenario (soot input indicated on upper x axis) and its associated percent reduction in global photosynthetically active radiation (PAR). The slope for each marker type shows the impact of the climatic perturbation (for a given socioeconomic response F+/-; see Table 1), while the vertical spread between marker types shows the effect of the socioeconomic responses. Statistics for linear regressions are given in *SI Appendix, Tables S1 and S2*.

and subsequent recovery in global fish biomass and catch in the decade postwar. In the 5-Tg case, global catch decreases by at most 3.6% ($\pm 1.4\%$), occurring in year 5 postwar (Fig. 3A). In contrast, with a 150-Tg soot input, the largest catch decrease is 31% ($\pm 9\%$) in year 3 postwar. Trajectories for the intermediate soot loads consistently lie in between. Eventually, both biomass and catch recover relative to the control climate, with recovery taking ~ 14 y and somewhat exceeding the BAU-control (Fig. 3A and B). Due to the climate-driven biomass decline, which renders fishing less profitable, modeled fishing effort begins to decrease immediately after the war and lags harvest and biomass (Fig. 3C and Eq. 1).

Increase in fish demand (F+, F++) in turn increases fishing effort. After an initial increase in catch, biomass is depleted, driving a fishery crash in all scenarios that lasts until the end of the simulation (Fig. 3D–F and *SI Appendix, Fig. S2 A–C*). Catches drop below the BAU control 2 to 3 y postwar, and stabilize about 45% and 75% lower by the end of the 15-y simulation. For all soot inputs, biomass under F+ decreases, at most by 50 to 60%, and under F++ by about 84%. This biomass depletion means that the largest intensification of fishing (F++) leads to the lowest total catch when integrated over the whole 15-y postwar period: Under the 5-Tg and F++ scenario, cumulative catch falls by 38%.

If the war induces a substantial decrease in fishing (F-, F--), global catches initially decrease and fish biomass rapidly begins to recover (Fig. 3G–I and *SI Appendix, Fig. S2 D–F*). The decline in catch, down to 49% ($\pm 8\%$) in the F- and 150-Tg scenario, is maintained for the first 4 y, but eventually the recovering fish biomass increases catches long-term. By year 5 postwar, catch has begun to exceed the BAU control catch for all

soot inputs. At the end of the simulations, global biomass is almost double and fourfold under F- and F--, respectively (Fig. 3H and *SI Appendix, Fig. S2E*), and catches increase by ~ 60 and 140% (Fig. 3G and *SI Appendix, Fig. S2D*). Thus, the total cumulative catches over the 15-y postwar period is almost 30% higher under the 5-Tg and F-- scenario (in contrast to the cumulative 38% decrease under 5 Tg and F++). The greatly decimated effort (Fig. 3I and *SI Appendix, Fig. S2F*) and higher biomass lead to increased catch efficiency, similar to observations in the North Atlantic after the end of World War II (42), which makes the fisheries more economically efficient.

Regional Patterns of Change. While the climatic perturbations decrease the total global fish catch postwar, there is substantial spatial variability, with increasing catch in some regions (Fig. 4). Averaged over the first 5 y postwar under BAU fishing, catch increases patchily in the tropics and subtropics, particularly in the Atlantic Subtropical Gyres under higher soot input scenarios. The largest decreases in catch occur along the equator and midlatitudes. These spatial patterns generally follow spatial changes in NPP following the war predicted by CESM (*SI Appendix, Fig. S3*), with some influence from changes in water temperature (*SI Appendix, Fig. S4*). Spatial patterns of catch change under increasing or decreasing fishing pressure are similar to the patterns under BAU (*SI Appendix, Figs. S5 and S6*).

The spatial patterns translate into differential impacts on the catches of individual fishing nations (Fig. 5, *SI Appendix, Table S5*, and *Materials and Methods*). Here, we focus on the 5-Tg BAU scenario for comparison with the investigation of crop yields by (28). Under this lower-impact scenario, several major fishing nations, such as Russia, Canada, Japan, and the United States, see substantial catch losses in their territorial waters under the modeled climatic perturbations. Some lower-latitude fishing nations like Mexico, Peru, Greece, and Somalia experience increased catch potential. However, equatorial island nations, who are most dependent on marine food supply, suffer some of the largest declines. A comparison with the country-level dependence on marine ecosystems for nutrition (47) suggests that these island states are particularly vulnerable to the predicted fall in catches (Fig. 5B), among which Indonesia is the most populous country by far.

Benefits of Fisheries Regulation. Strong prewar management of fisheries greatly increases the capacity of marine fisheries to mitigate agricultural losses (Fig. 6). If global fisheries are strongly regulated to maintain a healthy biomass before the onset of the conflict (*SI Appendix, Fig. S8* and *Materials and Methods*), the short-term catch increase under intensified fishing postwar is greatly enhanced (*SI Appendix, Fig. S9*). Under a 150-Tg and F+ scenario (Fig. 6), shown here to illustrate the extent to which intensified fishing could alleviate an extreme food crisis, global catch increases by 430% ($\pm 350\%$) relative to the unregulated BAU control. This increase is achieved despite the substantial climatic impact associated with the 150-Tg soot input (Fig. 2A). Catch rapidly decreases in the second year but remains somewhat higher than in the unregulated case until ~ 10 y postwar.

Discussion

In summary, nuclear-war-driven climatic perturbations have an overall negative effect on fisheries that increases with soot input, despite positive impacts in some subtropical regions. However, socioeconomic responses to the nuclear war could greatly influence the trajectories of global fish catch and biomass. In the absence of strong prewar management, if the nuclear war leads to intensified fishing (for example due to terrestrial food shortages) a small increase in the global catch is possible for the first

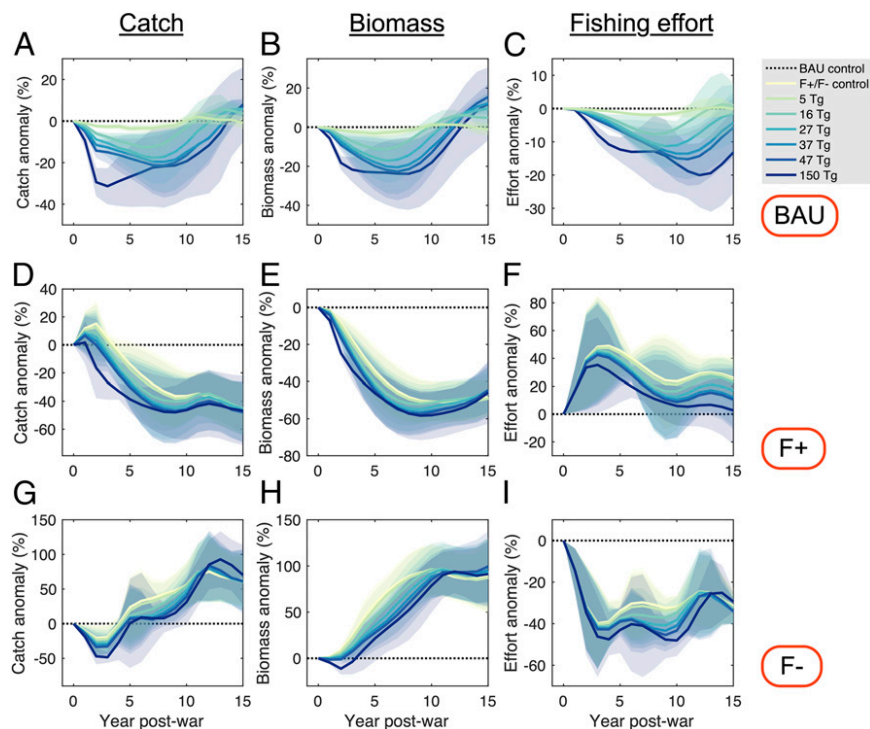


Fig. 3. Global fishery developments postwar. Panels show the percent anomaly from the BAU control scenario (dashed line) for all soot inputs (solid lines). Upper row (A–C) shows trajectories of catch, biomass, and fishing effort under BAU fishing, middle row (D–F) shows trajectories under the intensified fishing scenario F+, and lower row (G–I) shows trajectories under the decreased fishing scenarios F–. The shaded areas show SD for the five parameter ensemble runs, while the solid lines are the ensemble mean. The light yellow lines in D–I show the F+ and F– responses in the absence of a climatic perturbation, i.e., the F+ or F– control.

few years postwar. This however rapidly depletes the fish stocks and is followed by a precipitous decline in catches. Strong fisheries regulation prewar could instead allow catches to become many times higher than normal in the first year postwar, even despite large soot inputs. A decrease in fishing because of damaged infrastructure would lead to relatively large short-term catch decreases in a potentially critical time for global food security.

Role of NPP, Temperature, Fishing, and Adaptation. The effect of the nuclear-war–driven climatic perturbations on global fish catch can largely be explained by the effects of NPP, temperature, and fishing pressure. Cooling slows the growth rates of fish, while lower NPP input decreases the amount of energy available for the ecosystem, causing the postwar decrease in simulated biomass and catches (43, 48). However, cooling also has a positive impact on the steady-state fish biomass, by increasing the efficiency with which energy supplied by NPP can accumulate as biomass in large organisms (43, 48). This accumulation is most apparent for the simulations in an unfished ocean (*SI Appendix, Fig. S7*), but is less pronounced in fished systems, where growth rates limit fish biomass more than NPP. We underline that the representation of ecological processes in BOATS greatly simplifies trophic exchanges and does not include fish movement, and that it has a relatively high sensitivity to temperature when compared with other models (23). Still, integrated globally, the modeled catch decrease under BAU fishing is similar to the decrease in global oceanic NPP caused by the different soot inputs (*SI Appendix, Fig. S7B*) and is consistent with macroecological theory.

We note that both the nuclear-war–driven climatic perturbations and anthropogenic global warming have negative impacts on marine fisheries, even though the former causes cooling and the latter, warming. Model projections of the long-term (year 2100) decrease in global fish biomass or catch potential under

unmitigated climate change (RCP 8.5), range from ~12 to 25%, while strong mitigation (RCP 2.6) likely limits the decrease to <5% (23, 45, 49, 50). In comparison, the 150-Tg case yields maximum declines in catch and biomass of 31% and 24%, respectively, under BAU fishing (<4% in the 5-Tg case). Thus, the negative impacts of unmitigated climate change on fisheries almost reach those of a large-scale nuclear war between the United States and Russia. However, the abruptness and duration of the negative impacts differ greatly, as do the underlying causal mechanisms. A nuclear conflict generates a net global decrease in oceanic NPP (*SI Appendix, Fig. S7*), likely attributed to a reduction in sunlight reaching the ocean surface (51), in turn leading to a decrease in global catch and biomass. In contrast, the reductions under global warming result from a combination of NPP decreases driven by increased stratification (52), the decrease in the size of phytoplankton (53), and the metabolic effects of warming on fish physiology (48).

Our results also suggest that the marine fish catch is relatively more robust to the effects of a nuclear conflict than land-based food production. While total global fish catches here decrease by ~4% under the 5-Tg scenario, Jägermeyr et al. (28) found an 11% decline in global crop production for 5 y under the same soot input. This difference arises because the ocean does not cool as much as land (cf. figure S6 in ref. 3), and because of the assumed adaptability of fish, and in turn fisheries, to a cooling environment. In contrast to crops, most fish stocks rapidly move and migrate in response to climate variations (54). Here, fishing fleets in turn increase their fishing effort in regions with climate-driven biomass increases, and vice versa, which alleviates global catch losses. This assumption is supported by the global ubiquity of fishing and the fleet’s ability to track seasonal fish movements (55, 56). For agricultural systems, where the war-driven climate effects are most severe in regions that produce several major

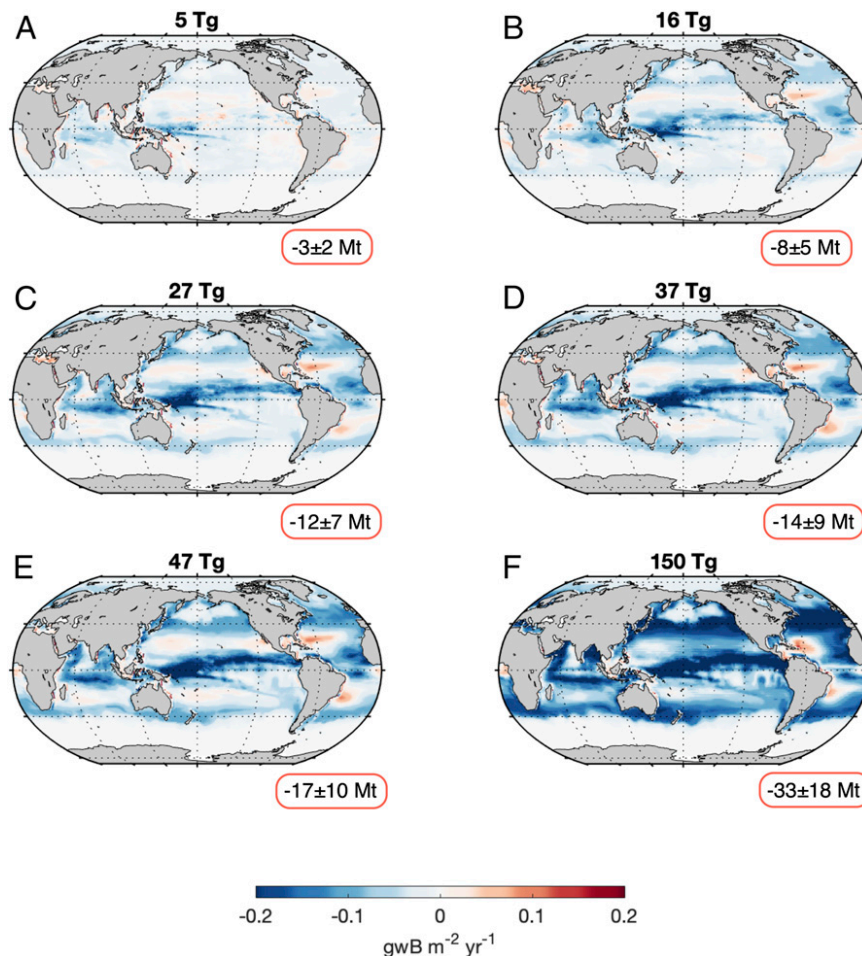


Fig. 4. Spatial distribution of changes in fish catch. Panels show six different soot inputs under BAU fishing, averaged over the first 5 y postwar. A–F show the mean difference in annual fish catch per square meter between the control (0 Tg) and the 5- to 150-Tg soot inputs of the five ensemble runs. In the *Lower Right* corner, the global catch difference in the 5-y period is indicated (ensemble mean and SD).

crops, the limited ability to rapidly adjust production to the changing climatic conditions (57) exacerbates crop losses.

Food System Linkages. Both the drivers of fishing and the importance of global fish catches are interlinked with the impacts of nuclear war on other parts of the global food production system. Cereal production is about 25 times larger than fish catches globally (58), with the caloric content per gram of cereals being almost six times that of fish (59). This makes offsetting the losses of calories from agriculture very difficult. Still, it is reasonable to expect that cereal production losses postwar, estimated at 11% already under the 5-Tg case (28), would impair the production of other animal protein and increase the overall need for other foods. Here, the increase of global catch under greatly intensified fishing is limited to at most 30% in the 5-Tg case (and less under larger climate perturbations), $\sim 30 \text{ Mt}\cdot\text{y}^{-1}$ if using the present-day catch of $\sim 100 \text{ Mt}\cdot\text{y}^{-1}$ as a baseline (32, 33). Such an increase would constitute a significant but small contribution to global food security. However, strongly regulated global fisheries could theoretically generate “emergency catches” several hundred percent higher than unregulated fisheries. Since a catch of $\sim 100 \text{ Mt}\cdot\text{y}^{-1}$ makes up roughly 10% of the total animal protein supply (32), our results suggest that the 430% ($\pm 350\%$) increase in global catches enabled by strong prewar management (Fig. 6) could offset a loss of $\sim 43\%$ ($\pm 35\%$) of the present-day annual supply of all other animal protein (cultured fish, meat, dairy, and eggs). Although short-lasting, such a buffer could be extremely

valuable to mitigate a global food emergency and allow time for adaptation.

We also underline that the direct impacts of cereal production losses on fish demand are uncertain considering the differences in nutritional values and total production. The demand for fish may be more strongly connected to the production of other animal protein products (60), in particular aquaculture products, for which the effects of nuclear war are poorly explored (61). Furthermore, the capacity to adapt conventional agricultural production systems (28) and to scale up production of alternative foods (fungi, bacteria, etc.) in the event of a crisis (62) could impact the demand for fish as well as the consequences of falling global catches.

Contamination of food due to nuclear fallout is a further concern for food security. Close to sites of nuclear power plant accidents, fish can become highly contaminated by radioactive pollution (63, 64). However, radionuclides are strongly diluted in the ocean given the large volume of water, and the range and intensity of contamination of marine systems have been limited in past accidents (64–68). Although it is yet unexplored how the nuclear war scenarios used here would affect oceanic radionuclide concentrations, seafood appears less likely to be sensitive to nuclear fallout than terrestrial foods. This suggests that fish caught outside of the immediate war areas could provide a relatively safe food source, which might further increase demand.

It is important to underline that the fish biomass in BOATS represents only the fish and shellfish that have historically been

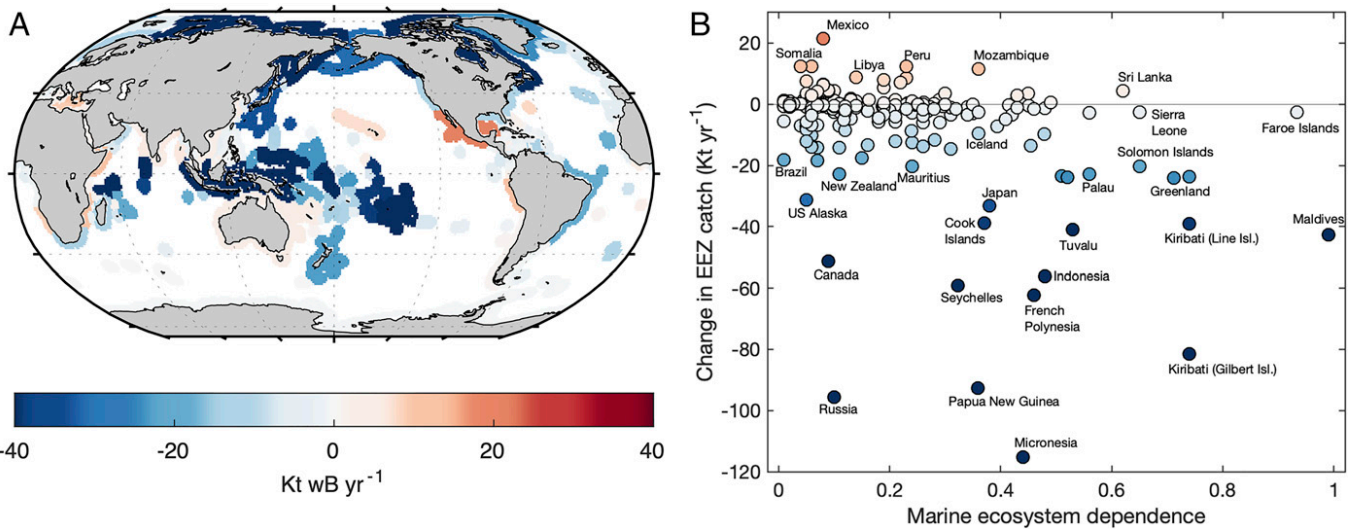


Fig. 5. Country-level fish catch changes under the 5-Tg and BAU fishing scenario. In **A**, the color of each exclusive economic zone (EEZ) shows the total change in modeled catch (1,000 ton wet biomass \cdot yr $^{-1}$) relative to the BAU control scenario, averaged over the first 5 y postwar. In **B**, change in EEZ catch vs. national-level dependence on marine ecosystems for nutrition is shown.

targeted by fisheries (i.e., those reported in the Sea Around Us Database) (33). In the event of global food shortage, it is possible that new marine organisms would become targeted by fisheries, expanding the scope for increasing marine catches. The total biomass of all fish species is highly uncertain (69), meaning that this potential is poorly known, but the biomass of unexploited mesopelagic fishes is believed to be larger than the total global biomass of currently exploited wild finfish (70). If a global food crisis would induce the rapid development of more effective harvesting technologies for these dispersed fish and other currently unexploited species, fisheries could further mitigate terrestrial crop failures, but with potentially large and poorly understood consequences for marine ecosystems (71, 72).

The conflict-driven changes in the global fish supply would likely have highly variable regional impacts, given the importance of factors like local food production capacity, purchasing power, and trade network functionality (73). We here find that the modeled climatic perturbations would cause the largest fall in fish catches in developed high-latitude countries, which are also the hardest hit by crop failures (28), and in developing equatorial island nations, which are highly fish dependent (47). This suggests potential synergistic effects on regional food security, in particular if the drop in global food production reduces the willingness or ability to trade. At the same time, regional variations in management effectiveness and the resulting biomass levels (35) (*Uncertainties and Limitations*) should also strongly impact the regional consequences. Overall, further investigation of the interdependencies between fishing, aquaculture (mediated through wild-caught fish being used as feed), and the rest of the food production system in the event of a global food crisis is needed.

Uncertainties and Limitations. This work quantifies the response of global marine ecosystems and fisheries to abrupt, extreme climatic cooling. As a result, the associated uncertainties are bound to be large. An advantage of BOATS is that its key ecological processes (growth, metabolism, mortality, and reproduction) are affected in a mechanistic way by changes in temperature and NPP (43, 48), increasing the model's generalizability. The modeled fish productivity response to anthropogenic climate change in BOATS agrees well with fish population-based (rather than ecosystem-based) estimates (23, 74). This, together with the use

of an optimized ensemble of parameterizations that allow us to explore a large part of the uncertain parameter space (44, 45), increases the confidence in the model results.

Still, the extreme rate and magnitude of climatic change modeled here may have consequences that are not accurately captured by BOATS. The model implicitly assumes that species will quickly migrate and adapt to the changing environmental conditions, and is unable to capture the importance of keystone species, or the seasonal timing of reproduction and feeding interactions. These factors may severely and perhaps irreversibly affect marine ecosystem productivity under rapid climatic change (75–77). The importance of such unresolved mechanisms is expected to be larger in ecosystems where the rate of adaptation is lower than the rate of climatic change (78)—which is especially rapid in this study. For example, nearshore and coral reef systems have previously been suggested to be the most sensitive to rapid cooling (75). The maintained biomass growth in BOATS may therefore be optimistic in such regions, as it disregards the risks for climate-driven nonlinear ecosystem and productivity shifts due to noninstantaneous adaptation. Nonetheless, the increase in the productivity of some species and decrease in others in the Gulf of Maine after the 1815 Tambora eruption (41), which had a greater radiation anomaly than the 5-Tg case modeled here (Table 1), lends some credibility to the assumption of regional species substitutability in BOATS even under the rapid climatic changes that could be caused by a nuclear war. We also emphasize that neither BOATS nor CESM resolves the potential impacts of nuclear-war-driven changes in ocean acidification (as described in ref. 38) on marine organisms. Work is currently underway to simulate the response of coccolithophores to acidification in CESM (79); future studies will explore this idea further.

An important simplification in the present study is that the prewar fisheries baseline (Fig. 1) assumes that there is no effective fisheries management. Fishing effort instead evolves as predicted in an open access fishery, where effort only decreases when profit becomes negative (Eq. 1) (80, 81). We use this assumption because it better reproduces the development of global catches (Fig. 1), but note that it leads to a progressive decrease of fish biomass (45, 82) that is pessimistic. Indeed, while there is evidence of widespread biomass depletion worldwide (34, 83, 84), current management methods have curtailed overfishing

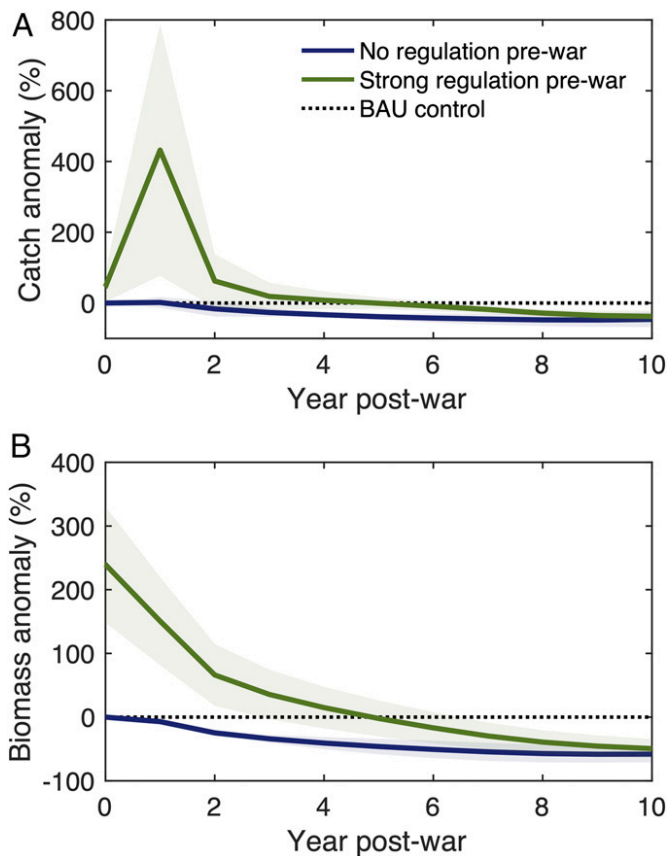


Fig. 6. Contribution of well-regulated fisheries to postwar food security. (A) Catch anomaly (percentage) relative to the BAU control (dashed line), and (B) the associated anomaly for commercially targeted fish biomass. Both panels show trajectories under the 150-Tg and intensified fishing (F+) scenario and contrast the impact of strong (green) vs. no (blue) prewar fisheries regulation. Despite the substantial negative impact of the 150-Tg soot input (Fig. 2A), strong prewar regulations allow a many-fold catch increase immediately after the war by providing a large buffer of fish biomass.

and increased biomass to a significant degree in more than half of the fisheries where stock assessments are made (which themselves make up 40 to 50% of the total global fish catch) (35). Thus, the fisheries in several well-managed regions would respond more like in the simulation with a strongly regulated global fishery prewar (Fig. 6 and *SI Appendix*, Fig. S9).

Furthermore, we emphasize that the impacts that nuclear conflicts themselves might have on the effectiveness of management are highly unpredictable, but potentially important. Lack of resources for fisheries regulation, stronger incentives for illegal fishing, and collapse of international management organizations could impair management. On the other hand, war fosters increased (parochial) cooperative behavior, which is a key element in effective fisheries management (85). This, or strict war-induced (possibly military) protection of countries' exclusive economic zones (EEZs) and their marine food resources could actually improve management effectiveness.

Since the realized effect of nuclear war on global fishing behavior is highly uncertain, the socioeconomic scenarios were chosen to bracket a large possible range of alternative behaviors. This approach provides a generalizable understanding of the system's response to perturbations, but not a prediction of the most likely outcome. Consequently, the socioeconomic scenarios generally have a larger impact on global catches than the climatic perturbation (Fig. 2B). We speculate that a war might increase both fish prices and fishing costs (with opposing effects on fishing

effort), that a larger war would cause larger increases, and that the prices and costs could eventually return to the prewar level. Further socioeconomic scenario development could explicitly address such counteracting effects and potential responses in the spheres of governance, markets, and fisheries technologies (86).

Resilience of Fisheries in the Face of Large-Scale Shocks. The findings presented here are instructive for understanding possible global fisheries responses also under other shocks, both climatic and market-related. Large-scale volcanic eruptions would cause similar climatic perturbations (Table 1) with the associated effects on ecosystems and food production systems, while global fuel crises or food price spikes may also arise due to other factors (87). Volcanic eruptions large enough to have substantial global impacts have a global return period of about 500 to 1,000 y but are unpredictable and have been associated with widespread famine and plagues (29, 88–91). Furthermore, the unfolding COVID-19 pandemic is expected to cause a global food emergency (92), which is already having diverse and rapidly evolving impacts on fisheries (93). Beyond crises, fish prices have been rising over the past 20 y (58, 94), and intensified demand, for example mediated by a slowdown of aquaculture growth (32), could induce intensified fishing if unregulated.

Most importantly, our results show that poorly managed fisheries have a much lower capacity to contribute to global food emergencies than do well-managed fisheries (Fig. 6). For a short pulse in fishing intensity, the magnitude of this emergency catch potential is essentially proportional to the management-induced increase of fish biomass left in the ocean. Thus, management interventions that increase the biomass of fish globally help to buffer against food shocks. This result shows that effective fisheries management serves not only to achieve sustainability (34, 50), but also provides a proactive contribution to the resilience of the global food supply. Beyond showing how global marine fisheries are impacted by climatic and socioeconomic perturbations after a nuclear war, our generalizable findings thus also add to the imperative of effective fisheries management (95).

Materials and Methods

To explore the potential impacts of nuclear conflicts on fisheries, we investigate six climatic perturbations of regional and larger-scale nuclear wars (Table 1) (3, 15), an ensemble mean of three control climate runs without soot injection, and five socioeconomic fishing responses (Table 2). The climate control run is first used to create the prewar fisheries baseline up until 2019. Using the state of the fishery in 2019 as the initial condition, we model how a nuclear war in the following year (year 1 postconflict), with and without accompanying changes in fishing behavior, impacts global fish biomass and catches.

Climatic Perturbations after Nuclear War. The climate impacts of nuclear war are modeled using the CESM, version 1.3, a state-of-the-art coupled climate model consisting of atmosphere, ocean, land, and sea ice components. CESM implements the Parallel Ocean Program physical ocean model (96), here at nominal 1° horizontal resolution and with 60 vertical levels, and the Biogeochemical Elemental Cycling (BEC) ocean ecosystem–biogeochemistry module, which represents the lower trophic levels of the marine ecosystem, and a dynamic iron cycle (51, 97–101). Similar to other Coupled Model Intercomparison Project (CMIP) class models (102, 103), BEC simulates three phytoplankton functional types: diatoms, small phytoplankton, and diazotrophs as well as one zooplankton functional type. The productivity (carbon fixation) of the three phytoplankton groups are combined to generate NPP (104), which is used, along with model-derived sea surface temperature, to drive the offline fisheries model. The CESM-BEC ecosystem and biogeochemistry model is well validated in a variety of scenarios and performs favorably when compared with other CMIP class models (e.g., refs. 101, 105, and 106, and references therein).

The climatic response to nuclear war is simulated by injecting black carbon (soot) into the atmosphere above the South Asian subcontinent (India and Pakistan exchange) (3), or over the United States and Russia (15). Atmospheric circulation and chemistry is simulated in CESM using the WACCM (107) with nominal 2° resolution and 66 vertical levels, a model top at ~145 km,

and uses the Rapid Radiative Transfer Model for GCMs (108) for the radiative transfer. The Community Aerosol and Radiation Model for Atmospheres (109, 110) is coupled with WACCM to simulate the injection, lofting, advection, and removal of soot aerosols in the troposphere and stratosphere, and their subsequent impact on climate (111). The India–Pakistan scenarios (5 to 47 Tg; Table 1) and United States–Russia scenario (150 Tg) build on previous work by Mills et al. and Miller et al. (12, 14) and Robock et al. (29), respectively.

Global Fisheries Model. The BOATS model is used to estimate climatic and socioeconomic impacts on global marine fish biomass and catch through time. We use the model thoroughly described in previous publications (43–45), with improved accuracy of fish biomass in high-nutrient, low-chlorophyll regions (112) and a newly developed regulation component from (46). BOATS calculates fish biomass of three independent fish groups categorized as small, medium, and large fish (defined by maximum sizes of 0.3, 8.5, and 100 kg, respectively) in noninteracting oceanic grid cells with a 1° horizontal resolution. Fish in each group grow to their maximum size from a common smallest size (0.01 kg) along the so-called size spectrum (113), and the resulting biomass depends on the amount of energy available from oceanic NPP, temperature-dependent metabolic growth and mortality rates, the fraction of energy allocated to reproduction, and reproductive success (43). Gridded maps of vertically integrated NPP along with sea surface temperature from CESM are used as input to the model. We underline that BOATS resolves only the subset of marine fish biomass that has been targeted by fisheries, for which model estimates can be compared with and constrained by global catch data (33).

In BOATS, fishing effort evolves dynamically in each grid cell and fish size group, responding to changes in the biomass and the model's economic forcings (44, 46). As is common in models simulating fishing activity (114), it is assumed that profit is a main driver of fishing behavior, but also that fishing behavior can be more or less strongly influenced by regulation (management). BOATS represents the effort put into fishing each of the three fish size groups ($k = 1, 2, 3$) as nominal fishing effort, E_k (in watts per square meter; reflecting the boat power), which evolves over time as a function of the average profit, the regulation target for fishing effort, $E_{\text{targ},k}$ (in watts per square meter), and the regulation effectiveness S (dimensionless; $S \geq 0$) in a grid cell:

$$\begin{aligned} \frac{dE_k}{dt} &= K_e \frac{\text{revenue}_k - \text{cost}_k}{E_k} e^{-S} + K_s (E_{\text{targ},k} - E_k) (1 - e^{-S}) \\ &= K_e \frac{p q E_k B_k - c E_k}{E_k} e^{-S} + K_s (E_{\text{targ},k} - E_k) (1 - e^{-S}), \end{aligned} \quad [1]$$

where p is the ex-vessel price of fish (the price at which the catch is sold when it first enters the supply chain; \$-grams wet biomass⁻¹), c is the cost per unit of fishing effort (\$-watts⁻¹-second⁻¹), q is the catchability (meters²-watts⁻¹-second⁻¹), B_k is the fish biomass (grams wet biomass-meter⁻²), K_e (watts²-meter⁻²-\$⁻¹) is the fleet dynamics parameter (which scales the rate of effort change with respect to profit), and K_s (meters²-second⁻¹) is the regulation response parameter (which scales the rate of effort change with respect to regulation). The catch is the product $q E_k B_k$, where the catchability q reflects the effectiveness with which a given unit of fishing effort catches fish, and incorporates both gear technologies, fish finding or aggregating technologies, and skill and knowledge of the crew.

As Eq. 1 states, the key factors determining the level of fishing effort in BOATS are B_k , p , c , and q (44) and the regulation parameters $E_{\text{targ},k}$ and S . If S approaches zero (no regulation), the nominal fishing effort will decrease if c increases (increasing total cost), and increase if p or B_k increase (increasing revenue), all else being equal. In line with the theory of open access fisheries (80, 81), at unregulated equilibrium fishing effort stabilizes at a level that generates zero profit.

Prewar Fisheries Baseline. We use BOATS with simple historical representations of fish price, fishing cost, and catchability, to create a prewar fisheries baseline simulation determining the prewar state of fisheries and ecosystems. Based on the findings in ref. 45, the prewar fisheries trajectory is hindcasted by forcing the model with constant c (1.8×10^{-4} \$ kW⁻¹), constant p (1.1 \$ kg⁻¹), increasing q (5% y⁻¹), and no regulation ($S = 0$), with the climate control from CESM as input. Although these socioeconomic approximations are simplistic, they are within the ranges of empirical estimates (82, 115–117), and reproduce the historical evolution of global fisheries, with an increase, plateau, and slight decline of global catches and a continuous decrease in global fish biomass (Fig. 1). The global distribution of fish biomass and fishing effort in model year 2019 are saved to use as initial conditions for the nuclear war simulations.

To investigate the benefits of strong preemptive fisheries management, we create an alternative prewar simulation. We use the dynamic fisheries

regulation component described in ref. 46, and assume strong regulation effectiveness ($S = 10$) and regulation toward the local MSY target ($E_{\text{MSY},k}$). $E_{\text{MSY},k}$ is estimated for the long-term monthly mean of the climate control from CESM in each grid cell. This approach results in global catch and biomass trajectories similar to the unregulated baseline, but with higher catch and biomass in the last decades thanks to strong management (SI Appendix, Fig. S8).

Socioeconomic Responses. Due to the large uncertainty of the effects of a nuclear war on global fishing behavior, we here use simple, exploratory socioeconomic responses. We modify two of the key economic model forcings, ex-vessel price of fish (p) and cost of fishing effort (c), to induce intensified or decreasing fishing as a response to a nuclear war. Intensified fishing is modeled by an instantaneous step increase in p , either a doubling (F+) or a factor-of-5 increase (F++) in the year of the war. Decreased fishing is modeled here by an instantaneous twofold (F-) or fivefold (F--) step increase in c . Finally, as a comparison, we model a BAU scenario where c and p remain unchanged throughout the war scenarios. When investigating the effect of preemptive management, we use the BAU, F+, and F++ scenarios combined with an immediate reduction of the regulation effectiveness to zero ($S = 0$). Reduced regulation effectiveness is not necessarily the most likely socioeconomic response (*Uncertainties and Limitations*), but was applied for consistency with the other postwar scenarios. In all simulations, fishing effort evolves dynamically with a monthly time step, in response to the changes in p , c , q , and B_k (Eq. 1).

The cost and price increases used here (two and five times) were guided by the sparse available observations. First, the increases are substantially higher than historical variations (56, 94, 115, 118), since there is a large potential for extensive socioeconomic changes postwar. In particular, the risk of unprecedented food shortage even under the 5-Tg emission scenario (28), the relatively high volatility of fuel prices (119), and the hundredfold intensification of fishing recorded in one region after the Tabora eruption (41), warrant an investigation of large variations. Still, intensified fishing requires real fishing capital; boats, gears, and crews. Although the substantial overcapacity present in many regions today could be mobilized postwar, the need for capital still constrains fisheries expansion. Therefore, we do not investigate higher price increases.

Model Runs. Impacts of nuclear conflict and accompanying behavioral changes in the fishery were modeled for a 15-y period postwar using a total of seven soot inputs (including the controls) and five socioeconomic responses. We use the combination of BAU fishing and unchanged climate conditions—the “BAU control”—for comparison with all other scenarios, generating the percent changes given in the results. In addition, we simulate the impact of the climate scenarios on fish biomass in an unfished global ocean (see SI Appendix, *Impacts of nuclear war on the unfished ocean and Fig. S7*), and the impact of the BAU, F+, and F++ scenarios on a strongly regulated global fishery (Fig. 6 and SI Appendix, Fig. S9). To estimate the uncertainty in BOATS model predictions, each of the model runs (including the prewar baselines) was repeated five times using different sets of parameter combinations derived from the model calibration process (44) (values given in table S1 of ref. 45). The five different parameter sets (the parameter ensemble) span a large range of the possible parameter space (SI in ref. 45), and results are presented with the ensemble mean and SD.

EEZ Catch Changes and Marine Ecosystem Dependence. The total catch change is calculated for each EEZ by summing over the area, taking the average of the ensemble runs and over the first 5 y postwar. We use the country-level nutritional dependence from ref. 47 to indicate vulnerability, or the integrated dependence on marine ecosystems for countries lacking values for nutritional dependence. Dependent territories lacking data in ref. 47 were assigned the same value as their controlling central state. Disputed areas and joint regime areas were excluded from the analysis in Fig. 5B.

Data Availability. Model output data and code for the fisheries model have been deposited in Zenodo repositories (<http://doi.org/10.5281/zenodo.4110876> and <http://doi.org/10.5281/zenodo.4117477>).

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Chapter 4

Global fisheries employment 1950-2015

1 Introduction

The global marine capture fishery has seen tremendous changes over the past century. Data reconstructions suggest that catches have increased by more than an order of magnitude since the beginning of the 21st century (Watson and Tidd, 2018) and by more than a factor of four since 1950 (Pauly and Zeller, 2016). Further, since 1950 the number of fishing vessels in the world has doubled, and their total engine power increased by a factor of six (Rousseau et al., 2019). However, it is poorly known how this great expansion of fisheries, driven by rapid industrialization and technological advances, influenced their most fundamental human dimension: the number of people employed. The long-term evolution of the world's population of fishers must be better understood before it can be incorporated into a global model framework. Therefore, reconstructing historical global fisheries employment is the focus of this chapter.

Across the globe, it has been estimated that 50 million people fish for income, livelihood and food (Teh and Sumaila, 2013). For many of these fishers, their occupation is an integral part of their culture and identities, appreciated for the independence, adventure and connection with nature it provides (Acheson, 1981; Pollnac and Poggie, 1988; Seara et al., 2017). Simultaneously, fishing is one of the world's most hazardous occupations, with high fatality rates and many associated health problems (FAO, 2020b; Woodhead et al., 2018). Thus, changes in the global fisher population affect important wellbeing aspects of a large group of people (OECD, 2007). Yet, officially reported data on the number of fishers from the FAO only covers 1995-2015, and previous work has only provided a single average estimate

representative for the period 1950-2010 (Teh and Sumaila, 2013). This greatly limits the extent to which we can understand, and project, the long-term evolution of the fishing occupation.

Beyond the wellbeing aspects, the evolution of the fishing occupation has potential sustainability dimensions. To tackle widespread (economic and ecological) overfishing and rebuild fisheries, management institutions worldwide strive to reduce fishing capacity and fishing effort (Duarte et al., 2020; Worm et al., 2009). While the focus is mainly on reducing the number vessels, their engine power or their catch, capacity reducing management measures often force fishers to leave their occupation (Abbott et al., 2015). Often, the human dimensions are “treated as an afterthought in the policy process” (OECD, 2007), a tendency that can easily result in conflict between fishers and managers about regulation (Charles, 1992). Further, generating alternative livelihoods so that people can leave the fisheries is also presented as a solution to overfishing problems in highly-populated low-income areas where poverty forces people to continue to overexploit declining marine resources – often termed Malthusian overfishing (Finkbeiner et al., 2017; Pauly et al., 1989). Thus, the development of the number of fishers is often linked to the question of effective fisheries management.

However, fishing effort, and thus the impact on marine ecosystems, is the product of human labour and their “capital”, the fishing technology they possess (e.g. Hannesson, 2007; Pollnac et al., 2015). Today, the catching capacity of an individual fisher can be multiplied many times over by the gear and vessel he or she uses. Likely because of this, the amount of capital is usually the main point of concern when reducing fishing pressure (Kirkley and Squires, 1999), leaving human labour as an implicit and somewhat hidden factor in the fishing effort. High technology levels greatly decrease the number of fishers that would be ecologically sustainable, causing difficult socio-political trade-offs and conflicting interests between stakeholders. Thus, it is important to estimate how the contribution of human labour to the total fishing effort has changed over time.

Several processes should influence the number of fishers over long time scales. The fisher population is a subset of the total human population, so population growth could increase the

number of fishers. The effects of other processes beyond population growth can be discerned from changes in the fisher fraction, i.e. the number of fishers divided by the total population. Technological progress and mechanization, which has had a major impact on both catch and fishing fleets (Finley, 2016; Galbraith et al., 2017; Squires and Vestergaard, 2013), is suggested to greatly reduce the need for labor in fisheries over time (Garcia and Rosenberg, 2010; Hamilton and Duncan, 2000). Further, the perceived (future) benefits from fishing relative to other possible occupations, in terms of catch, profit or other less tangible benefits, should affect people's decision to commit to fishing as an occupation (Ikiara and Odink, 1999; Pollnac et al., 2015; Pradhan and Leung, 2004; Tidd et al., 2011). Thus, declining catches due to overfishing (Link and Watson, 2019), an increase in attractive alternative occupations from economic growth (Cinner et al., 2009), or targeted reductions in fishing capacity through management (OECD, 2007) could also be expected to drive a long-term decrease in the fisher fraction.

Here, we reconstruct global fisheries employment over the period 1950-2015. We assemble national level data on fisheries employment, and use a recently published global fleet dataset (Rousseau et al., 2019) and the relationship between mechanisation level and level of economic development (using GDP per capita as a proxy) to reconstruct data for missing years and countries. We then investigate the growth of the fisher population relative to that of the overall population, allowing us to evaluate the hypothesized impact of technological progress and other processes. Finally, the implications of our findings are discussed.

2 Methodology

We reconstruct historical global fisheries employment at the country level using three types of estimates, all with different levels of accuracy. Empirical values for the national work force of marine fishers were first sourced from the peer reviewed literature, organizations and national governments. Time gaps in the empirical data were filled through linear interpolation. Finally, when no anchor points for interpolation were available, we reconstructed the number of fishers from a relationship between GDP per capita and mechanization level. Details are provided in the following sections. Statistical analysis was performed in R.

2.1 Empirical data on national employment

Discontinuous data on the national work force of fishers (number of fishers, n_F) was available for most countries for the years 1995-2015 from the UN Food and Agricultural Organization (FAO, 2017; hereon the "FAO data set"). However, this FAO data set does not disaggregate inland and marine fishers. Therefore, we complemented the data with information from the FAO Fishery and Aquaculture Country Profiles (FAO, 2020c), which also provided additional empirical data for the years 1980 and 1990 for some countries. If disaggregated data for marine fisheries employment was available directly on the country profile page, we used these values instead of those reported for the total number of fishers in the FAO data set. In years lacking data disaggregated by marine and inland, we multiplied the numbers reported in the FAO data set with the fraction of marine fishers from the available year(s). If the marine fisher fraction stayed relatively constant over time, we used the average marine fisher fraction, while for countries with large temporal variations in the marine fisher fraction, we used the value from the closest year. If no inland versus marine disaggregation was made, we used disaggregated catch data as a proxy, assuming that the marine catch fraction is roughly proportional to the marine fisher fraction. Countries with less than 1% of catch from

inland fisheries, or with explicit statements that inland catches were negligible, were left unchanged.

We also assembled long-term (>50 yr) time series of the number of marine fishers from government censuses, statistical publications and reports. Long-term time series of employment in marine fisheries were obtained for China, South Korea, Canada, Italy, Ireland, Norway, Sweden, Denmark and Iceland, for which continuous data was available for between 50 and 100 years (Table 1). A few or single data points pre-1980 were obtained for a handful of other countries like India, Peru, Indonesia, Japan, Sri Lanka, Pakistan, Thailand, Myanmar, Pakistan and Eritrea.

Table 1 – Summary of long-term time series on employment in fisheries.

<i>Country</i>	<i>Time period</i>	<i>Vessel characteristic(s)</i>	<i>Employment data</i>	<i>Source / Comments</i>
Iceland	1898-2017	Total gross register tonnage (active vessels and boats)	Total number of crew members	Hagskinna, FAO and Statistical Yearbook of Iceland
Sweden	1918-2017	Engine power (kW), Rousseau et al., 2019	Full and part time fishers	Statistical abstract of Sweden
Norway	1948-2018	Total horse power (motorized boats)	Number of fishers	Fiskeritelling, Statistikk Fiskefartoy 2018, Gullestad 2013
China	1956-1965 1971-2019	Engine power (kW), Rousseau et al., 2019	National fisheries labor force, full time/ professional and part time	China Fishery Statistics 40 years, China fisheries yearbok 1980-2011 from Shen and Heino, (2014)
South Korea	1962-2019	Engine power (kW), Rousseau et al., 2019	Fishery workers	Statistics Korea (KOSIS), Fishery Survey

Italy	1871-1915 1929, 1938 2002-2012	Gross tonnage of fishing fleet	-	Annuario Statistico Italiano, OECD, FAO and EUROSTAT
Ireland	1893-1985 1995-2017	Engine power (kW), Rousseau et al., 2019	Full and part time fishers (men and boys)	Report of the Sea and Inland Fisheries of Ireland, FAO after 1995.
Denmark	1946-1977 1995-2017	Engine power (kW), Rousseau et al., 2019	Professional and occasional fishers	Statistisk Årbog, FAO after 1995

Finally, in order to be able to compare our reconstruction with the fisheries employment reported by FAO (2017), we subtracted the estimated number of inland fishers from the FAO data. If disaggregated data was not available on the country profile page, we used either the inland fraction or the inland catch fraction to estimate the number of inland fishers, similar as described in the previous section. With this approach, the number of marine fishers was estimated to make up somewhat more than half of the number of fishers reported by FAO (2017) over the period 1995-2016.

2.2 *Fleet power data and rates of labour substitution*

Unless fishing is undertaken from land, employment in fisheries is necessarily linked to fishing vessels. Recently, improved reconstructions have provided high-resolution estimates of the evolution of the worlds fishing fleet since 1950 (Rousseau et al., 2019). This progress lays the foundations for performing a time-resolved analysis of global fisheries employment.

The long time series of fisheries employment were used to investigate the long-term rate of labor substitution in national fisheries. We investigate the level of mechanization, which we represent by the power per fisher (PPF), the ratio between the total mechanic power in the fleet (P_i , Watts) of each country, i , and human labor (number of fishers, $n_{F,i}$). For the rate of labor substitution, we investigated how the inverse of the mechanization level (i.e. fisher per

power) developed over time. For the time period 1950-2015, Rousseau et al. (2019) provide the total fleet power. For Iceland, Italy and Ireland, which have pre-1950 employment data, we also assembled time series of the total gross tonnage of the national fleet from national reports and use tonnage as a proxy for fleet power.

2.3 *Relationship between GDP and mechanization level*

Across a range of regions and fields, there is strong evidence that economic growth is tightly linked to mechanization. The consumption of energy, a requirement for machinery, is highly correlated with GDP per capita (Nasreen and Anwar, 2014; Warr and Ayres, 2010; Zhang and Cheng, 2009), investment in equipment is strongly associated with economic growth (De Long and Summers, 1991), and GDP growth coincides with a decrease in the fraction of the population that is employed in the agriculture sector (FAO, 2015; Our World in Data, 2020). We therefore hypothesized a link between the national GDP per capita and the level of mechanization in the fishery and used this empirical relationship to infer missing data on the number of fishers.

Historical estimates of GDP per capita (2011 US\$) from the MADDISON database (Bolt et al., 2018), estimated with a multiple baseline approach, were used to derive a relationship between GDP and mechanization level, i.e. the $PPF = P_i/n_{F,i}$ (W pers⁻¹). Gaps in the GDP time series were replaced by linearly interpolated values. Through an initial linear regression using the whole dataset (Supplementary Fig. 1; Eq. 1), we found that several outliers were from early years. Therefore, considering the possibility that older estimates of $n_{F,i}$ (in particular the single data points pre-1980) are more uncertain, we used data only from the period 1995-present to derive the GDP- PPF relationship (Fig. 1). Using only this more recent subset of the data resulted in a higher R^2 than for the whole dataset despite the smaller dataset, yet regressions for the whole and recent data sets had similar slopes ($k = 1.15$ and 1.13 respectively; see Results).

$$\log(PPF) = \log\left(\frac{P}{n_F}\right) = k \log(GDP) + m \quad (1)$$

We also hypothesized that there would be a lag between the growth in GDP and increased mechanization level in the fleet, as the labor force adjusts to increased mechanization gradually as fishermen exit the fishery through retirement or finding alternative employment. We tested if using the GDP per capita 1 to 15 years before the year of the PPF data improved the regression. A 15-year lagged regression requires a continuous time series of GDP per capita from 1935, but while 113 countries had GDP data from 1950, only about 56 countries had data for the period 1935-1949. For missing entries, we therefore extrapolated the earliest available GDP value to all the preceding years. Given that GDP per capita has grown over time in the majority of countries, this generally results in a slight underestimate of the number of fishers. An 11-year lag for GDP per capita had the highest predictive power: $R^2 = 0.69$ for the 1995-present subset, and 0.59 for the whole dataset (Fig. 1 and S1). We also performed weighted regressions where each data point was weighted by the number of fishers. However, given that such a relationship will be heavily biased towards the development in the most populous countries (China and India), reconstructions using the weighted regression is only presented for comparison in Appendix III (Fig. S2).

We investigated the explanatory power of a range of additional predictors beyond GDP per capita, again using data from 1995. Multiple linear regressions were made with lagged GDP per capita and either Human Development Index (UNDP, 2020), Gini coefficient (World Bank, 2020a), wage (Purchasing Power Parity; ILO, 2020), national population growth rate (World Bank, 2020b) or the ratio of coastal length to country area (CIA, 2020) as the second predictor. We used log-transformed values for predictors with log-normal distributions, i.e. GDP, Gini, wage and coastal-area ratio, and filled data gaps with linear interpolation. While all predictors were statistically significant (all < 0.002), none of the predictors increased the predictive power of the regression more than marginally. The Gini coefficient and population growth increased R^2 the most, from 0.69 to 0.72. Since the wage data was sparse ($n = 169$), including it as a predictor required a significant reduction of the sample size. Given the limited increase in predictive power, and the lack of data before 1995 for several predictors, we did not include any other predictor than GDP per capita in the GDP-PPF relationship used for the reconstruction.

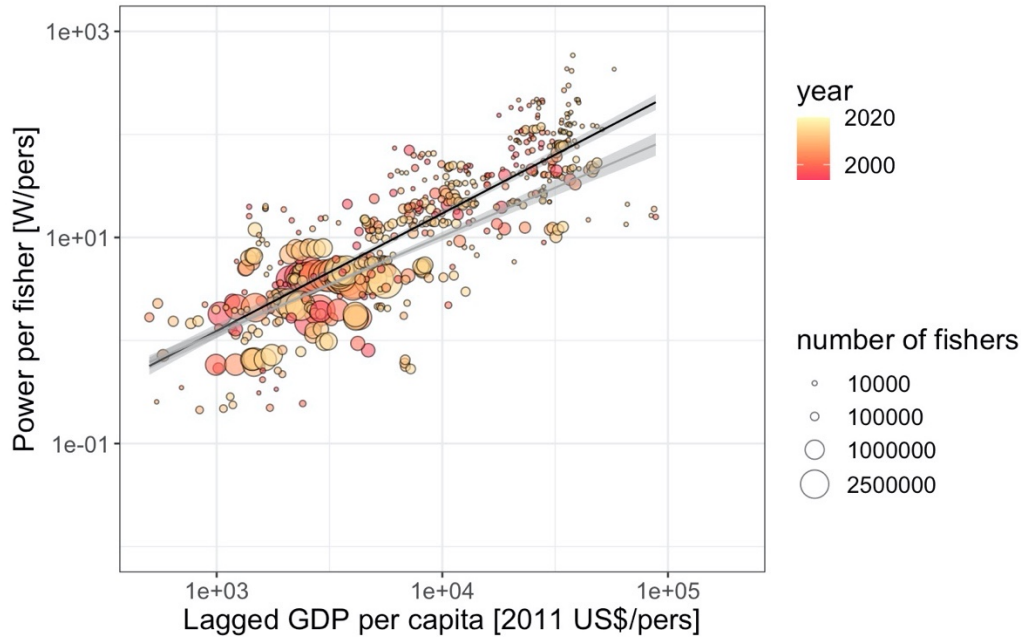


Figure 1. Relationship between GDP and mechanization level. The log-transformed data from the years 1995-2020 show a linear increase of the log-transformed power per fisher ($W \text{ pers}^{-1}$) with the log-transformed lagged (11 years) GDP per capita (2011 US\$ pers^{-1}). Black line shows linear regression for the unweighted data set ($R^2 = 0.69$, $p\text{-value} < 2 \cdot 10^{-16}$), while grey line shows regression when weighted by the number of fishers ($R^2 = 0.52$, $p\text{-value} < 2 \cdot 10^{-16}$). Envelopes show the standard error. Slope of regression is 1.15 for unweighted and 0.93 for weighted regression.

Table 2. Statistics for multiple linear regression with $\log(\text{GDP per capita})$ and one additional predictor. Standard error is indicated for the slope. The sample size (n) for linear regression using only GDP is 563.

<i>Predictor</i>	<i>Slope</i>	<i>p-value</i>	<i>R2</i>	<i>n</i>
Population growth	-0.06 ± 0.01	$3.80e-6$	0.72	555
Human Development Index	1.09 ± 0.36	0.0027	0.71	547
Coastline-to-area index (log)	0.15 ± 0.02	$5.38e-9$	0.71	562
Gini index (log)	-0.58 ± 0.21	0.0064	0.72	439
Wage (log)	0.42 ± 0.12	0.00076	0.61	169

2.4 Reconstructing the number of fishers

For countries and years lacking empirical or interpolated data, we used the GDP-PPF unweighted regression for the post-1995 data subset with an 11-year lag for GDP (Fig. 1) to reconstruct the number of fishers from the fleet data (Rousseau et al., 2019). Solving for $n_{F,i}$ in Eq. 1, the reconstructed number of fishers of country i , $n_{F,i}^*$, was given as:

$$n_{F,i}^* = \frac{P_i}{10^{k \log(GDP_i) + m}} \quad (2)$$

The global fishing fleet contains a significant number of unpowered fishing vessels (e.g. manually propelled or sailing vessels), as detailed in the fleet data set from Rousseau et al., (2019). Since we use the engine power of the fleet (P) to reconstruct $n_{F,i}^*$, we estimated the segment of “unpowered” fishers separately from the data on the number of unpowered vessels by calculating the average crew size of unpowered vessels.

The number of unpowered fishers is difficult to disaggregate from the empirical values, $n_{F,i}$, but Rousseau et al. (2019) provide data on the number of unpowered vessels. We derive the average crew size of unpowered vessels from a subset of data points that either 1) are from before year 1900, thus ensuring that all fishers were employed on unpowered vessels, or 2) had more than 97% unpowered vessels in the fleet. Due to the likely spurious inclusion of inland fishing vessels in the data for the Democratic Republic of the Congo and Tanzania, these two countries were excluded from the subset. The remaining countries included Ireland, Iceland, Italy, Japan, Djibouti, Sri Lanka, Kirbati, Haiti, Indonesia, China, Comoros, Mozambique and Sweden. By dividing $n_{F,i}$ in these countries with their number of vessels, the average crew size of unpowered vessels was estimated to be 3.8 ± 1.7 persons (mean and standard deviation).

The total number of unpowered fishers for each country and year was estimated by multiplying the average crew size with the number of unpowered vessels. While we add these unpowered fishers to the reconstructed number of fishers, $n_{F,i}^*$, to avoid double counting we do not add unpowered fishers to the empirical or interpolated data ($n_{F,i}$). We underline that

the number of unpowered fishing vessels made up a relatively small proportion of the total global fishing fleet (30%) during the years 1995-2020 - from which we derive the GDP-PPF relationship - while 60% of all vessels were unpowered during 1950-1995. This further motivates a separate reconstruction of unpowered fishers.

Finally, to avoid sudden shifts in the reconstructed number of fishers, $n_{F,i}^*$ was joined with $n_{F,i}$ for each country using a gradual smoothening. The reconstructed values 10 years before the earliest year with available empirical data were replaced by a simple linear interpolation.

We assess the predictive skill of the GDP-PPF relationship for the post-1995 data through cross-validation. A 10-fold cross-validation repeated three times had root mean square error (RMSE) = 0.40, $R^2 = 0.70$. Plotting the observed versus predicted values for the whole dataset (including pre-1995 values; Fig. 2) shows that while there is somewhat more variability for the earlier data points, overall the GDP-PPF model estimates fisher population sizes pre-1995 relatively well.

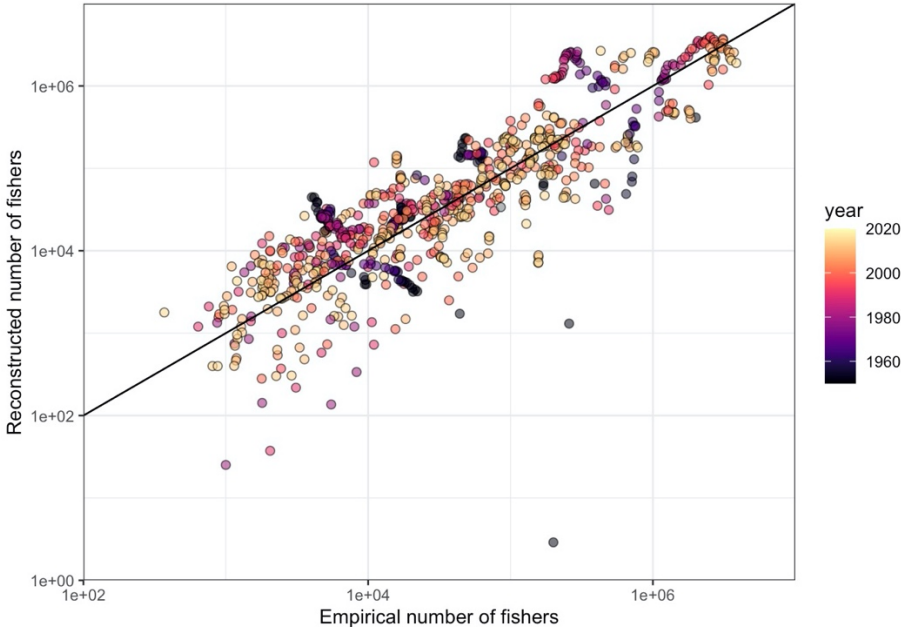


Figure 2. Empirical ($n_{F,i}$) versus reconstructed ($n_{F,i}^*$) number of fishers for each country and year for the complete dataset. The color indicates the year of the data point, and the black line shows the one-to-one reference line.

3 Results

3.1 Long-term labour substitution

In the countries with available long time series of fisher populations, we found that labor substitution has been significant over the past century. Out of the six countries shown in Fig. 3, the fisher populations of South Korea, Norway, Iceland and Ireland declined over the whole time period and the Italian fisher population grew substantially until year 1938 and then decreased greatly (Fig. S3). Only China showed a sustained growth in the number of fishers. Still, the ratio between fishers and fleet power (either engine power or gross tonnage) has declined greatly over the past century in all countries (Fig. 3). Exponential functions fitted to the data suggest that the rate of decrease in fisher per power has been 10%, 22%, 11%, 7% and 4% yr⁻¹ respectively for South Korea, China, Ireland, Norway and Iceland. These cases support the notion that technological progress has led to widespread rationalization and labor reductions (Garcia and Rosenberg 2010).

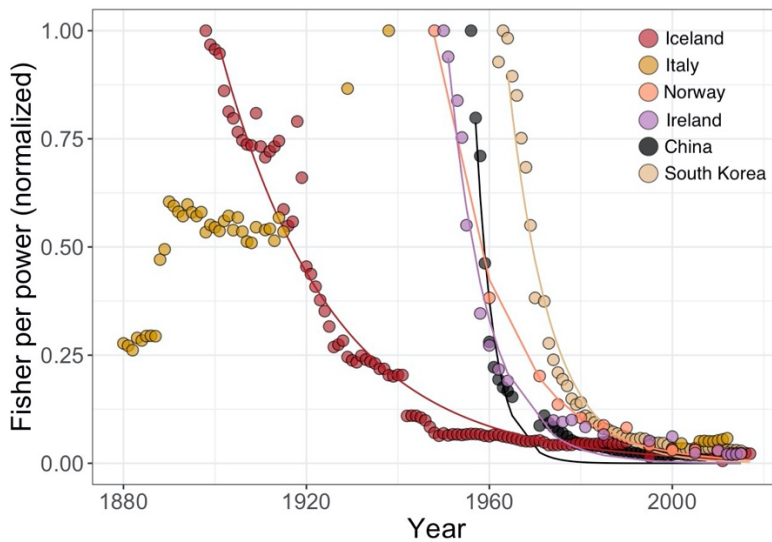


Figure 3. Long-term labor substitution in six fishing nations. Number of fishers per unit of fishing power, normalized by maximum values, for South Korea (beige), China (black), Ireland (purple), Norway (orange), Italy (yellow) and Iceland (dark red). For Italy and Iceland,

total gross tonnage of the fishing fleet is used as the power unit, while total engine power (kW, Rousseau et al. (2019) except for Norway) is used for the remaining countries.

3.2 Reconstructed employment

Despite the dramatic change in labor intensity in the countries with long-term data series (Fig. 3), our data reconstruction suggests that the global fisher population has grown continuously since 1950 (Fig. 4). The total fisher population (including fishers that use unpowered vessels) started at about 8 million in 1950, and after a period of relative stability until 1970, it grew rapidly at an average rate of $\sim 2\%$ yr^{-1} until the beginning of the 21st century. Overall, this development resulted in an approximate doubling of the fisher population in 50 years. As suggested by the FAO data (Fig. 4), the global number of fishers is currently reaching a plateau, similar to both the global catch (Pauly and Zeller, 2016) and the number of fishing vessels (Rousseau et al., 2019).

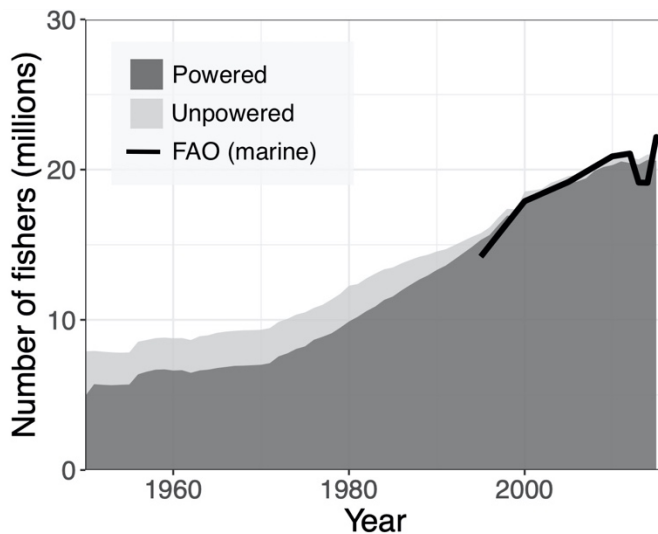


Figure 4. Reconstructed global fisheries employment 1950-2015. Dark grey shows the reconstruction from either linear interpolation or the relationship between lagged GDP per capita and power per fisher (PPF) and the fleet power data from Rousseau et al. (2019). Separate reconstruction for fishers that use unpowered fishing vessels is in light grey. Black line shows data reported by the FAO 1995-2016, with inland fishers subtracted.

The trends in fisher numbers differ significantly between regions (Fig. 5). Disaggregating by geographic regions shows that the global development is largely driven by the development in East Asia and the Pacific and South Asia, where our reconstruction suggests that fisher populations have increased three- and seven-fold respectively. Sub-Saharan Africa, Latin America and Caribbean and Middle East and North Africa also show similar trends, with growing fisher populations during most of the period and a stagnation in recent years, although with a temporary peak in the mid 1960's in Latin America and the Caribbean. In contrast, the European and Central Asian fisher population has declined to only about a third of its size in 1950. Beyond slight decreases in 1950-1955 and 2005-2015, the fisher population of North America has been relatively stable.

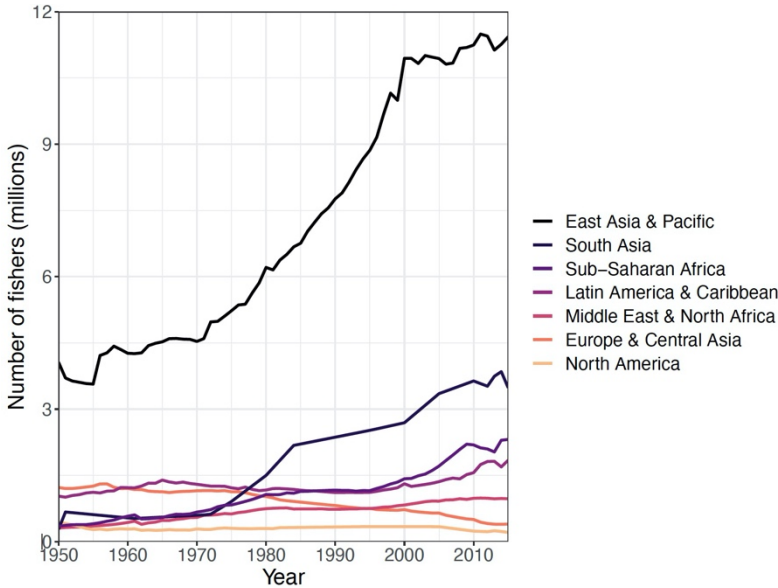


Figure 5. Reconstructed number of fishers by region. Color legend is ordered according to the size of the regional fisher population in 2015. Only North America and Europe and Central Asia have had decreasing fisher populations over time.

When disaggregating the reconstruction by income group (high, upper-middle, lower-middle and low-income countries; Fig 6a), we find that the lower-middle income countries have the largest number of fishers. This group also saw the most rapid growth in the number of fishers, with an approximate ten-fold increase since 1950. Rapid growth also took place in the low-income countries, which had the smallest fisher population until 2005 when it exceeded the

steadily shrinking population of fishers in high-income countries. The upper-middle income group, dominated by China, exhibited more modest growth.

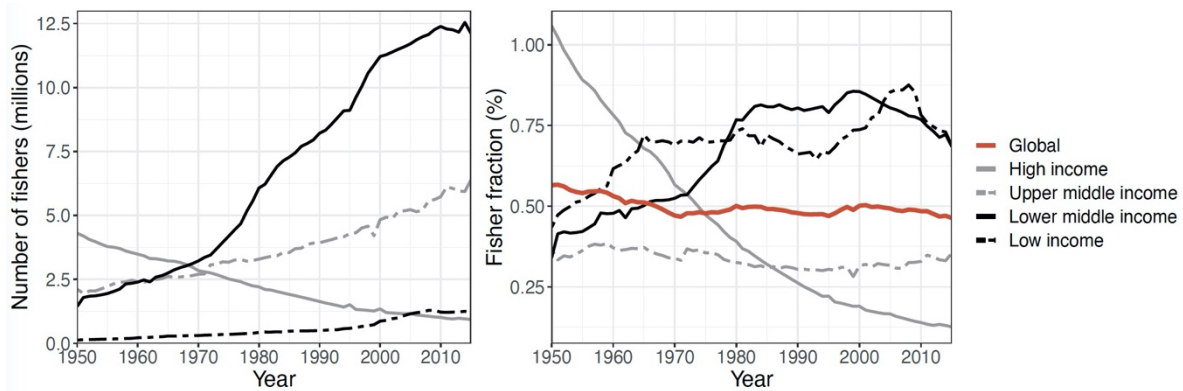


Figure 6. Reconstructed number of fishers and fisher fraction by country income group. While the high-income countries have had a decline in the number of fishers over time, the fisher populations of the other three income groups have stabilized somewhat in recent years. The average global fisher fraction (weighted by the fisher population size) has thus been relatively stable at around 0.5% of the total working population since the 1970s.

In Fig 6b, we investigate how the number of fishers has changed over time relative to the total population. Using age-structured national population data and including all individuals of working age (here age 15-64), we calculate the fisher fraction, i.e. the proportion that fishers made up of the national work force. A stable fisher fraction over time suggests that the fisher population grows at the same rate as the working population, and the metric helps to disentangle the effects of population growth from that of other factors. Globally, the working population-weighted average fisher fraction has remained relatively stable around 0.5 % after a small initial drop in the period 1950-1970. That is, over the whole 65-year time period, about 1 in 200 of the total work force or 1/200th of the total working hours have supplied wild-caught seafood to the world. However, the development differs greatly between income groups. While the fisher fraction has declined by more than an order of magnitude in the high-income countries since 1950, our reconstruction suggests that it has remained relatively stable in upper middle-income countries, and increased significantly in lower-middle- and low-income countries.

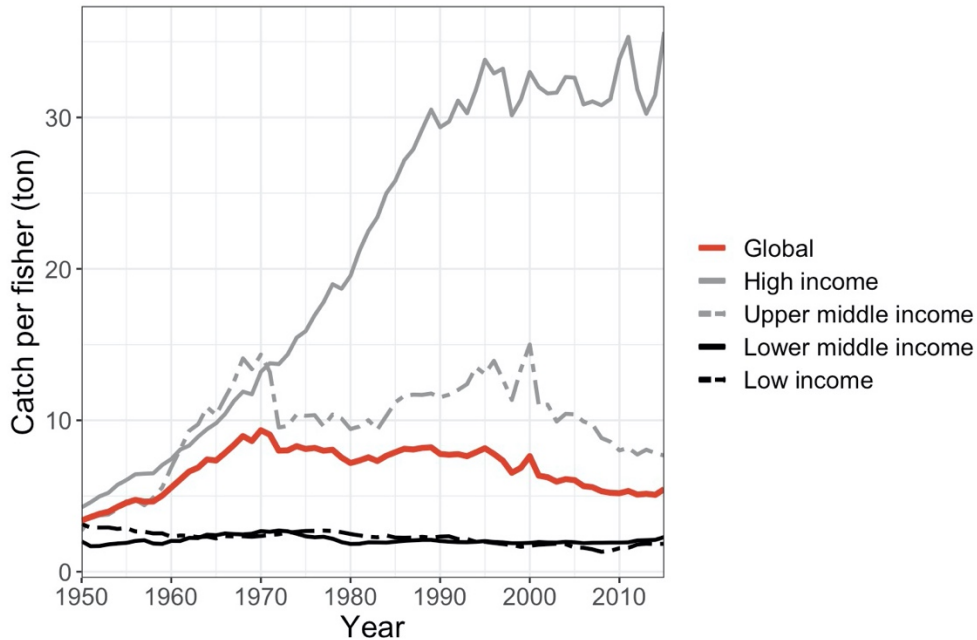


Figure 7. Catch per fisher (metric tons) by country income group. Figure shows the average across all countries weighted by the reconstructed number of fishers, using catch reconstruction from the Sea Around Us project. The decline in catches in upper middle income countries during the last 15 years, and continued growth of the fisher population, drives a decline in the catch per fisher both in upper middle income countries and globally.

Finally, we use reconstructed global marine catches by country from the Sea Around Us project (Pauly and Zeller, 2016) to estimate the catch per fisher (Fig. 7). Again, the global average catch per fisher has been surprisingly stable over the time period. After an initial doubling from 1950-1970, the catch per fisher remained around 8 ton per person until the beginning of the 21st century, and then decreased until 2015. Our reconstruction suggests that the catch efficiency per fisher is today the same as in 1960, despite extensive technological progress and the large quantities of fuel used in the process (Tyedmers et al., 2005).

4 Discussion

Our reconstruction suggests that the global fisher population has grown continuously over the past 65 years. Further, the growth of the global fisher population has kept a similar pace as that of the total working population, resulting in a relatively stable global fisher fraction. We find this surprising, given the rapid technologic and economic development that has taken place not only in high-income countries, but throughout the world since 1950 (Gapminder, 2020). Since the 1950s, the extent to which machines and engines, rather than human labor, propel the fishing vessels, search for fish, haul the nets and perform the handling of the catch could be expected to have increased greatly. In agriculture, another primary sector, this kind of mechanization has been clearly demonstrated (Debertin et al., 1990; Hayami and Ruttan, 1970; Herrendorf et al., 2014; Lianos, 1971; Ruttan, 2002), and the global farmer fraction decreased from 44% to 26% only between 1991 and 2020 (ILO, 2020b). Garcia and Rosenberg (2010) sum up this expectation in their review of global fisheries, when writing that “[technology’s] unbridled use will continue to direct fisheries on a trajectory of progressive automation and reduction of labor, with negative implications for coastal communities”. However, several factors could explain why this is not a universal pattern in our reconstruction.

First, the general understanding of trends in fisheries employment may be dominated by findings from highly industrialized countries (e.g. Donkersloot and Carothers, 2016; Hamilton and Duncan, 2000; Hannesson, 2007; Heen, 1988; Johnson and Mazur, 2018), where more resources and long-term data is available. Extrapolating such an understanding to other regions of the world may fit poorly with reality, as previously pointed out in reconstructions of global fishing fleets (Rousseau et al., 2019). While our approach avoids such extrapolation problems by covering a broad range of countries and economic levels (GDP per capita), a biased preconception may still mean that one, a priori, overestimates the global effect of mechanization.

Cultural preferences, sociopolitical interventions and the distribution of wealth may explain part of the observed stability in the fisher fraction. Despite the strong overall relationship between GDP per capita and PPF, countries like Canada, China, Iceland and Peru have had long periods of essentially unchanged fisher-to-power ratio (Fig S4). Possibly, this could be a result of a strong fishing culture and political interventions aiming to maintain high employment in fisheries (Cao et al., 2017; Hongzhou, 2015; Icelandic Parliament, 2006; Schrank, 1998). In other instances, economic inequalities both between fishers and non-fishers, and between different fisher groups may contribute to low rates of labor substitution. While global inequality between countries has decreased, 70% of the world's population is experiencing increasing income inequality in their own countries (United Nations, 2020). In countries with high internal inequality, poor worker's rights or corruption, the rising tide may not lift all fishing boats. Increasing wealth from fisheries may only benefit a few of the fishers, leaving the majority of fishers without access to technologies and other capital (Jentoft et al., 2011).

Supporting the notion of inequality within groups of fishers, Teh et al. (2020) show that large-scale/commercial fishers earn twice as much as small-scale fishers and that a significant proportion of crews worldwide earn below the national poverty line. In the Caribbean, boat owners earn twice the income of captains and almost six times the income of crew. If income inequality is high, and fishers a poor or marginalized group, neither wealth generated by the fishery nor the national economy may translate to decreased fisheries employment. As an illustrative counterexample, Hannesson, (2007) demonstrates how since 1950 in Norway, one of the countries with the world's highest income equality, fisher's wages have been maintained at high levels, comparable with alternative occupations, but only through an 85% reduction in the number of fishers. The importance of equality is supported by the significance of the Gini index as a predictor in our multiple linear regression (Table 2).

The analysis of fisher incomes by Teh et al. (2020) provide another possible explanation for the continued high fisheries employment in many geographic regions. In East Asia and the Pacific, Latin America and the Caribbean, South Asia and Sub-Saharan Africa, the fishing

occupation yields an average income 1.5 – 2.3 times higher than in agriculture. Given that low and lower-middle income countries have high shares of the total labor force in agriculture (World Bank, 2020c), the higher income in fisheries relative agriculture could explain why these regions in particular have had growing fisher fractions during large parts of the past 65 years (Fig. 6b). This is likely also a key reason for the continuously growing fisher fraction we have found for China (Hongzhou, 2015).

We underline that the approach used here aimed primarily to extrapolate and fill in data gaps, while other global fisheries reconstructions have strived to also reconstruct unreported and hidden numbers (Pauly and Zeller, 2016; Rousseau et al., 2019; Teh and Sumaila, 2013). Small-scale and subsistence fishers are often left out of official statistics, motivating specific modelling approaches to estimate this subset of the global fisher population (Teh and Sumaila, 2013). This explains why our estimated number of fishers is less than half of that previously reported (Teh and Sumaila, 2013) (yet close to the number of marine fishers estimated by FAO, 2017). By using a separate estimate of small-scale fishers for the unpowered segment of the fleet, we partly offset this difference for the historical reconstructions. Yet, the remaining hidden subset of global fishers is potentially important and could alter our findings.

It is for example possible that the tendency for underreporting fisher numbers has decreased over time. The FAO attributes the increase in global fisheries employment 1995-2010 partly to “improved estimation procedures” (FAO, 2018a) suggesting that earlier data points may underestimate the true fisher population to a greater extent. The same difficulty to estimate numbers with high accuracy further back in time also applies for fishing vessels (Rousseau et al., 2019). A higher proportion of hidden fishers in earlier years would mean that (1) the number of fishers has increased less since 1950 than what is suggested in Fig 4; (2) that the fisher fraction started from a higher value in Fig. 6b; and (3) that the catch per fisher has increased more since 1950 than suggested in Fig. 7. It would thus be more in line with the notion that mechanization has greatly diminished the need for labor in fisheries (Garcia and Rosenberg, 2010).

We emphasize that we aggregate full and part time fishers (professional versus occasional). Although some of our long-term data sources give separate numbers, the FAO data set did not allow this kind of disaggregation. Further, we have not estimated employment in secondary sectors like processing, manufacturing, wholesale, transport, boat and gear construction or repair. Scarce data and a potentially large influence of mechanization that is difficult to quantify prevented an estimate of secondary fisheries employment over the time period studied here.

Finally, we see some tendencies for a recent stagnation in the growth of the fisher population (Figs. 4-6). For several major fishing countries (e.g. China, Egypt, India, Indonesia, Malaysia, Nigeria and Taiwan), the rate of increase in the fisher population over the past five years is lower than over the past ten years (not shown). Possibly, the global slowdown could be linked to management interventions aiming to reduce fishing pressure (OECD, 2007; Rousseau et al., 2019). However, we underline that stabilizing fisher numbers does not equal stabilizing fishing pressure, since technological progress greatly alters the per capita fishing power. For example, catches in the North East Atlantic and Mediterranean have been relatively stable since the 1980's (Pauly and Zeller, 2016), although the European fisher population decreased by more than 60%.

5 Concluding remarks

The reconstruction in this chapter finds that despite the influence of mechanization, the global fisher population has grown continuously, in total by a factor of 2.6, since 1950. Despite large regional and economically-determined variation, the fraction of the total global working population employed in fisheries, has remained surprisingly stable around 0.5% over the 65-year time period. The extent of rationalization in medium and low-income countries has been low relative to their rate of economic progress. However, there have been remarkable ~80% and ~90% declines in the number of fishers and fisher fraction respectively in high-income countries. If other regions were to follow this development, this would mean

an even more dramatic socio-economic transformation. The global fisher population is highly heterogeneous, and the benefits of being a fisher varies greatly. The priorities of policymakers and managers, who's task it is to help steer the mix of labor and capital inputs to a level that meets societies' objectives, thus have a great potential to influence the future wellbeing of the world's marine fishers.

Chapter 5

1 Discussion and conclusion

I will now conclude with a discussion of the contributions and limitations of this thesis, and of the future work for which it paves the path, adding to the discussions presented in each individual chapter. I begin by detailing how the work presented in Chapters 2-4 has achieved my research aims.

1.1 Achieving the research aims

In this thesis, I have developed new ways to explore the dynamics of the global marine fishery. The focus has been on understanding key human processes, incorporating them in the model framework, and performing global experiments – both over long and short time scales.

My first research aim was to advance the representation of humans and their activities in global marine ecosystem models. The development of a regulation module to the BOATS model (Chapter 2) and of scenarios for fisheries during an extreme climatic and socio-political shock (Chapter 3) achieve this aim. Further, the reconstruction of historical global fisheries employment (Chapter 4) is a first and necessary step towards representing fishing activity in terms of human labor in this kind of global model.

The second research aim was to improve the understanding of how the global fishery responds to key macroscale drivers of changes. This goal has been achieved first through the investigation of the importance of regulation effectiveness, technological progress and climate change in long-term projections, as undertaken in Chapter 2. Further, Chapter 3 has investigated the response of global catch and biomass to large and abrupt shifts in climatic drivers, fish prices and fishing costs. Finally, through the work performed in Chapter 4, I have

begun to untangle the mechanisms that drive long-term changes in the world's fisher population.

1.2 Contributions

The work in this dissertation has contributed new insights and methods to the area of global fisheries analysis. On the methodological side, the work in Chapters 2 and 3 has advanced the application of global, spatially-resolved fisheries models for future projections. The long-term effects of climate change on marine fisheries have recently been projected by a suite of different global marine ecosystem models (Lotze et al., 2019), but the simultaneous inclusion of major determinants of fisheries outcomes, such as technological progress, regulation and economic parameters (Fulton et al., 2011; Galbraith et al., 2017; Palomares and Pauly, 2019; Squires and Vestergaard, 2013), are missing in most of these - and other (Costello et al., 2016; Gaines et al., 2018) - global projections. Chapters 2 and 3 show how these processes can be dynamically incorporated into global models. Further, the work in Chapter 3 provides one of the first quantitative investigations of the effects of sudden climatic and socio-economic shocks on the global fishery. The work lays out ways to incorporate such shocks and demonstrates a new type of application for global fisheries models that could be re-examined and further evaluated by future modelling efforts (see 1.4).

As long-term future projections are becoming central in the field (Cheung et al., 2016; Dueri et al., 2016; Lotze et al., 2019; Stock et al., 2017) the kind of investigation undertaken in Chapter 2 is of large importance. The work builds on Galbraith et al. (2017) to investigate the impact of regulation effectiveness and technological progress on fisheries projections over multi-decadal time scales. The concept of a race between technology and regulation (that we term the Red Queen race) is far from new, but rather a well-known phenomenon in fisheries science (Whitmarsh, 1990). But by quantifying the global implications of this race over the upcoming century, I demonstrate that these human factors have a potentially large impact on projections, in some instances larger than that of human-driven climatic change. Further, the findings underline that the poor mechanistic understanding of technological progress

(Nagy et al., 2013), which is a key driver of change over multi-decadal time scales (Squires and Vestergaard, 2013), is a source of major uncertainty in long-term projections.

With a completely different time-frame, Chapter 3 treats the large-scale impacts of abrupt shocks on global fisheries. While regional analyses, for example of marine heat waves (Caputi et al., 2016; Cheung and Frölicher, 2020; Lenanton et al., 2017; Roberts et al., 2019), socioeconomic shocks (Gephart et al., 2017), or historical catastrophic climate events (Alexander et al., 2017) have been performed, the work in this thesis is to my knowledge the first global model simulation of this kind. The work suggests that after a nuclear war-induced climate perturbation, it is mainly the low light, and to lesser extents the cooling and circulation changes that drive a decrease in the total global fish biomass. The results also reinforce the findings that a nuclear war could jeopardize the whole world's food security (Jägermeyr et al., 2020). Given its relatively small contribution to global food security (FAO, 2018b), increased fishing would not be a panacea. This knowledge is important both for the general public and for global leaders and policymakers negotiating treaties regulating the future of nuclear weapons. The work finally demonstrates a simple and intuitive fact that is rarely used to motivate the importance of effective fisheries management; that it creates a large source of emergency animal protein in the event of a global (or local) food emergency.

While Chapters 2 and 3 contribute directly to advancing global fisheries modelling approaches, Chapter 4 contribute a new empirical description of historical employment. The reconstruction creates a new temporal understanding of labour in fisheries, extending the previous global syntheses (FAO, 2017; Teh and Sumaila, 2013) and supplementing country-level analyses (Donkersloot and Carothers, 2016; Hamilton and Duncan, 2000; Hannesson, 2007; Heen, 1988; Johnson and Mazur, 2018). It suggests that mechanisation has had a relatively small impact on labour in large regions of the world, and that this combined with the stagnation of global catches has led to a surprisingly small increase in the catch per fisher over 65 year study period. The work lays the foundation for improving the mechanistic understanding of what drives changes in labour in the global fishery.

1.3 Limitations

Many limitations of the work have already been discussed in the respective chapters. In Chapter 2 (Scherrer and Galbraith, 2020), I discussed the uncertainty of future technological progress, the assumed homogeneity in regulation effectiveness and the simplifying assumptions about economic drivers. In Chapter 3 (Scherrer et al., 2020), I focused on limitations in the ecological realism of the BOATS model, its limited accuracy in modelling the current status of fisheries management, and the great uncertainties about how global fishing activity would respond to the many types of shocks caused by a nuclear war. In Chapter 4, the discussion treats the influence of underreporting, extrapolation and deviations from the model used for reconstruction. Some of the discussed limitations deserve a deeper analysis.

First, it is worth repeating that the studies in Chapters 2 and 3 explore different potential futures, but do not try to predict it. The findings are results of projections; alternative possible futures with different scenarios for the developments of technological, socioeconomic and climatic drivers of change, that may or may not be realised (Bray and von Storch, 2009). The outcomes of these projections depend on a number of assumptions about how the system works (the mechanisms included in the model) and how the conditions (model forcings) might change. For such future model projections, it is notoriously difficult to confront the model results with data. The relevance, or validity, of the results thus hinge upon whether 1) the system works the same way under different conditions, and 2) the assumptions about how the conditions might change are reasonable.

Beginning with point 2), the scenarios in Chapter 2 and 3 are characterized by very high, or “deep” uncertainty (Lempert et al., 2003) about key drivers of change. The largest uncertainty is on the human side, and the uncertainty about technological and socioeconomic drivers also carries through to the projections of changes in the “natural” system, i.e. the climatic changes. In Chapter 2, the multi-decadal time scale makes the developments particularly uncertain, especially given the possibility for non-linear, difficult-to-predict

changes (Merrie et al., 2018). And in Chapter 3, the nuclear war - itself an example of such a non-linear change - is an unprecedented event with multiple coupled effects (see Biggs et al., 2011) and highly uncertain outcomes. My approach to address these uncertainties has throughout been to investigate a wide range of alternative possible developments (see Maier et al., 2016). Further, a goal in Chapter 2 was to explicitly investigate how much the assumptions about the socioeconomic drivers (particularly technology-driven increases in catch efficiency) could affect the long-term future projections.

Limitations in the universality of the key model mechanisms in BOATS should also be acknowledged. BOATS uses relatively mechanistic bio-energetic and bio-economic relationships (Carozza et al., 2019, 2017, 2016; Scherrer and Galbraith, 2020), which increases the model's generalizability. Slow progressive change like that in Chapter 2 should pose a smaller problem, but an extreme shock (Chapter 3) has a larger potential to throw off both the macroecological relationships that determine the growth and abundance of fish, and the socioeconomic dynamics that determine fishing pressure. For the socioeconomic aspect, this is addressed by the fact that the F+ and F- scenarios in Chapter 4 are intended to serve as illustrative, pre-determined experiments. Given the great uncertainty about how the war would affect human behaviour, the main aim of the modifications of price and cost was simply to induce sudden increases or decreases in fishing intensity. As discussed in Chapter 4, there are still large uncertainties about how ecological processes that are not resolved in BOATS would affect our results, that need to be addressed through further simulations with alternative marine ecosystem models.

Finally, while a global modelling approach can tell us a range of interesting things, trade-offs between generalizability and detail limit its ability to represent potentially important small-scale processes. In this work, details about the spatio-temporal heterogeneity of technology level and regulation effectiveness have been left out for tractability. While these factors could possibly be estimated for the present day, estimating their historical (and future) evolution over time is a challenge. My aim has been to use simple idealized scenarios for model forcings that convey the uncertainty about their actual developments.

1.4 Future work

My work with this thesis has outlined a range of avenues for future work. For Chapter 2, next-steps would include improving the representation of spatially and temporally variable management effectiveness by tapping into and interpreting the available literature (e.g. Costello et al., 2016; Mora et al., 2009; Pitcher et al., 2009). This would improve BOATS' ability to accurately reproduce the present-day status of global fisheries, and the improved model could potentially help untangle the causes for the stagnating global catches. Further work on identifying key mechanisms behind (or good proxies for) socioeconomic processes such as compliance with regulation or technological progress is also needed.

For the work in Chapter 3, the robustness of the results should be tested by simulations with other, structurally different marine ecosystem models. Repeating the model experiments with for example species distribution models (Jones and Cheung, 2015) or more complex food web and size spectrum models (Fulton et al., 2011; Heymans et al., 2016; Maury, 2010) would give a more nuanced view of the effects of a nuclear war or another similar perturbation, and help address the ecological model uncertainty associated with sudden shocks. Further, the interactions between capture fisheries and other components of the global food system should also be explored, and analysis of global fisheries responses to the ongoing COVID-19 pandemic can provide additional insights about the coupled system's response to shocks. For Chapter 4, my longer-term goal is to include fisheries employment as an explicit component of BOATS. Thus, the drivers behind the evolutions of global fisheries employment need to be clarified, possibly through a combination of further data analysis and mechanistic model construction.

Finally, some of my ongoing work has not been presented in this thesis. Given the large heterogeneity in fishing activity worldwide, I am introducing separate representations of long-ranging versus short-ranging fishing fleets in the BOATS model. By analyzing global AIS data, I work to identify how distance dependent costs of fishing influence the dynamics of long-ranging fishing fleets. For modelling short-range coastal fishing, I am including the

gridded human population as a potential driver of change. Combined with an improved understanding of the links between human population growth and fishery labor, this inclusion lays the foundation for a global modeling framework where humans are an explicit and interactive component. My hope is that this approach can continue to advance our understanding of humanity's interaction with the ocean.

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Appendices

Appendix I – Supplementary material for Chapter 2

Supplementary figure

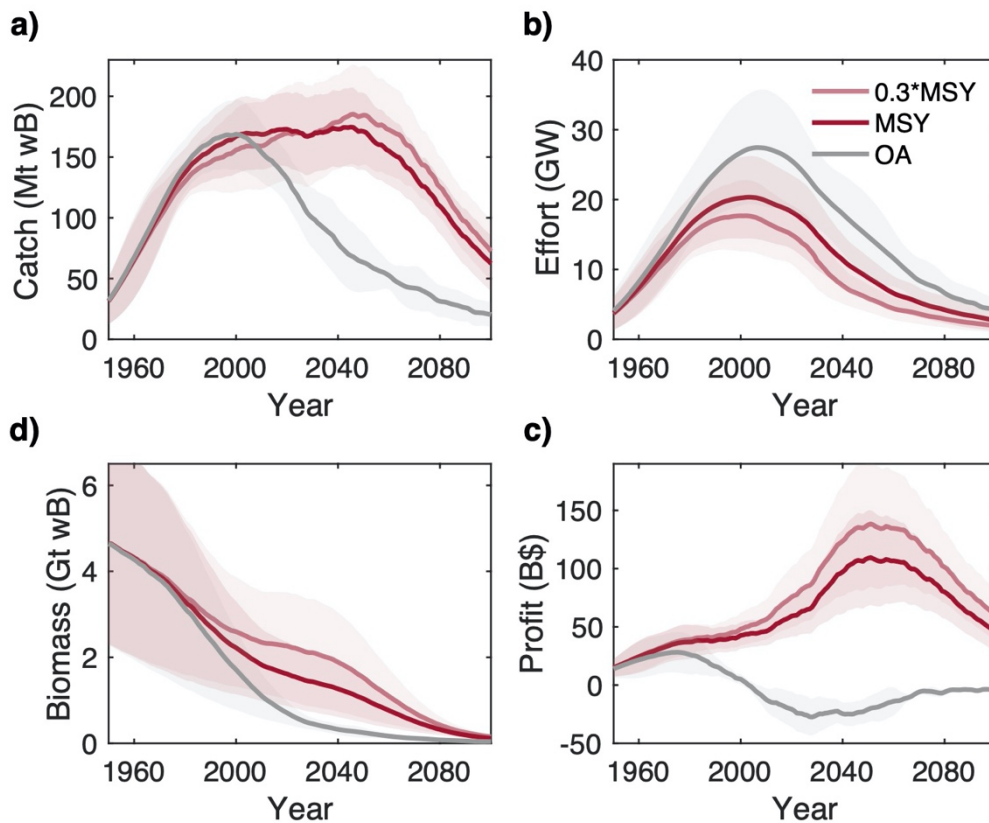


Figure S1 - Simulated trajectories of aggregated global a) catch, b) effort, c) profit (in year 2000 US\$) and d) biomass when the regulation target is either to maintain F_{msy} (dark red) or 30% of F_{msy} (light red). Projections are performed with continued technological progress, RCP 8.5 climate, and weak ($S = 3$, red) regulation. No regulation ($S = 0$, grey) is shown as a reference. Uncertainty intervals (one standard deviation among model ensemble members) are shown by shaded areas. A precautionary management target does not enable long-term sustainability under weak regulation, if technological progress continues at pace.

Appendix II– Supplementary material for Chapter 3

Supplementary text

Here we describe the methodology and results for the model simulations of the impact of soot input on the biomass in an unfished ocean.

Impacts of nuclear war on the unfished ocean

Industrial fishing has caused large, transient changes in fish biomass that are out of equilibrium, modifying how the nuclear scenarios impact fish biomass. Therefore, in addition to the simulations of nuclear war impact on the present-day ocean, we simulate the response of the unfished biomass to the climate perturbations described in the main text. The unfished biomass is determined by running BOATS for 100 years with a repeated time series of the control climate without the bio-economic fishing compartment. This allows the biomass of each fish size group in each grid cell to stabilize at the carrying capacity, determined by NPP and temperature (Carozza et al., 2016). Starting at this equilibrium state, we then force the model with each of the seven climatic perturbations (5, 16, 27, 37, 47 and 150 Tg soot input).

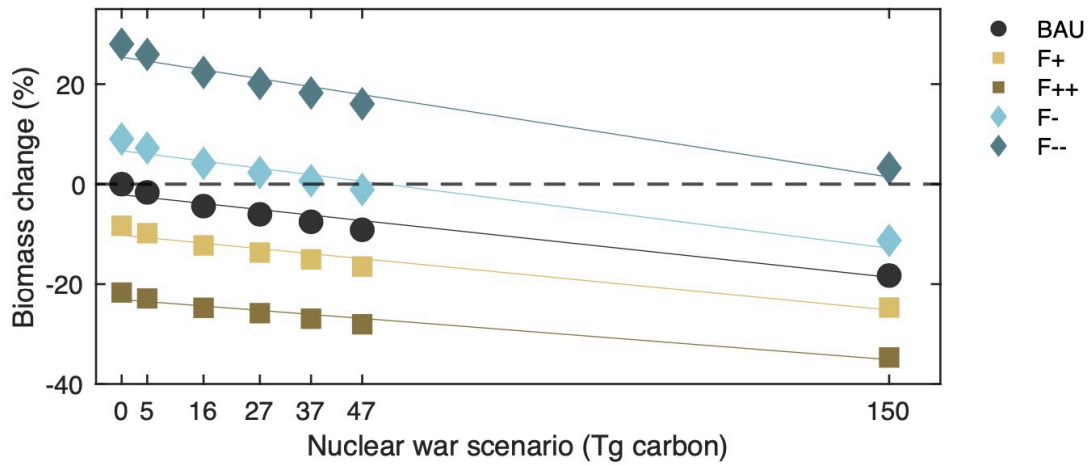
The pristine biomass (Fig. S7A) shows a much smaller negative response to the climatic perturbations than the fished biomass (Fig. 3A-C). At the point with the largest biomass decrease, year 2 post-war, biomass only falls by 10% in the 150 Tg scenario, compared with 18% under BAU fishing in the present-day ocean. At the same time, the global drop in NPP modeled by CESM (Fig. S7B) reaches almost 35% in the 150 Tg scenario, both due to deteriorating light conditions and ocean circulation changes. After the initial biomass decrease, biomass rapidly recovers and within five years it exceeds the pre-war levels by up to almost 15%.

This different outcome is caused by interacting effects of the changes in oceanic NPP and temperature (Fig. S7B,C). The decline in the food source of marine ecosystems is not matched by an equivalent decrease in the global fish biomass because colder temperatures generally

have a positive impact on biomass in BOATS (Carozza et al., 2019). This effect, where cooling attenuates the effect of losses in NPP on the biomass of higher trophic level organisms, is essentially the reverse of the trophic amplification of biomass losses under global warming observed in BOATS (Lotze et al., 2019). Thus, as global NPP starts to recover, the sustained cooling generates a global increase in unfished biomass. This effect is particularly pronounced in the 150 Tg case, where a modified ocean biogeochemical state causes a sustained NPP increases post-war (Fig. S7B).

Supplementary figures

A



B

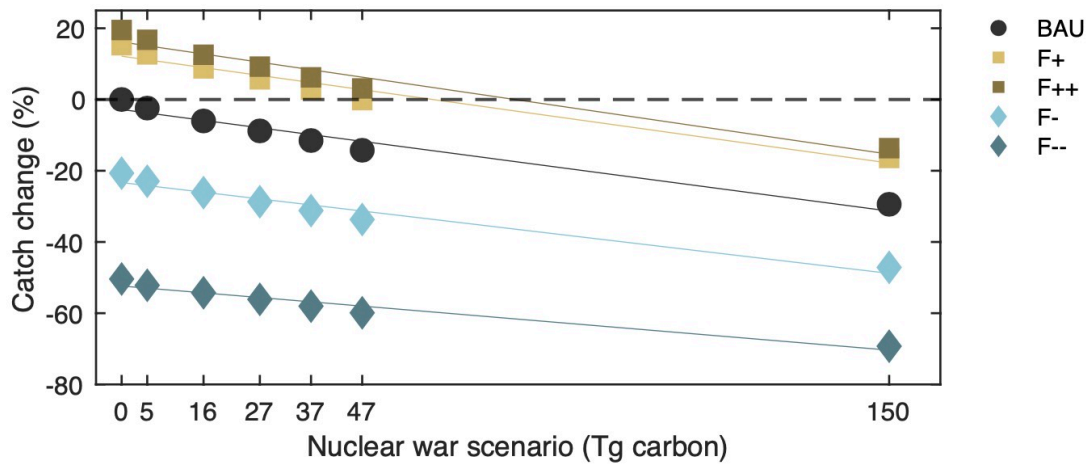


Figure S1 - Same as Fig. 2, but with the percent biomass and catch difference plotted against the soot input associated with each nuclear war scenario (Tg carbon). Statistics for linear regressions are given in tables S3 and S4.

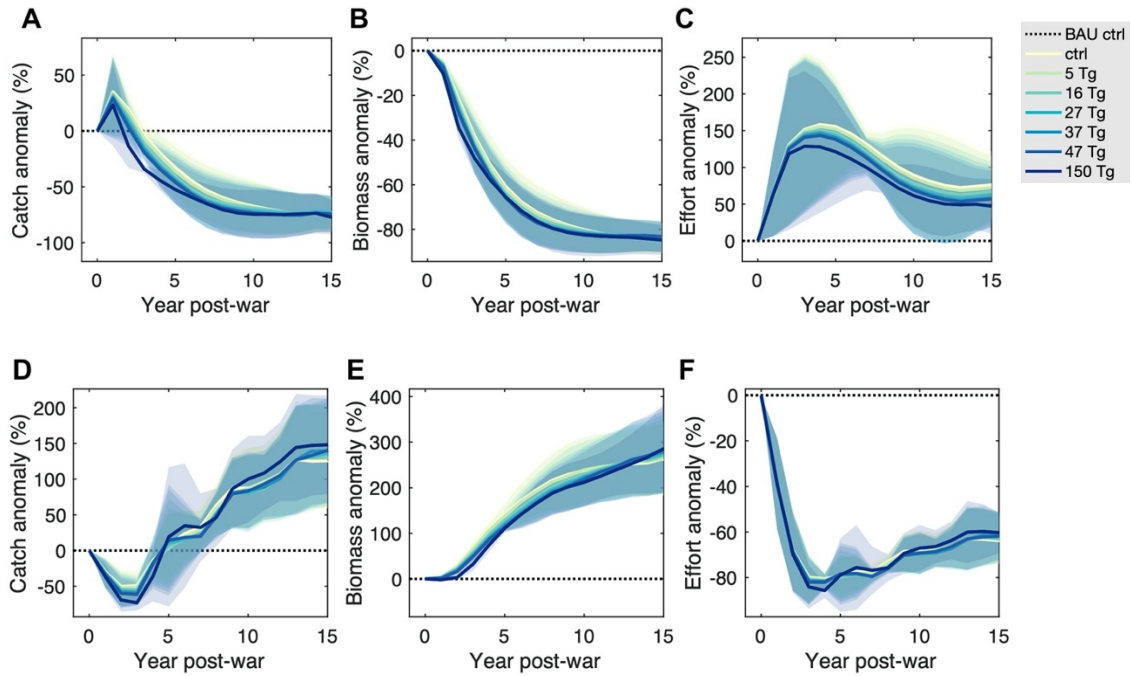


Figure S2 - Global fishery development shown using the % anomaly from the BAU control scenario (dashed line) under nuclear war-driven climate perturbation and altered fishing behavior. Upper row A-C show catch, biomass and fishing effort trajectories under greatly intensified fishing, F++, and lower row D-F show trajectories under greatly decreased fishing, F--.

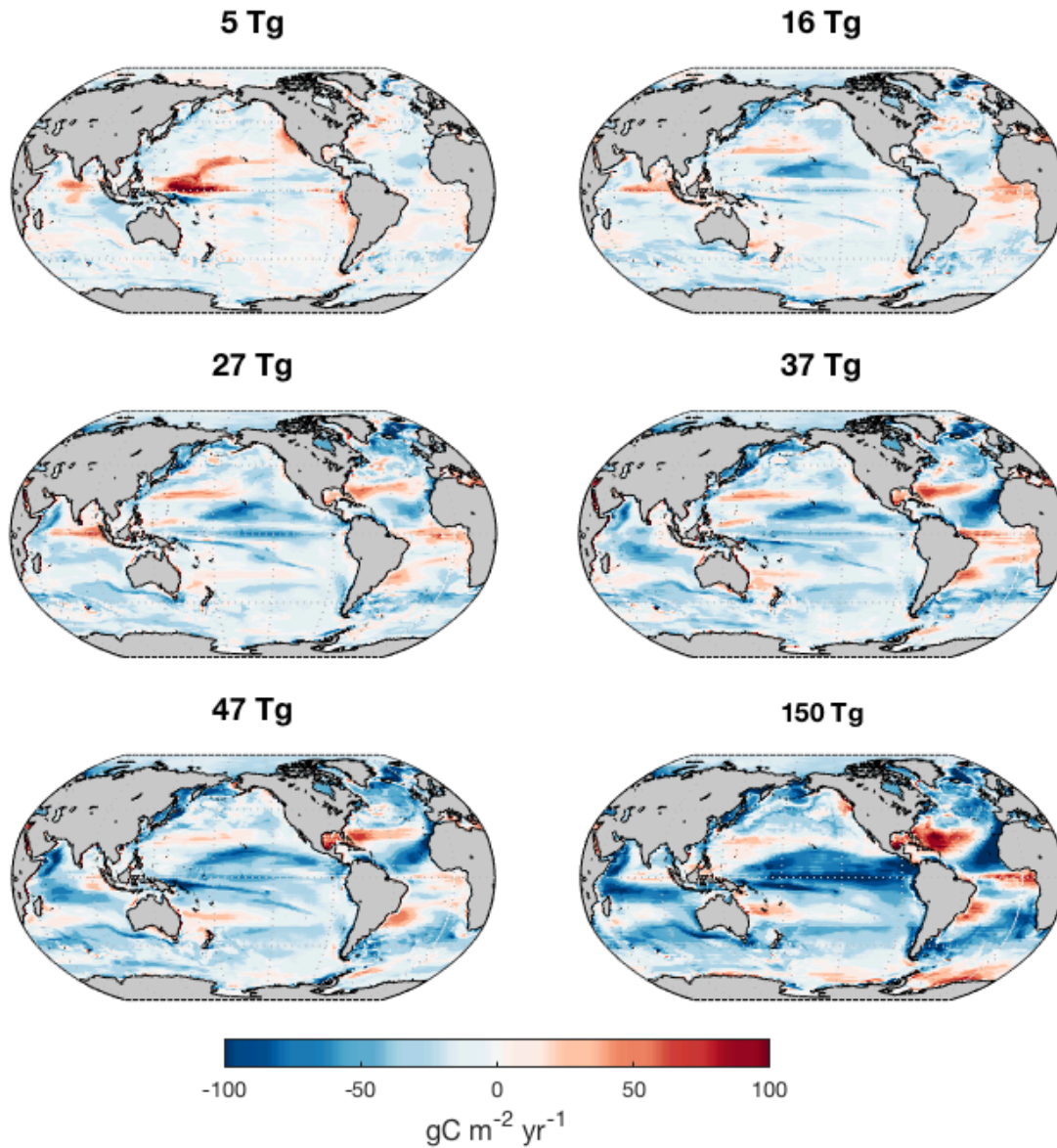


Figure S3 – Average changes in primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) relative to control over the first five years post-war for the six different soot input scenarios, as modelled by CESM.

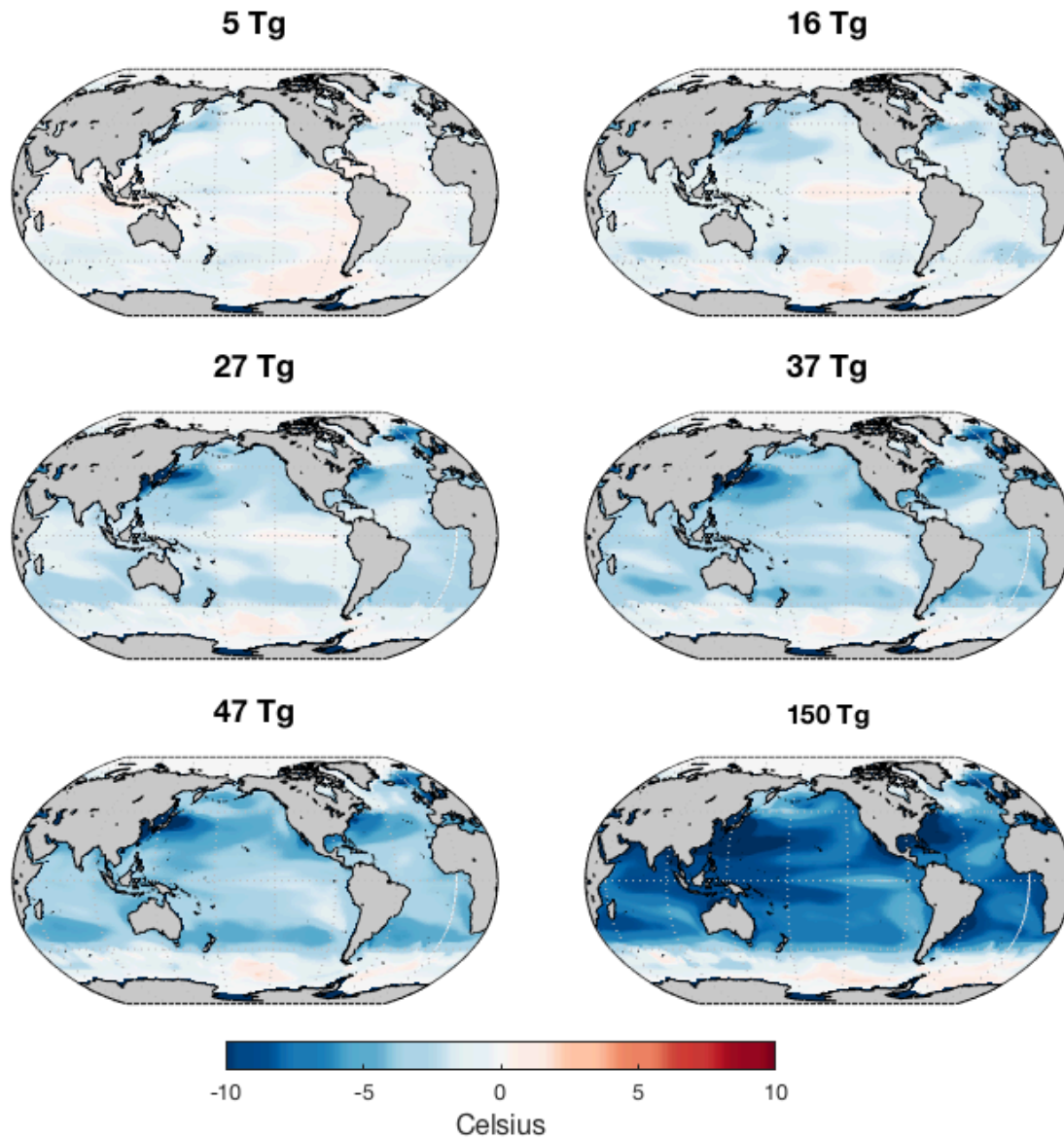


Figure S4 – Average changes in sea surface temperature (°C) relative to control over the first five years post-war for the six different soot input scenarios, as modelled by CESM.

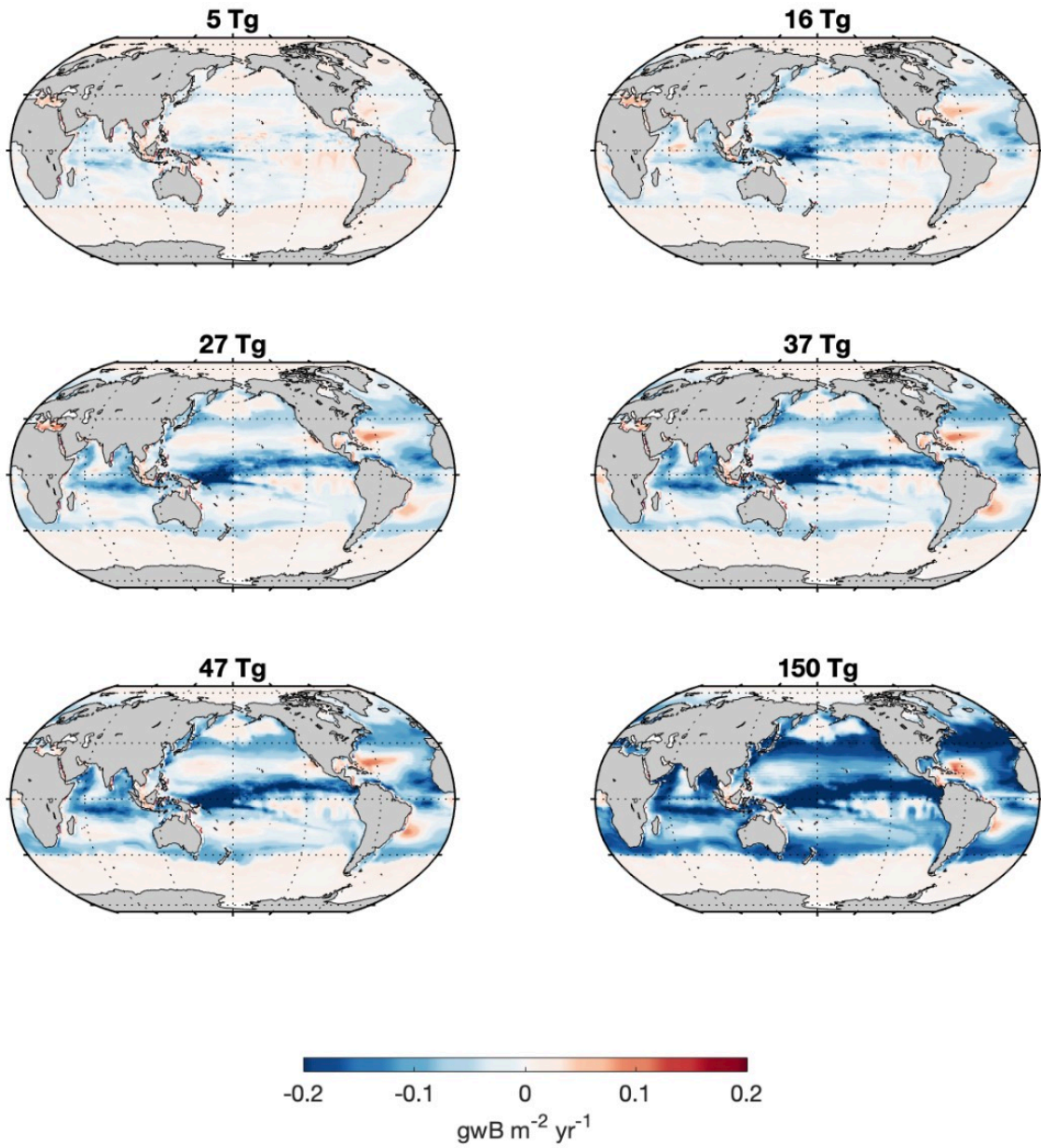


Figure S5 - Global maps of average change in fish catch under intensified fishing (F+) relative to the BAU control simulation (mean of the five first years post-war).

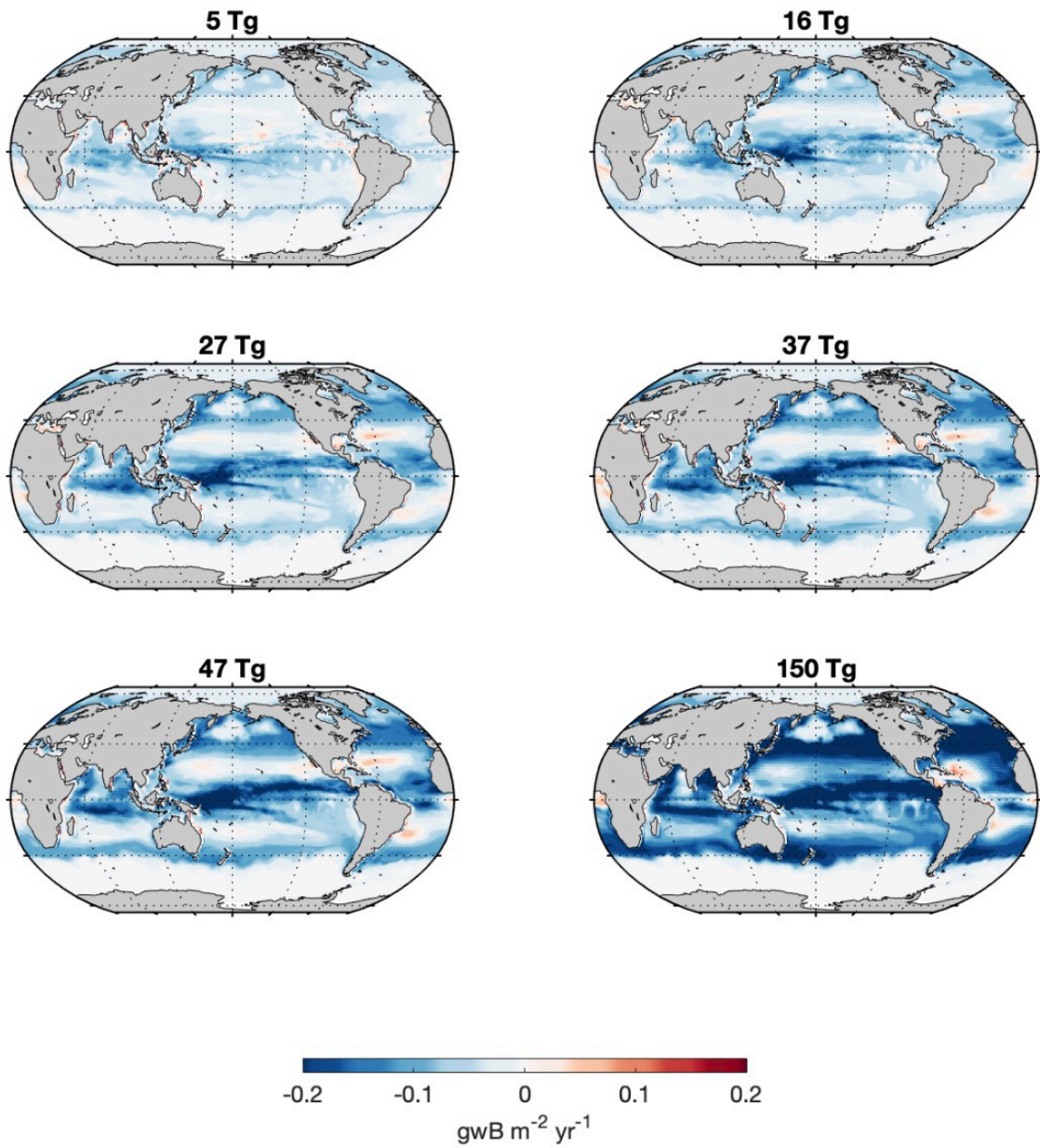


Figure S6 - Global maps of average change in fish catch under decreased fishing (F-) compared with the BAU control simulation (mean of the five first years post-war).

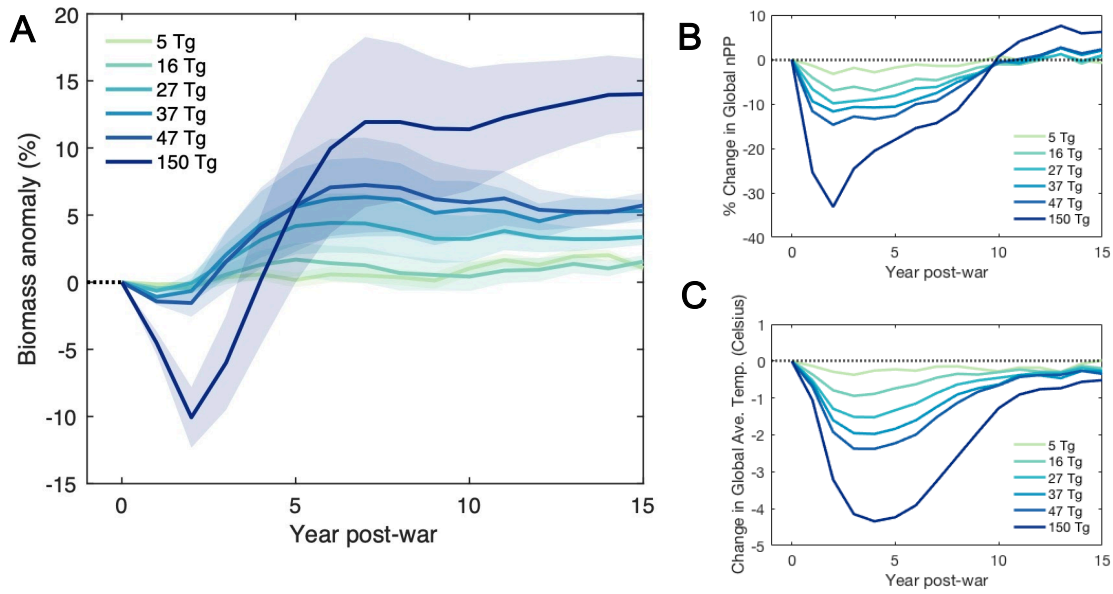


Figure S7 - Nuclear war impacts on the unfished biomass of fish in BOATS. A) shows the global % biomass anomaly relative to the no-fishing control run. The shaded areas represent the standard deviation of the five BOATS model ensemble runs. Panel B) shows the change in global oceanic NPP (%) and C) the change in global average sea surface temperature ($^{\circ}\text{C}$) relative to the control scenario, as modelled by CESM.

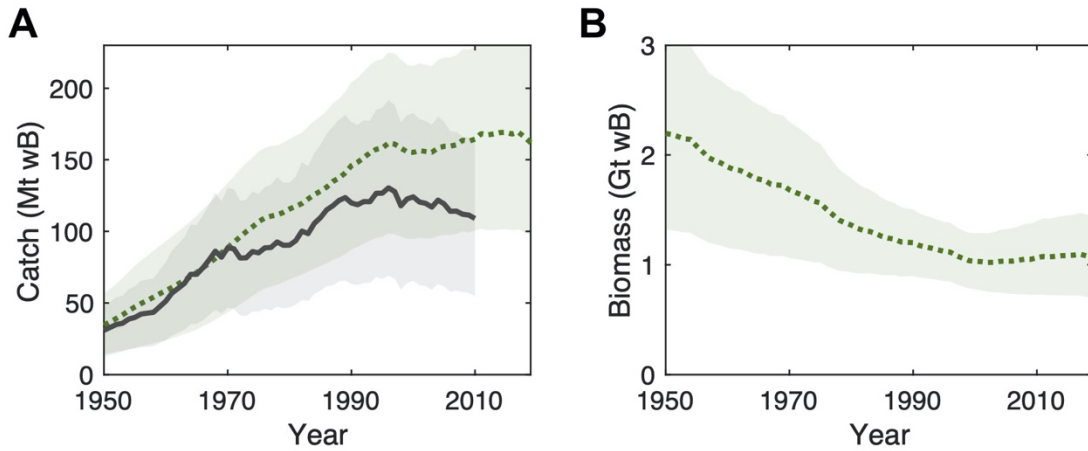


Figure S8 – Pre-war trajectories of perfectly regulated global fisheries. Simulated annual wild fish catch (A; Mt wet biomass) and total wild fish biomass (B; Gt wet biomass) over 1950-2019. Shaded areas show the standard deviation for the five parameter ensemble runs, and dotted lines show the ensemble mean. The fishery and ecosystem state in 2019 are used as initial conditions when investigating the effect of strong pre-emptive fisheries management (Figs. 6 and S9). Grey solid line and shaded area in A show empirical catches and uncertainty from Pauly and Zeller (2016).

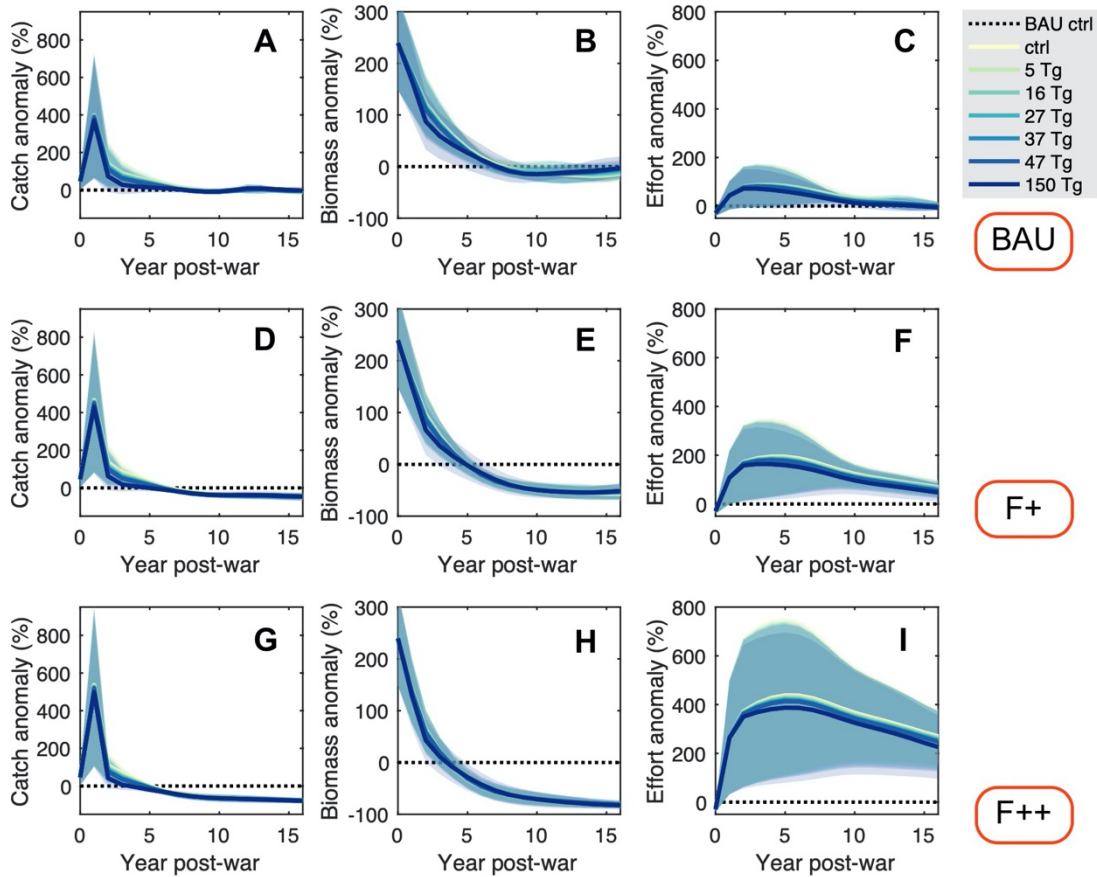


Figure S9 - Global fishery trajectories when starting from a well-regulated baseline (Fig. S8). All panels show the % anomaly from the BAU control scenario (dashed line) under nuclear war-driven climate perturbations (solid colored lines, ensemble mean). Upper row A-C show catch, biomass and fishing effort trajectories under BAU fishing, middle row D-F intensified fishing, F+, and lower row G-I show trajectories under greatly intensified fishing, F++. Shaded areas show the standard deviation for the five parameter ensemble runs.

Supplementary tables

Table S1 - Summary statistics for linear regressions of the effect of photosynthetically active radiation (PAR) change relative to control (%) on percent change in total global biomass (% change relative to BAU control for all scenarios), as shown in Fig. 2a.

<i>Scenario</i>	<i>Slope</i>	<i>Intercept (%)</i>	<i>R² (Adj)</i>	<i>p-value</i>
BAU	0.28	0.36	0.989	2.52 x 10 ⁻⁶
F+	0.25	-7.99	0.988	3.17 x 10 ⁻⁶
F++	0.20	-21.39	0.986	5.48 x 10 ⁻⁶
F-	0.31	9.43	0.989	2.69 x 10 ⁻⁶
F--	0.38	28.72	0.984	7.09 x 10 ⁻⁶

Table S2 - Summary statistics for linear regressions of the effect of PAR change relative to control PAR (%) on percent change in total global catch (% change relative to BAU control for all scenarios), as shown in Fig. 2b.

<i>Scenario</i>	<i>Slope</i>	<i>Intercept (%)</i>	<i>R² (Adj)</i>	<i>p-value</i>
BAU	0.46	1.11	0.982	8.83 x 10 ⁻⁶
F+	0.49	16.41	0.984	7.57 x 10 ⁻⁶
F++	0.52	20.63	0.986	4.79 x 10 ⁻⁶
F-	0.41	-19.76	0.984	6.60 x 10 ⁻⁶
F--	0.29	-49.81	0.986	5.51 x 10 ⁻⁶

Table S3 - Summary statistics for linear regressions of the effect of soot level (Tg) on percent change in total global biomass (% change relative to BAU control for all scenarios), as shown in Fig. S1a.

<i>Scenario</i>	<i>Slope</i>	<i>Intercept (%)</i>	<i>R² (Adj)</i>	<i>p-value</i>
BAU	-0.11	-2.12	0.936	2.29 x 10 ⁻⁴

F+	-0.10	-10.21	0.938	2.09 x 10 ⁻⁴
F++	-0.08	-23.13	0.944	1.64 x 10 ⁻⁴
F-	-0.13	6.68	0.937	2.23 x 10 ⁻⁴
F--	-0.16	25.41	0.948	1.38 x 10 ⁻⁴

Table S4 - Summary statistics for linear regressions of the effect of soot level (Tg) on percent change in total global catch (% change relative to BAU control for all scenarios), as shown in Fig. S1b.

<i>Scenario</i>	<i>Slope</i>	<i>Intercept (%)</i>	<i>R² (Adj)</i>	<i>p-value</i>
BAU	-0.19	-2.82	0.952	1.12 x 10 ⁻⁴
F+	-0.20	12.16	0.950	1.22 x 10 ⁻⁴
F++	-0.21	16.14	0.945	1.54 x 10 ⁻⁴
F-	-0.17	-23.32	0.948	1.35 x 10 ⁻⁴
F--	-0.12	-52.37	0.944	1.64 x 10 ⁻⁴

Table S5 – Catch difference by exclusive economic zone (EEZ) between the BAU 5 Tg scenario and the BAU control, and the national-level nutritional and/or integrated dependence on marine ecosystems from (Selig et al., 2018) (see Materials and Methods).

Exclusive Economic Zone	Catch difference (x 1000 ton)	Nutritional dependence	Integrated dependence
Micronesian EEZ	-115.2	0.44	0.49
Russian EEZ	-95.6	0.10	0.14
Papua New Guinean EEZ	-92.7	-	0.36
Kiribati EEZ (Gilbert Islands)	-81.5	0.74	0.72
French Polynesian EEZ	-62.4	0.46	0.36
Seychellois EEZ	-59.1	-	0.32
Indonesian EEZ	-56.2	0.48	0.36
Canadian EEZ	-51.3	0.09	0.12
Maldives EEZ	-42.7	0.99	0.71
Tuvaluan EEZ	-41.0	0.53	0.65

Kiribati EEZ (Line Islands)	-39.1	0.74	0.72
Cook Islands EEZ	-39.0	0.37	0.28
Disputed area Chagos Archipelago: UK/Mauritius	-38.1	-	-
Japanese EEZ	-33.2	0.38	0.25
United States EEZ (Alaska)	-31.2	0.05	0.05
Greenlandic EEZ	-24.2		0.71
Nauruan EEZ	-23.9	0.52	0.48
Kiribati EEZ (Phoenix Islands)	-23.7	0.74	0.72
Marshall Islands EEZ	-23.6	-	0.51
New Zealand EEZ	-22.9	0.11	0.15
Palau EEZ	-22.8	0.56	0.56
Mauritian EEZ	-20.3	0.24	0.35
Solomon Islands EEZ	-20.2	0.65	0.44
Cocos Islands EEZ	-18.4	0.07	0.10
Brazilian EEZ	-18.2	0.01	0.06
Cape Verdean EEZ	-17.6	0.15	0.27
Fijian EEZ	-14.7	0.31	0.34
Tokelau EEZ	-14.2	0.11	0.15
Christmas Island EEZ	-14.2	0.07	0.10
Venezuelan EEZ	-14.0	0.06	0.25
South African EEZ	-13.8	0.06	0.11
Norwegian EEZ	-13.7	0.26	0.25
Northern Mariana EEZ	-13.7	-	0.45
American Samoa EEZ	-13.3	-	0.16
Madagascan EEZ	-12.5	0.24	0.32
Portuguese EEZ (Azores)	-12.1	0.21	0.22
United States EEZ	-12.0	0.05	0.05
Tongan EEZ	-11.6	-	0.28
Tristan Da Cunha EEZ	-10.1	0.06	0.07
Guam EEZ	-9.8	-	0.48
Icelandic EEZ	-9.5	0.36	0.42
Omani EEZ	-8.8	-	0.24
Wallis and Futuna EEZ	-8.4	0.12	0.10
Howland and Baker Islands EEZ	-8.4	0.05	0.05
Ascension EEZ	-8.0	0.06	0.07
Disputed area Kuril Islands: Japan / Russia	-7.6	-	-

Pitcairn Islands EEZ	-7.4	0.06	0.07
Jarvis Island EEZ	-7.3	0.05	0.05
Réunion EEZ	-7.3	-	0.39
Costa Rican EEZ	-6.9	0.04	0.11
Yemeni EEZ	-6.9	0.11	0.25
United Kingdom EEZ	-6.9	0.06	0.07
Irish EEZ	-6.7	0.07	0.12
Guyanese EEZ	-6.0	0.29	0.37
Svalbard EEZ	-6.0	0.26	0.25
Portuguese EEZ (Madeira)	-5.9	0.21	0.22
Johnston Atoll EEZ	-5.8	0.05	0.05
Spanish EEZ (Canary Islands)	-5.7	0.18	0.20
Cuban EEZ	-5.6	0.01	0.14
Clipperton EEZ	-5.3	0.12	0.10
French Guiana EEZ	-5.1	-	0.12
Equatorial Guinean EEZ	-5.0	-	0.41
Panamanian EEZ	-4.7	0.13	0.18
Spanish EEZ	-4.4	0.18	0.20
Portuguese EEZ	-4.1	0.21	0.22
Jan Mayen EEZ	-3.9	0.26	0.25
Disputed area Senkaku Islands: Japan / China / Taiwan	-3.8	-	-
Ecuadorian EEZ (Galapagos)	-3.7	0.06	0.19
South Korean EEZ	-3.5	0.34	0.25
Nigerian EEZ	-3.4	0.42	0.33
Niue EEZ	-3.4	-	0.12
Moroccan EEZ	-3.4	0.19	0.28
Samoan EEZ	-3.3	0.31	0.33
Guinean EEZ	-3.0	0.35	0.29
Disputed area South China Sea	-3.0	-	-
French EEZ	-2.8	0.12	0.10
Barbados EEZ	-2.8	0.24	0.23
Ghanaian EEZ	-2.8	0.56	0.42
Myanmar EEZ	-2.7	0.36	0.43
Sierra Leonian EEZ	-2.6	0.65	0.52
Amsterdam Island & St. Paul Island EEZ	-2.6	0.12	0.10
Faeroe EEZ	-2.6	-	0.93

Dominican Republic EEZ	-2.5	0.10	0.15
Disputed area Liancourt Rocks: Japan / South Korea	-2.5	-	-
Disputed area Ukrainian EEZ	-2.5	-	-
Mauritanian EEZ	-2.4	0.11	0.31
Chilean EEZ (Easter Island)	-2.2	0.06	0.15
Grenadian EEZ	-2.2	0.27	0.30
Jamaican EEZ	-2.2	0.16	0.23
Joint regime area Japan / Korea	-2.1	-	-
Turkish EEZ	-2.0	0.06	0.08
Trinidad and Tobago EEZ	-1.9	0.20	0.15
Bassas da India EEZ	-1.9	0.12	0.10
Ile Europa EEZ	-1.9	0.12	0.10
Disputed area Falkland Islands: UK / Argentina	-1.7	-	-
Gabonese EEZ	-1.7	0.26	0.24
Antigua and Barbuda EEZ	-1.7	0.26	0.30
Thailand EEZ	-1.6	0.32	0.32
Surinamese EEZ	-1.6	0.23	0.29
Beninese EEZ	-1.6	0.28	0.18
Saint Vincent and the Grenadines EEZ	-1.5	0.12	0.22
Sao Tome and Principe EEZ	-1.5	0.46	0.41
Taiwanese EEZ	-1.4	-	0.10
Anguilla EEZ	-1.3	0.06	0.07
Senegalese EEZ	-1.2	0.48	0.50
Puerto Rican EEZ	-1.2	-	0.31
Disputed area Matthew and Hunter Islands: New Caledonia / Vanuatu	-1.2	-	-
Philippines EEZ	-1.1	0.43	0.37
Chilean EEZ (San Felix and San Ambrosio islands)	-1.1	0.06	0.15
El Salvador EEZ	-1.1	0.09	0.15
Danish EEZ	-1.1	0.14	0.17
Guadeloupean EEZ	-1.1	-	0.21
Wake Island EEZ	-1.0	0.05	0.05
Haitian EEZ	-0.9	0.19	0.25
Angolan EEZ	-0.9	0.34	0.26

Algerian EEZ	-0.9	0.07	0.16
Honduran EEZ	-0.8	-	0.27
Colombian EEZ	-0.8	0.02	0.08
Finnish EEZ	-0.8	0.10	0.07
Martinican EEZ	-0.8	-	0.30
Guinea Bissau EEZ	-0.8	0.01	0.17
Bonaire EEZ	-0.8	0.08	0.10
Aruban EEZ	-0.7	-	0.19
Juan de Nova EEZ	-0.6	0.12	0.10
Cayman Islands EEZ	-0.6	-	0.45
Argentinean EEZ	-0.5	0.02	0.06
Guatemalan EEZ	-0.5	0.01	0.10
Antarctic 200NM zone beyond the coastline	-0.5	-	-
Guernsey EEZ	-0.5	0.06	0.07
Latvian EEZ	-0.5	0.14	0.19
Swedish EEZ	-0.4	0.10	0.10
Disputed area South Georgia and South Sandwich: UK / Argentina	-0.4	-	-
Georgian EEZ	-0.4	0.08	0.08
Estonian EEZ	-0.4	0.06	0.14
Disputed area Mayotte: France / Comoros	-0.4	-	-
British Virgin Islands EEZ	-0.4	-	0.25
Polish EEZ	-0.3	0.08	0.10
Dominican EEZ	-0.3	0.19	0.26
Virgin Islander EEZ	-0.3	-	0.42
Saint-Pierre and Miquelon EEZ	-0.3	0.12	0.10
Dutch EEZ	-0.3	0.08	0.10
Joint regime area Nigeria / Sao Tome and Principe	-0.2	-	-
Saint Lucia EEZ	-0.2	0.21	0.25
Lithuanian EEZ	-0.2	0.25	0.24
Australian EEZ (Macquarie Island)	-0.2	0.07	0.10
Disputed area Western Saharan EEZ	-0.2	-	-
Montserrat EEZ	-0.2	0.06	0.07
South African EEZ (Prince Edward Islands)	-0.1	0.06	0.11

Joint regime area Iceland / Norway (Jan Mayen)	-0.1	--	-
Saba EEZ	-0.1	0.08	0.10
Belizean EEZ	-0.1	0.13	0.27
Saint Kitts and Nevis EEZ	-0.1	0.23	0.28
Joint regime area United States / Russia	-0.1		-
Gambian EEZ	-0.1	0.42	0.33
Disputed area: Puerto Rico / Dominican Republic	-0.1	-	-
Cambodian EEZ	-0.1	0.30	0.22
Kerguelen EEZ	-0.1	0.12	0.10
Disputed area: Canada / USA	-0.1	-	-
Uruguayan EEZ	0.0	0.02	0.08
Bouvet EEZ	0.0	0.26	0.25
Crozet Islands EEZ	0.0	0.12	0.10
Heard and McDonald Islands EEZ	0.0	0.07	0.10
North Korean EEZ	0.0	0.35	0.40
Joint regime area Colombia / Jamaica	0.0	-	-
Democratic Republic of the Congo EEZ	0.0	-	0.25
Qatari EEZ	0.0	-	0.05
Togolese EEZ	0.0	-	-
Bahraini EEZ	0.0	-	-
Djiboutian EEZ	0.0	0.07	0.10
Croatian EEZ	0.0	0.07	0.15
Disputed area Navassa Island: USA / Haiti / Jamaica	0.1	-	-
Bruneian EEZ	0.1	0.11	0.11
Colombian EEZ (Quitasueño)	0.1	0.02	0.08
German EEZ	0.1	0.04	0.04
Romanian EEZ	0.1	-	0.03
Kenyan EEZ	0.1	-	0.20
Israeli EEZ	0.1	0.03	0.03
Disputed area Glorioso Islands: France / Madagascar	0.2	-	-
Syrian EEZ	0.2	0.03	0.05
Lebanese EEZ	0.2	0.06	0.13

Congolese EEZ	0.2	0.28	0.31
Disputed area: Kenya / Somalia	0.2	-	-
Joint regime area Australia / East Timor	0.3	-	-
Curaçaoan EEZ	0.3	-	0.23
Joint regime area Costa Rica / Ecuador (Galapagos)	0.3	-	-
United Arab Emirates EEZ	0.4	0.19	0.15
Ivory Coast EEZ	0.5	0.49	0.39
Turks and Caicos EEZ	0.6	-	0.26
Brazilian EEZ (Trindade)	0.7	0.01	0.06
Norfolk Island EEZ	0.8	0.07	0.10
Chilean EEZ	0.8	0.06	0.15
Montenegrin EEZ	0.9	0.02	0.03
Maltese EEZ	1.0	0.14	0.18
Eritrean EEZ	1.0	-	0.24
Disputed area Ile Tromelin: Reunion / Mauritius	1.1	-	-
Cypriote EEZ	1.1	0.10	0.11
Bulgarian EEZ	1.2	0.01	0.05
Bahamas EEZ	1.4	0.21	0.30
Tanzanian EEZ	1.4	-	0.05
Tunisian EEZ	1.4	0.13	0.23
Comoran EEZ	1.4	-	0.29
Pakistani EEZ	1.5	-	0.16
Disputed area: Sudan / Egypt	1.5	-	-
St. Helena EEZ	1.8	-	0.09
East Timorian EEZ	1.9	0.13	0.20
Iranian EEZ	2.0	0.06	0.12
Saudi Arabian EEZ	2.1	0.06	0.06
Malaysian EEZ	2.8	0.43	0.30
Sudanese EEZ	2.9	-	0.07
Ecuadorian EEZ	3.0	0.06	0.19
Palmyra Atoll EEZ	3.1	0.05	0.05
Vietnamese EEZ	3.5	0.30	0.33
Liberian EEZ	3.5	0.05	0.09
Vanuatu EEZ	3.5	0.45	0.41
Egyptian EEZ	4.1	0.09	0.15

Australian EEZ	4.2	0.07	0.10
Sri Lankan EEZ	4.3	0.62	0.42
Nicaraguan EEZ	4.3	0.10	0.19
Chinese EEZ	4.5	0.08	0.12
Italian EEZ	4.5	0.09	0.09
New Caledonian EEZ	5.5	0.19	0.24
Indian EEZ	6.2	0.08	0.15
Indian EEZ (Andaman and Nicobar Islands)	6.4	0.08	0.15
Bangladeshi EEZ	7.0	0.22	0.27
United States EEZ (Hawaii)	7.4	0.05	0.05
Bermudian EEZ	7.9	0.19	0.30
Namibian EEZ	8.6	0.23	0.34
Libyan EEZ	8.8	0.14	0.16
Mozambican EEZ	11.5	0.36	0.30
Greek EEZ	12.3	0.06	0.15
Peruvian EEZ	12.3	0.23	0.24
Somali EEZ	12.4	0.04	0.18
Mexican EEZ	21.4	0.08	0.11

Supplementary figures

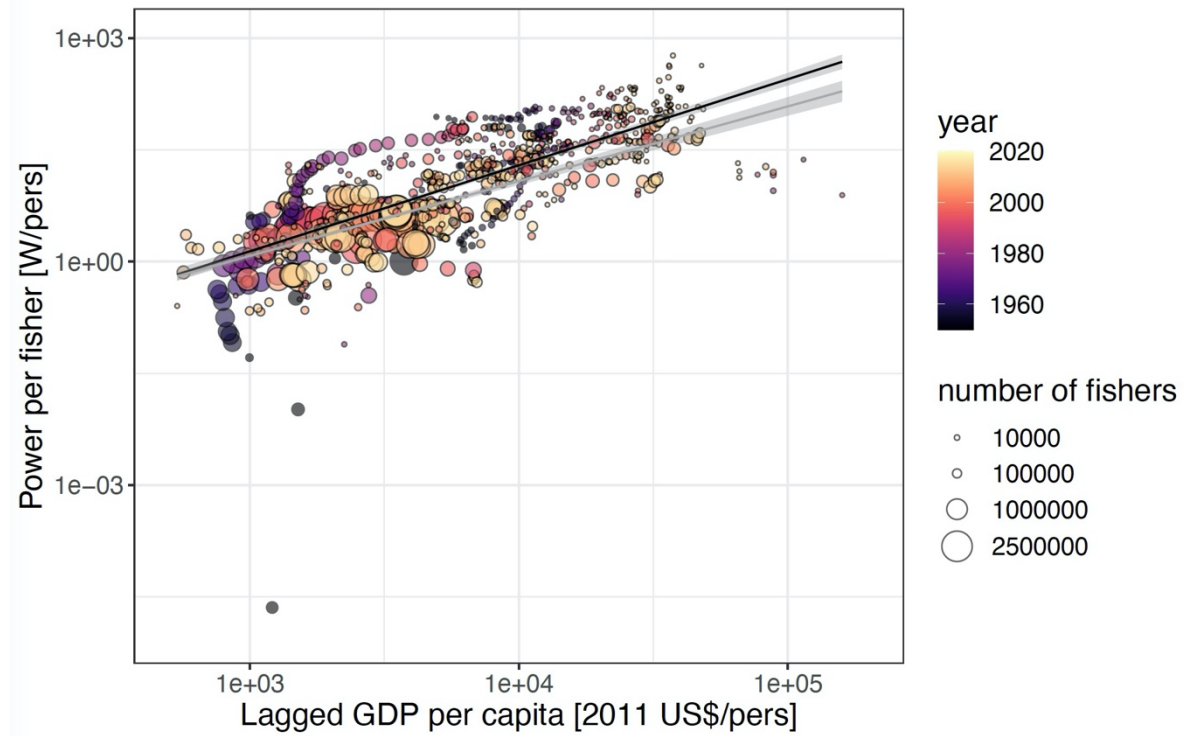


Figure S1. Relationship between lagged GDP per capita (11 years) and mechanization level for the full dataset. For the log-transformed data, the power per fisher ($W \text{ pers}^{-1}$) increases linearly with GDP per capita (2011 US\$ pers^{-1}). Black line shows regression for the unweighted full data set ($R^2 = 0.59$, $p\text{-value} < 2 \cdot 10^{-16}$), while grey line shows regression when weighted by the number of fishers ($R^2 = 0.48$, $p\text{-value} < 2 \cdot 10^{-16}$). Envelopes show the standard error. Outliers include Pakistan 1951 (lowest PPF), Indonesia 1951 (second lowest PPF) and the cluster of high-GDP countries consisting of Kuwait, United Arab Emirates and Qatar.

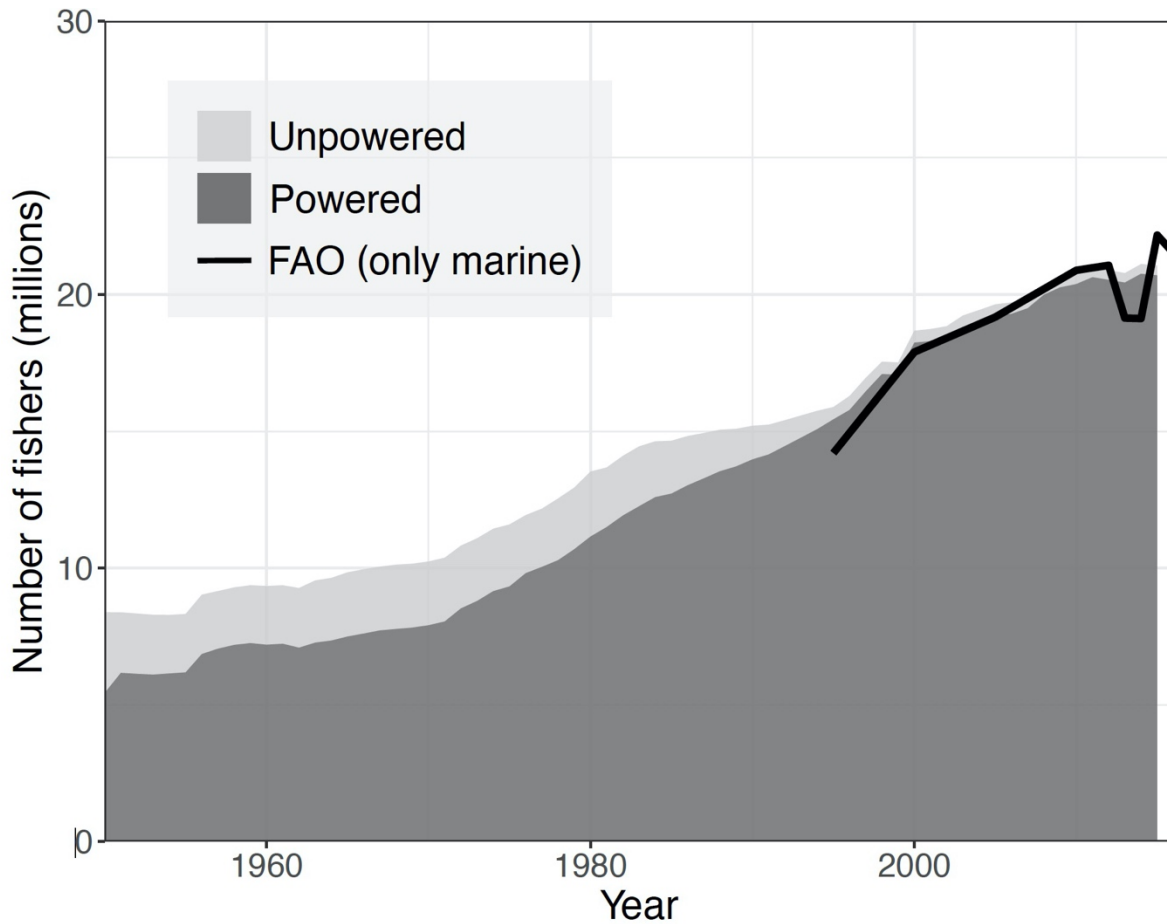
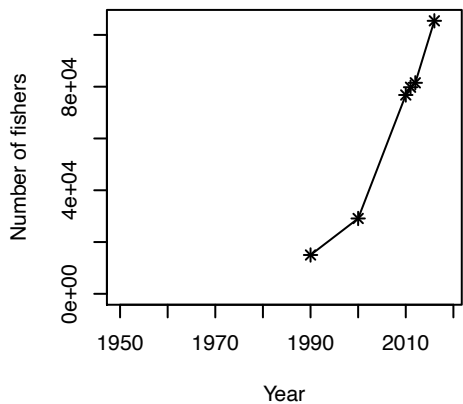
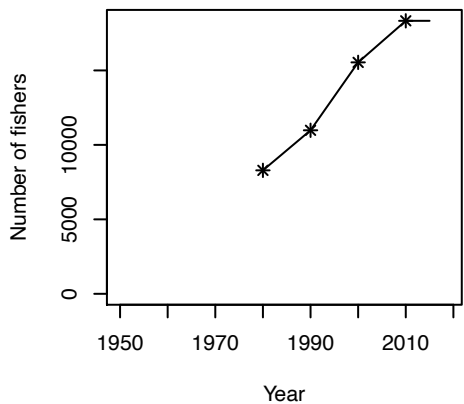
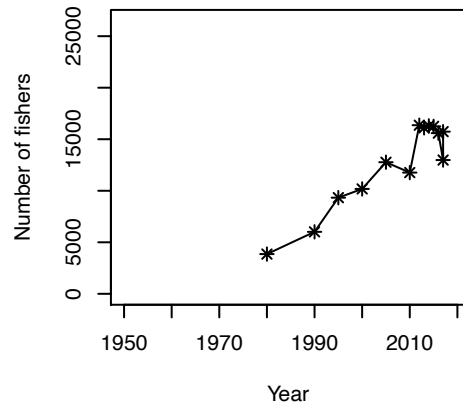
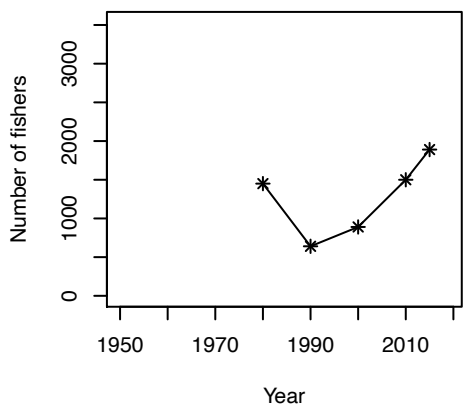
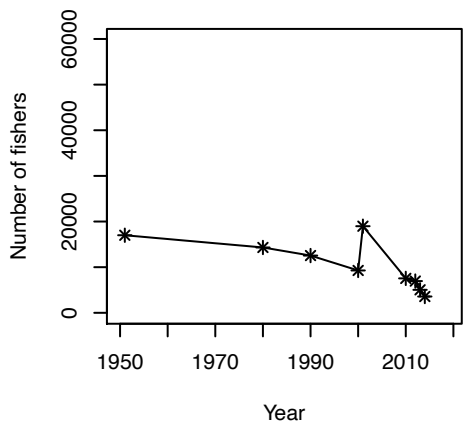
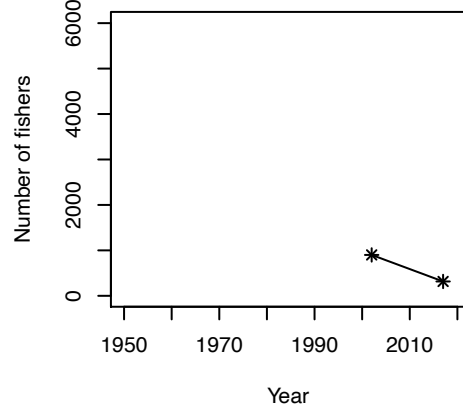
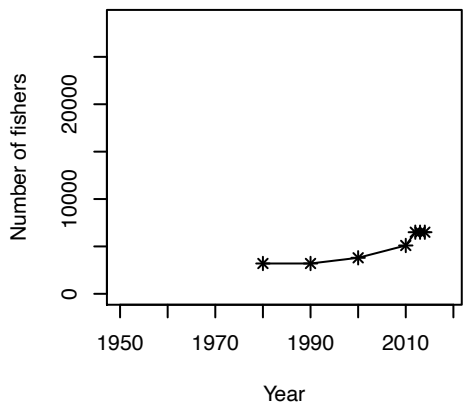
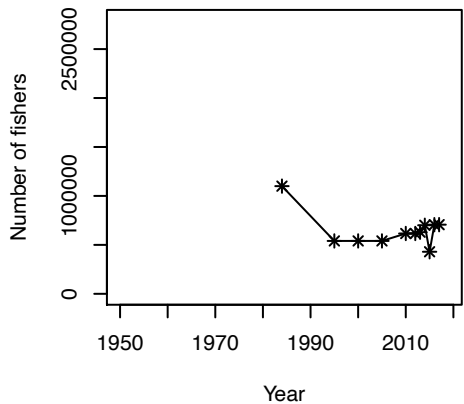
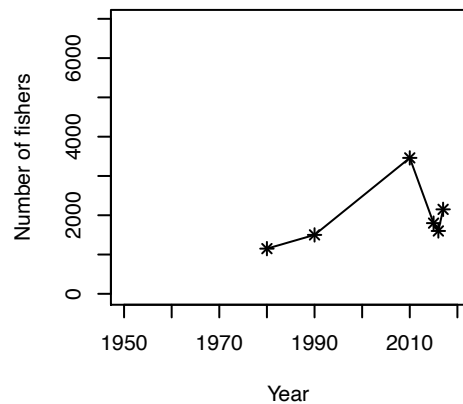
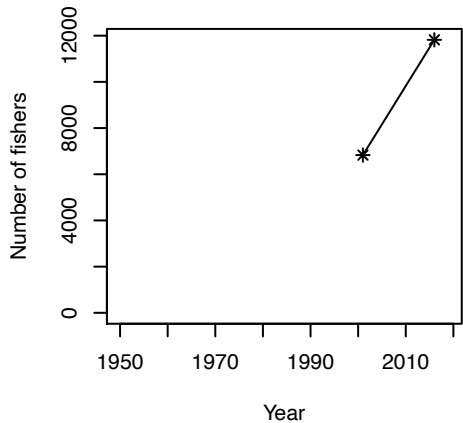
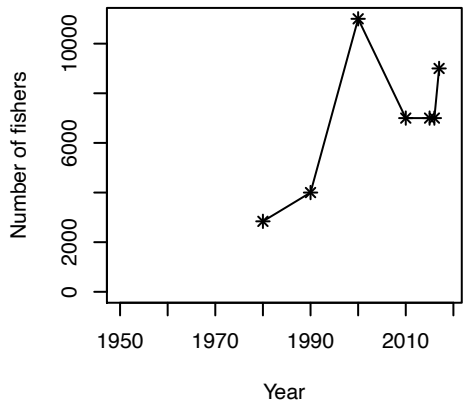
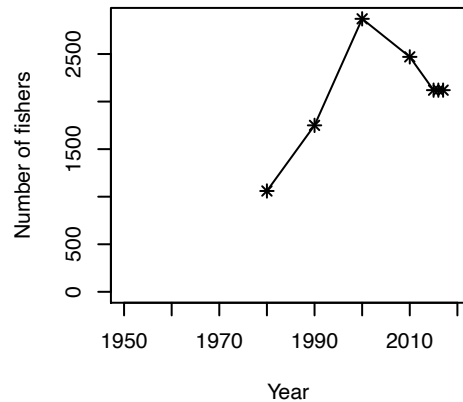


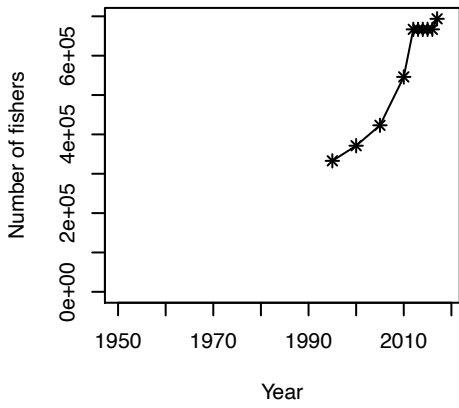
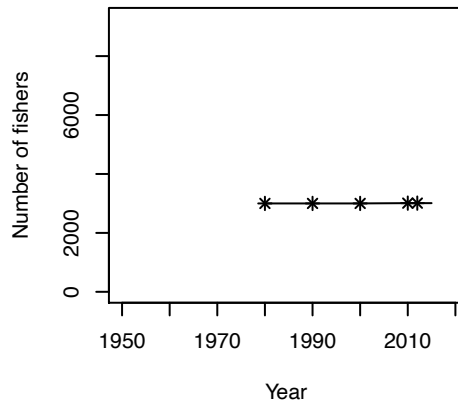
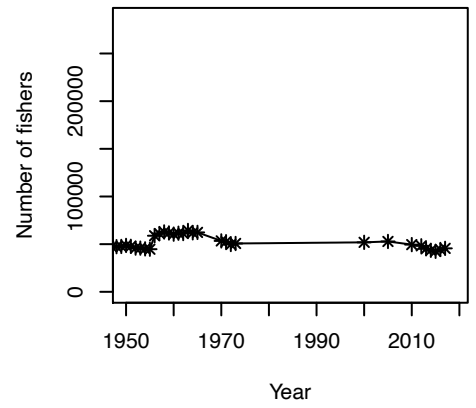
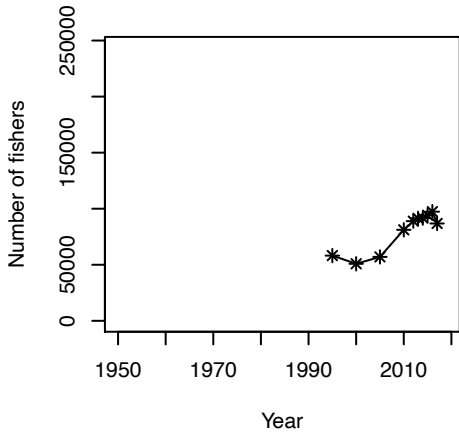
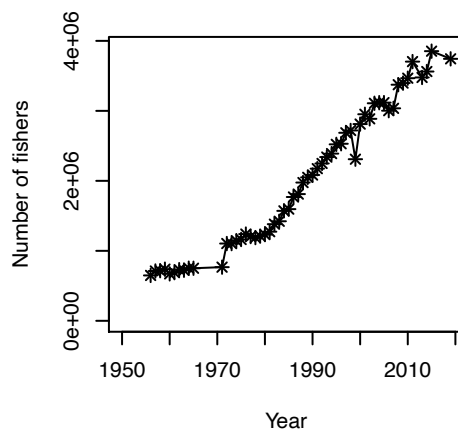
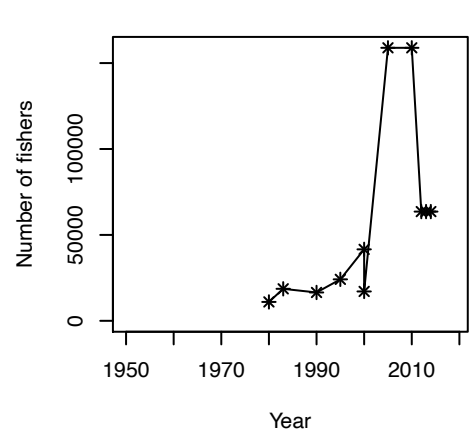
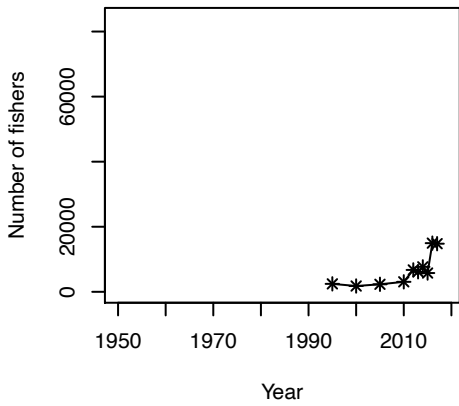
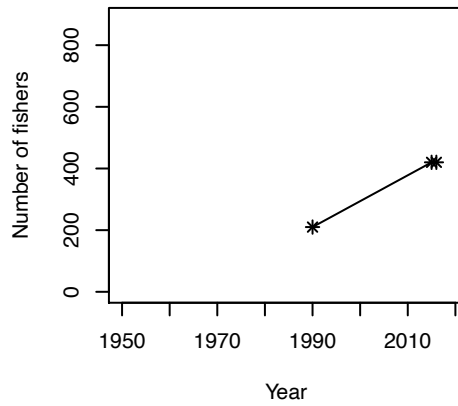
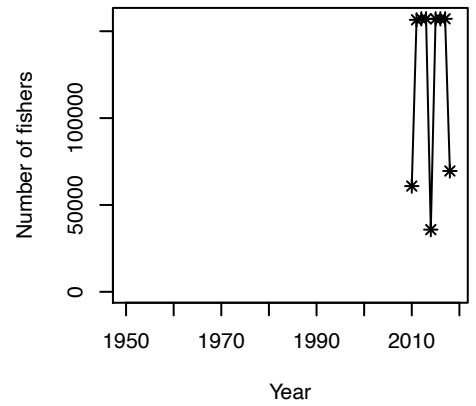
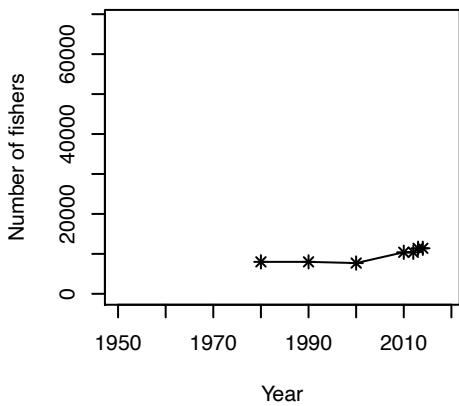
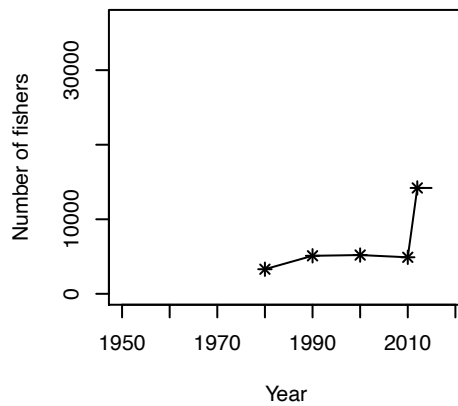
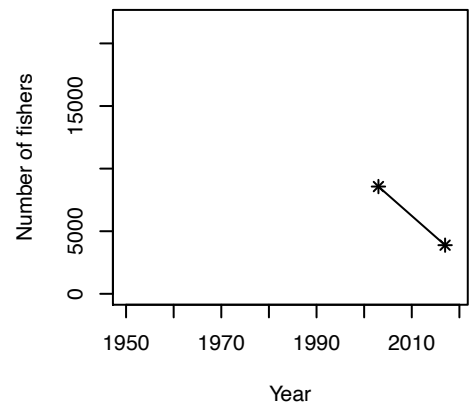
Figure S2. Reconstructed number of fishers when using the weighted GDP-PPF relationship.

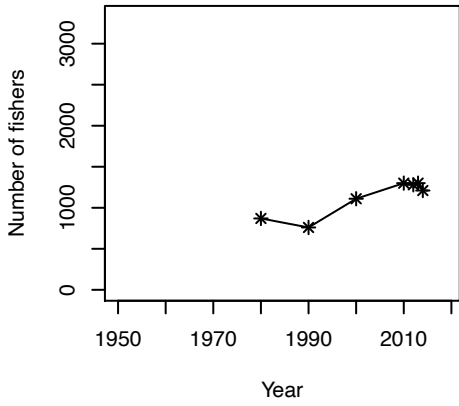
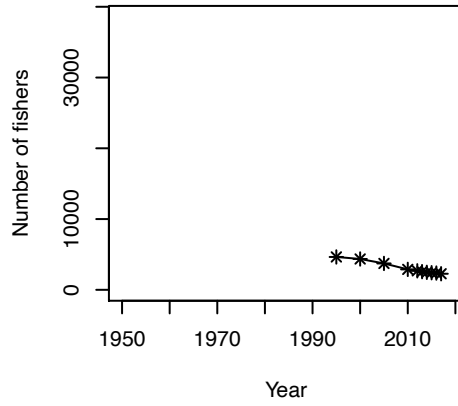
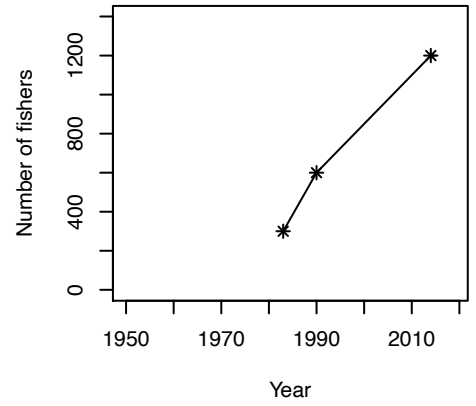
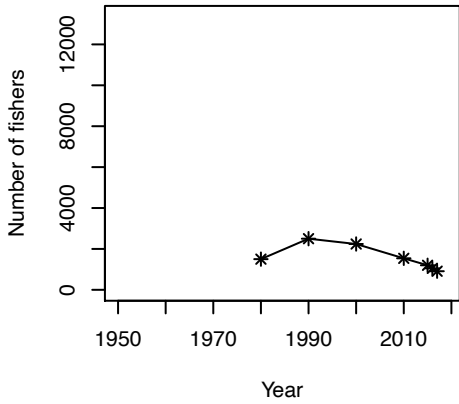
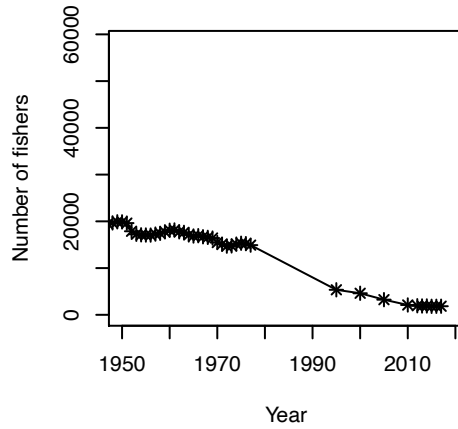
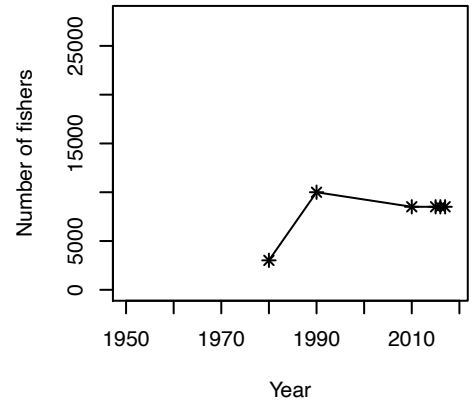
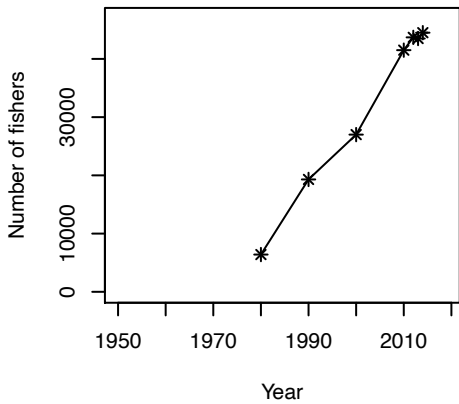
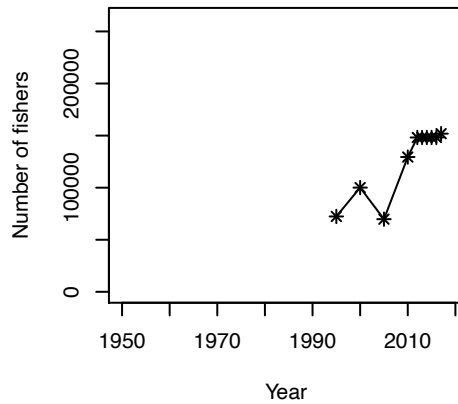
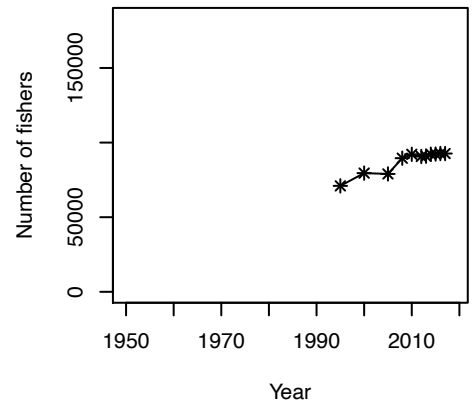
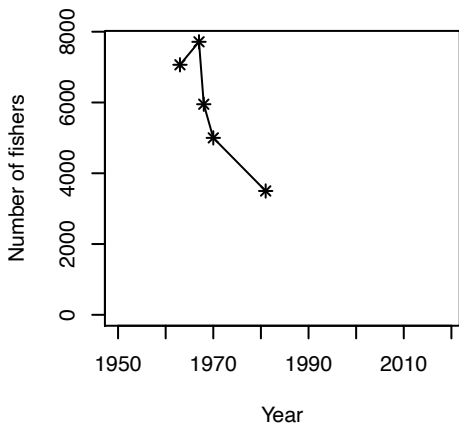
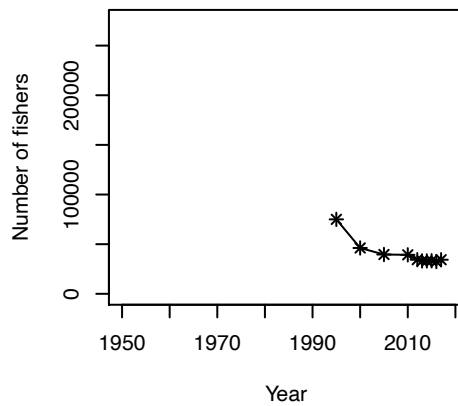
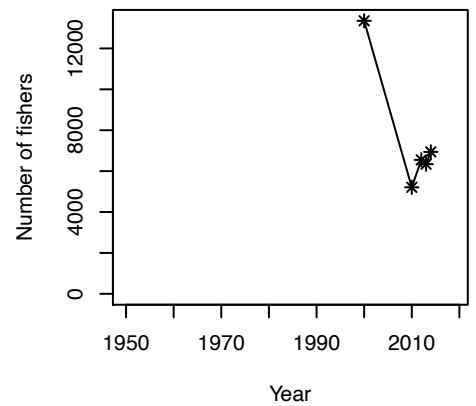
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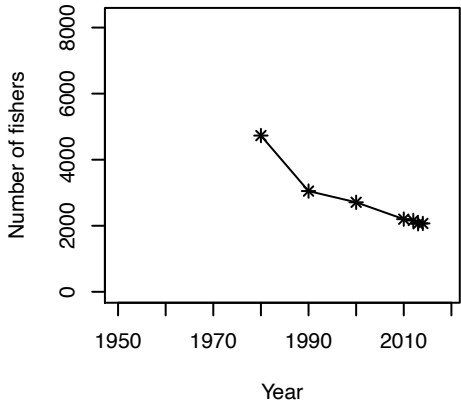
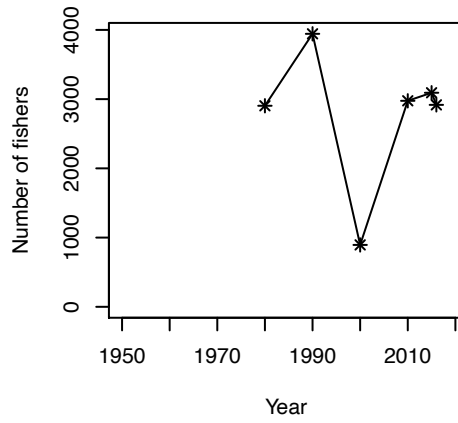
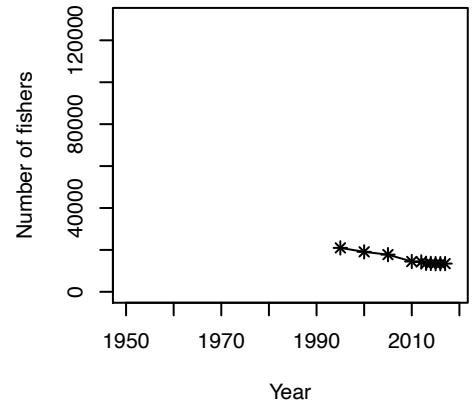
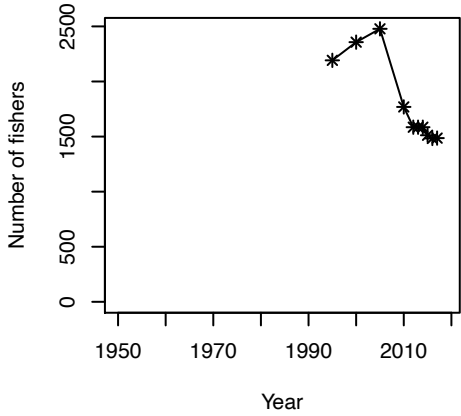
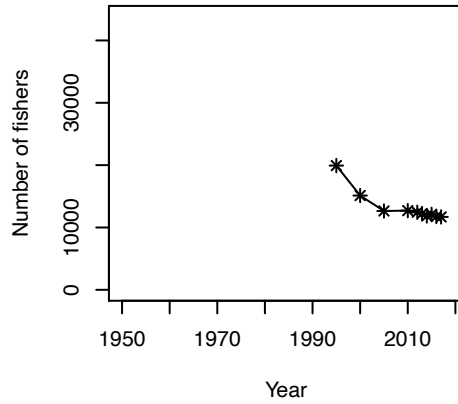
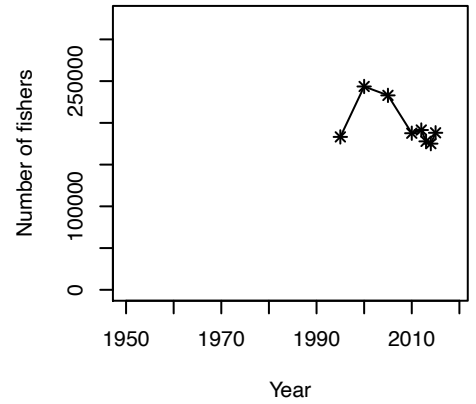
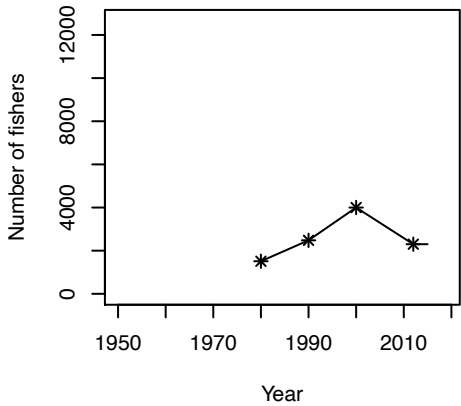
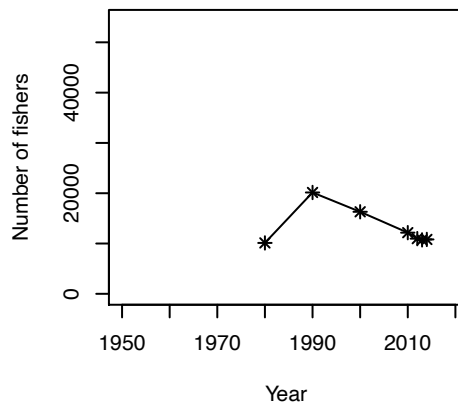
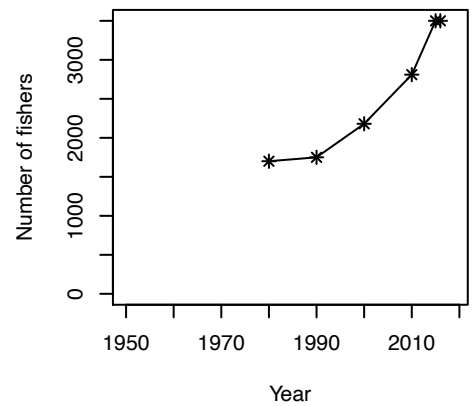
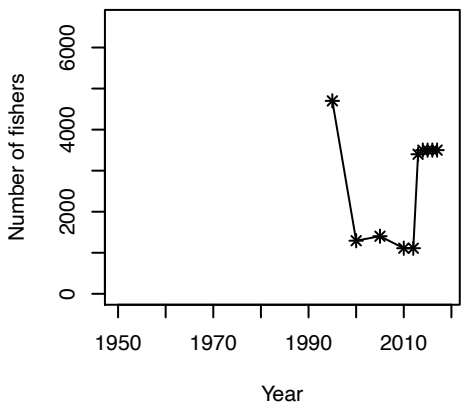
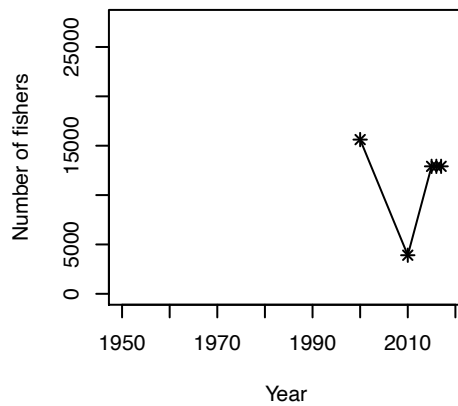
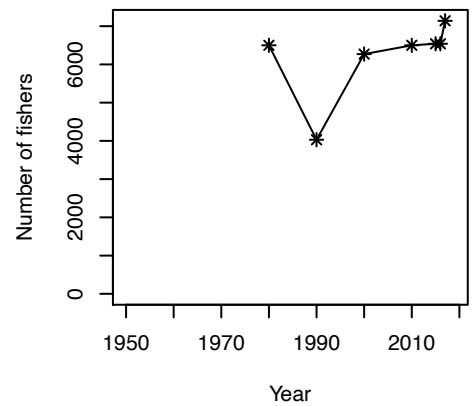
Figure S3. Empirical data on the number of fishers by country. Stars indicate the data points and black lines the interpolated values.

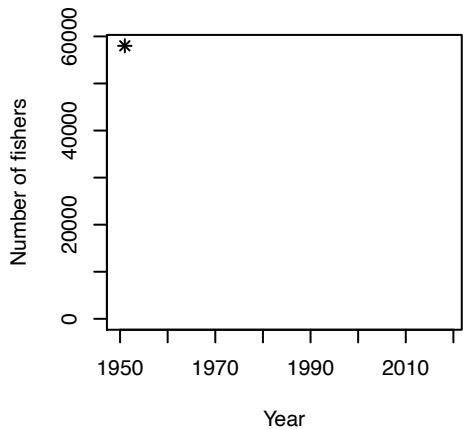
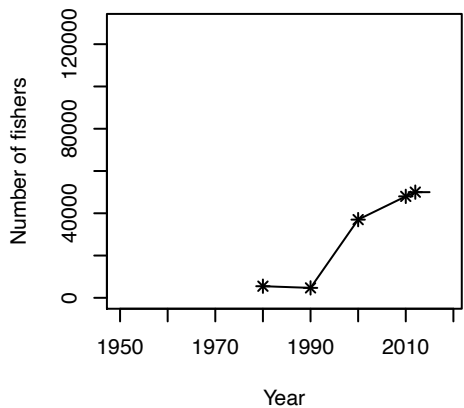
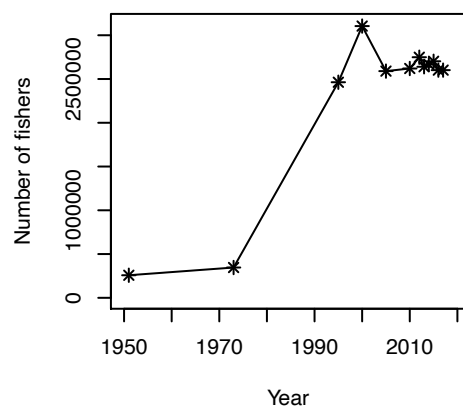
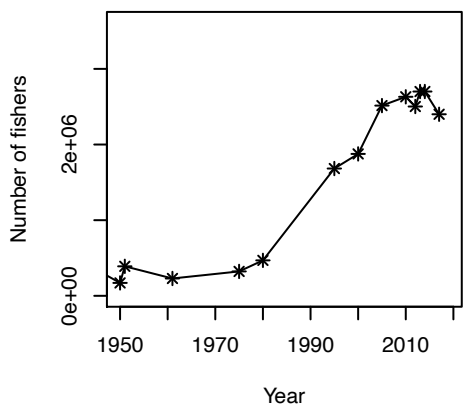
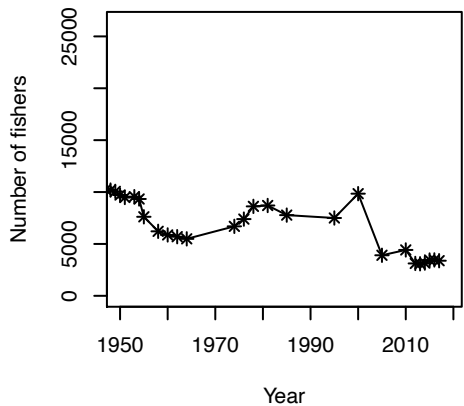
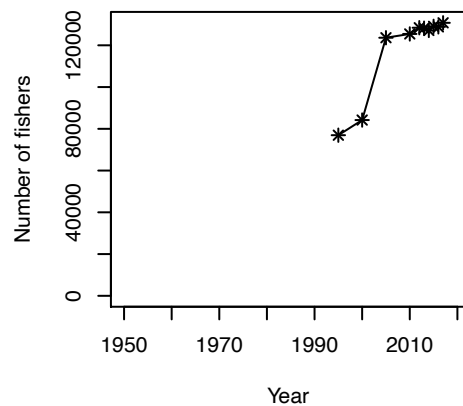
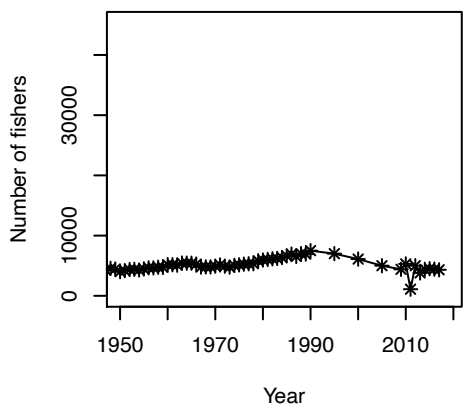
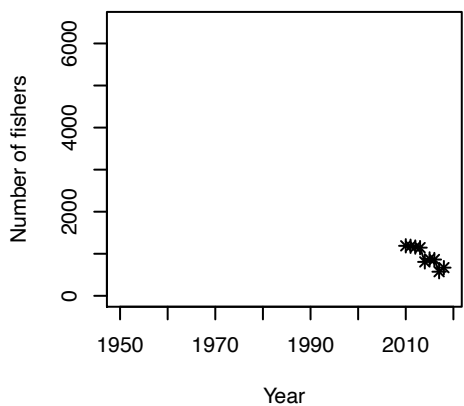
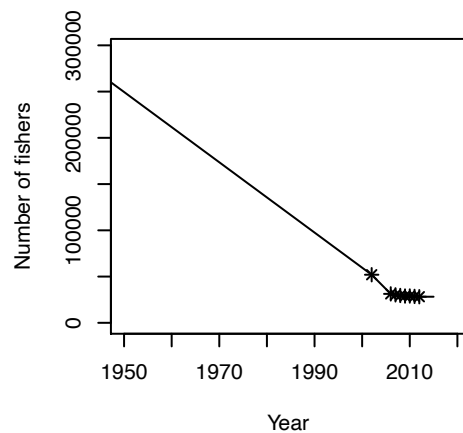
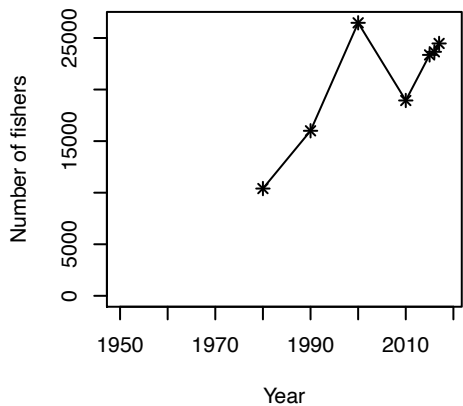
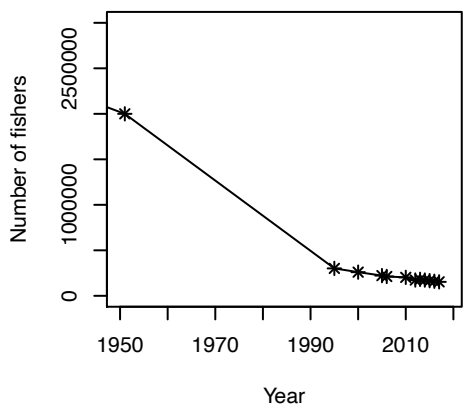
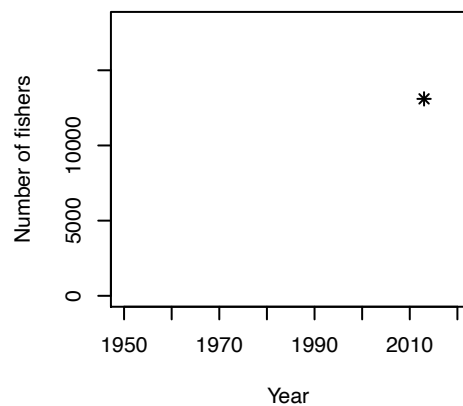
Figure S4. Relationship between GDP per capita and PPF by country. Color indicates year of observation. Black line shows linear regression line for global GDP-PPF relationship, i.e. corresponding to the black line in Fig. 1.

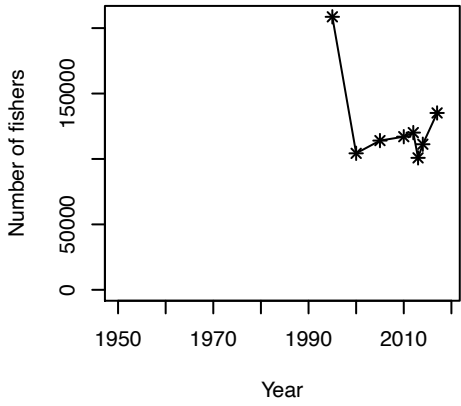
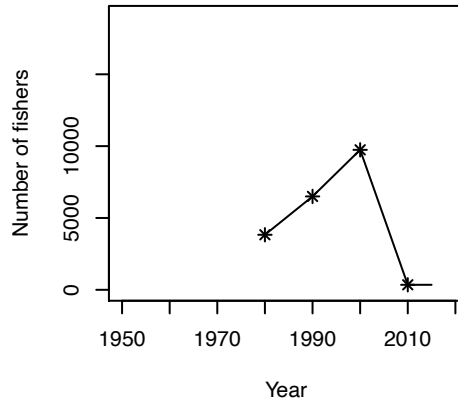
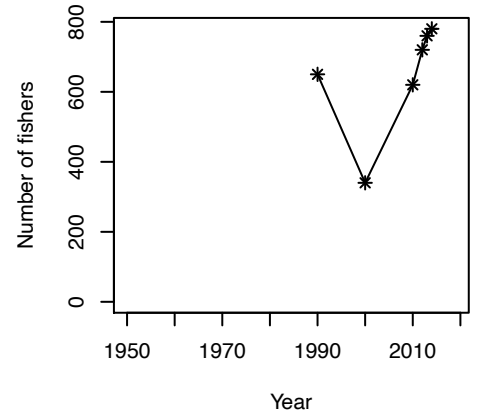
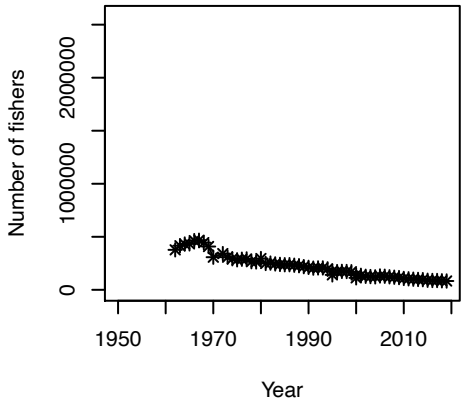
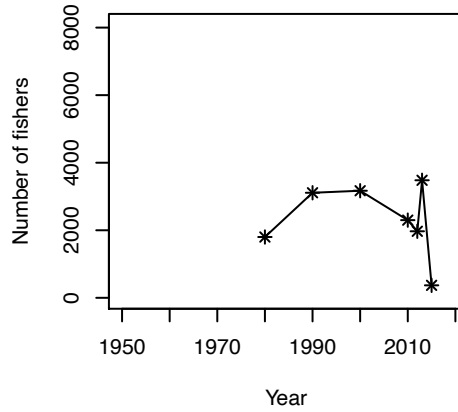
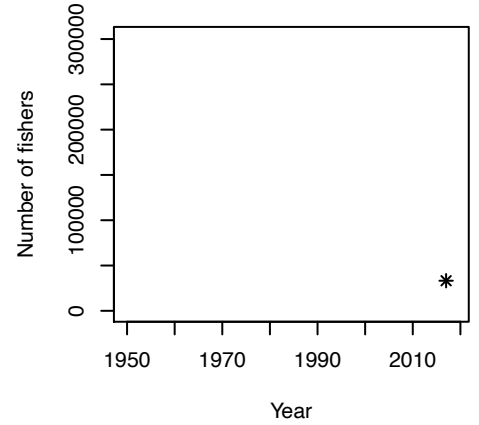
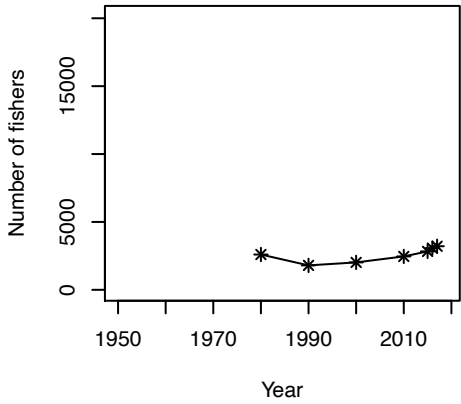
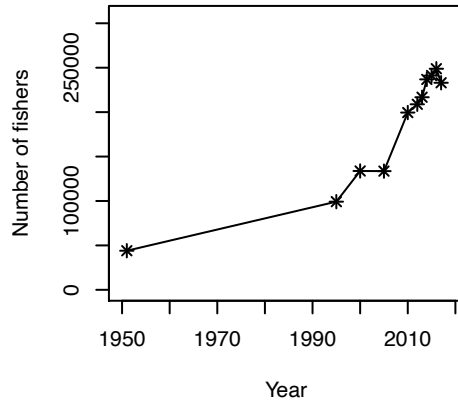
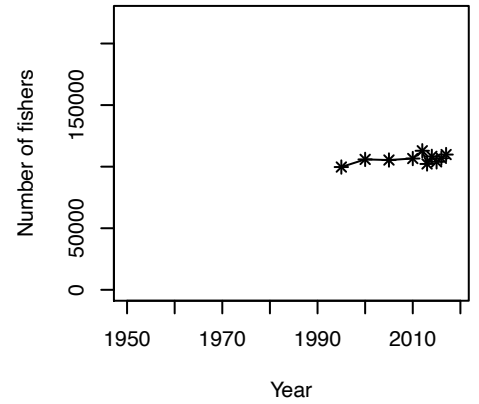
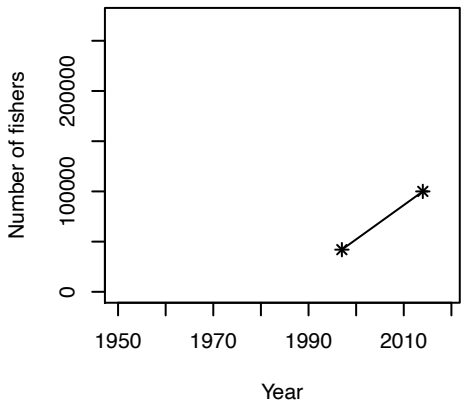
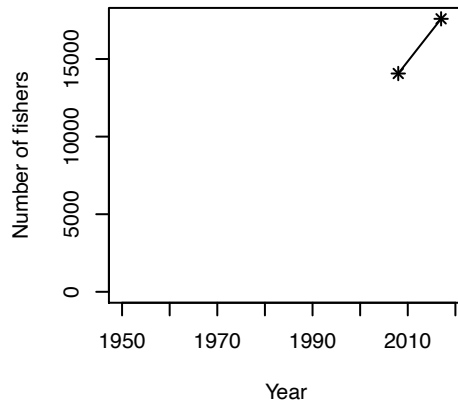
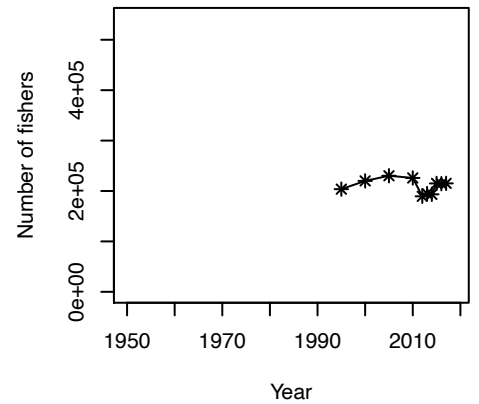
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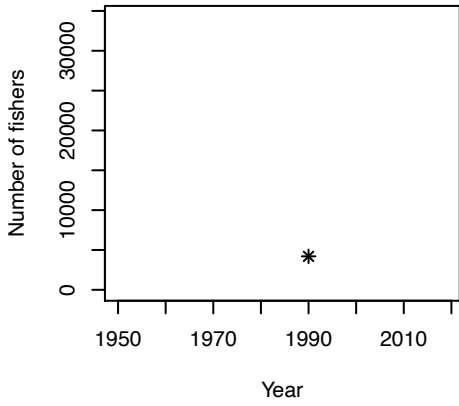
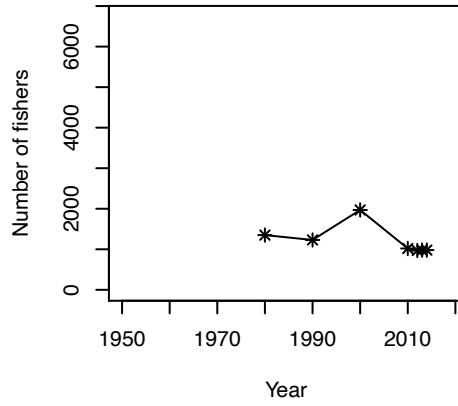
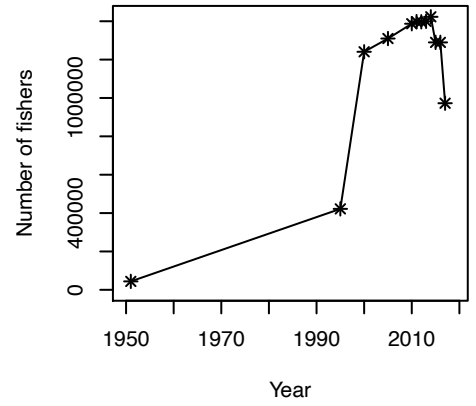
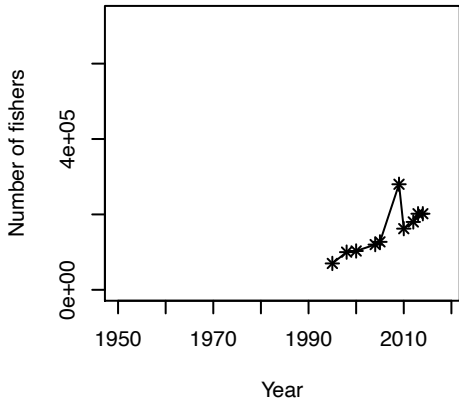
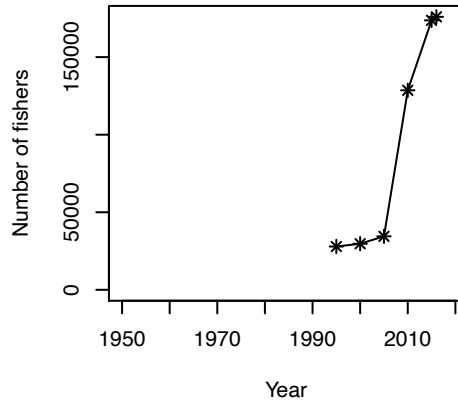
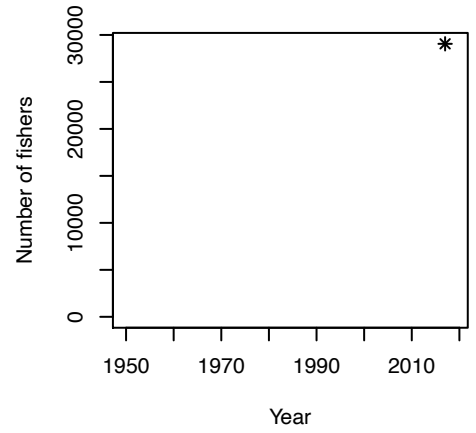
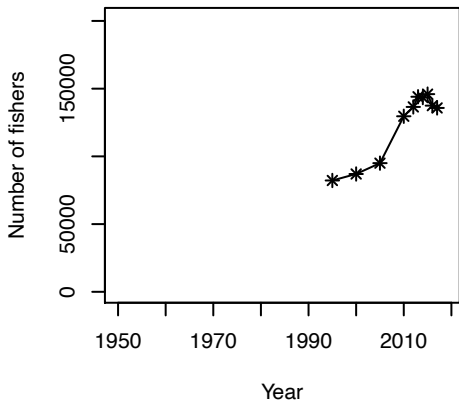
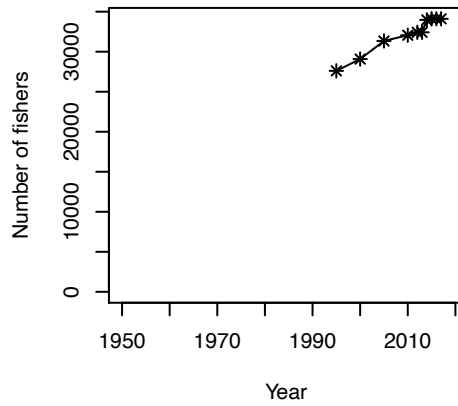
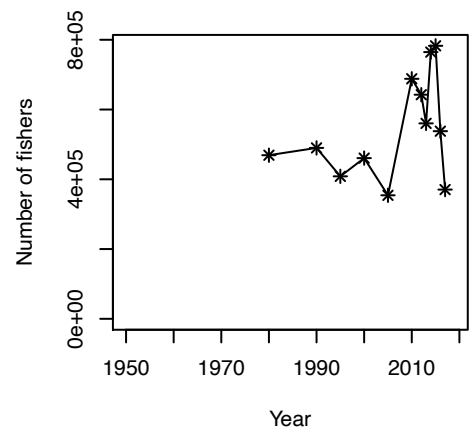
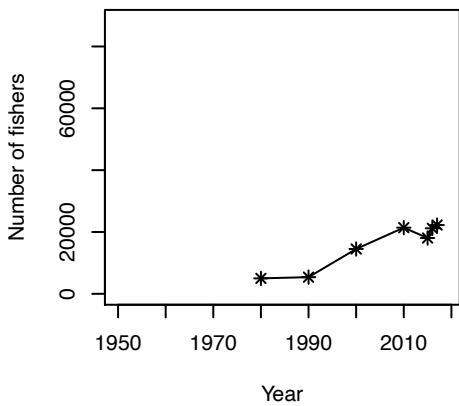
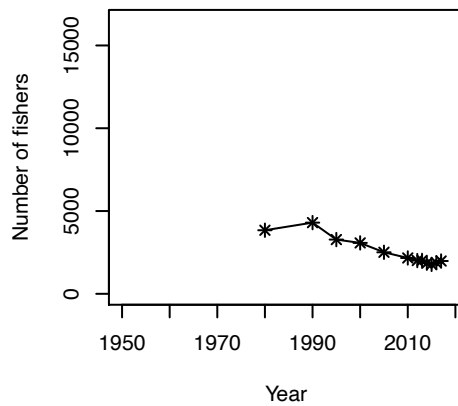
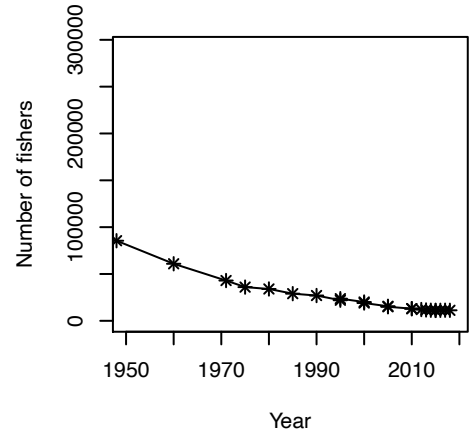
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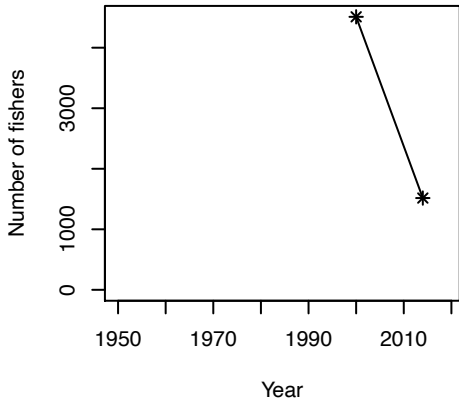
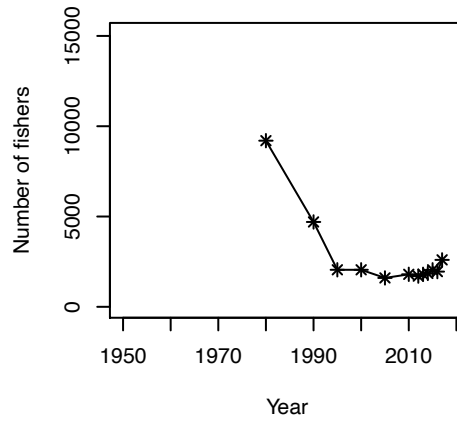
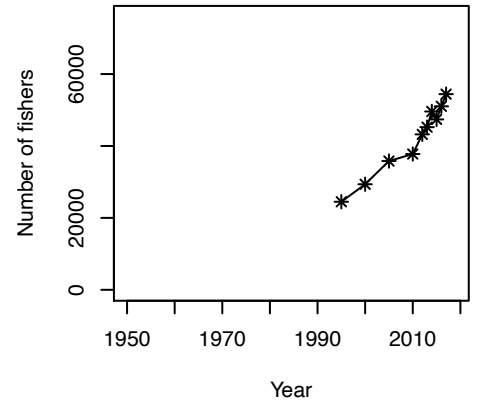
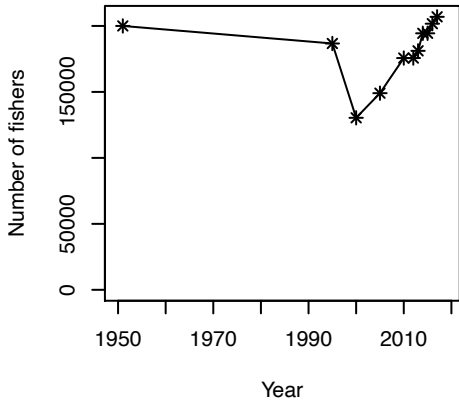
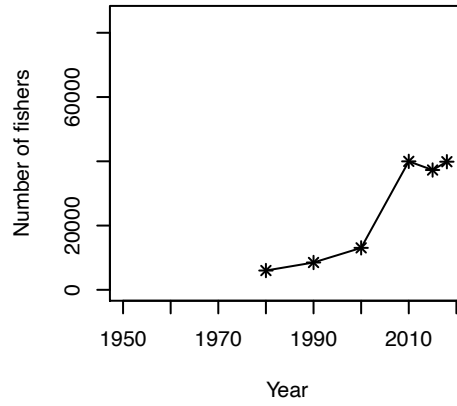
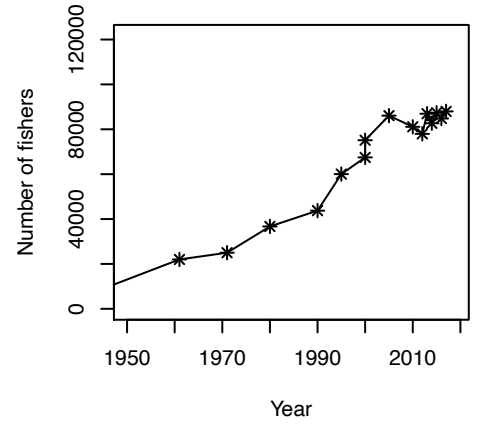
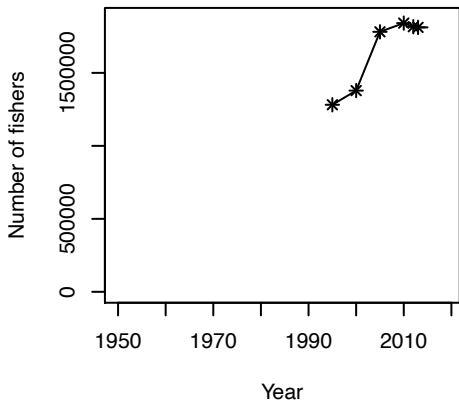
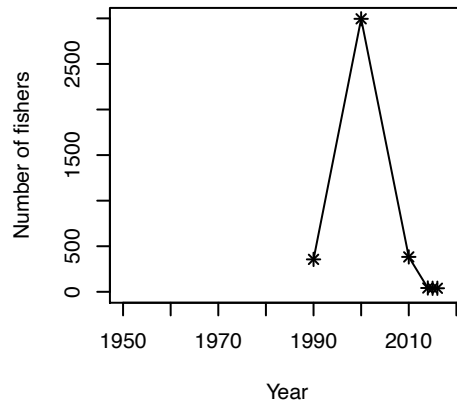
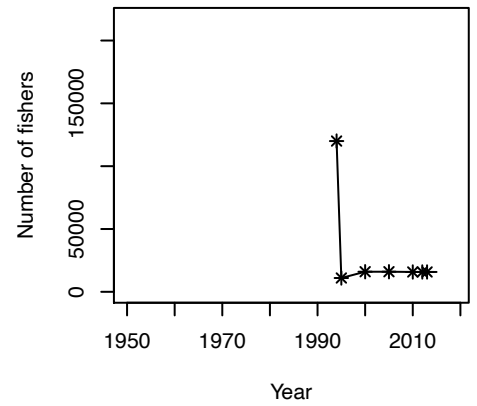
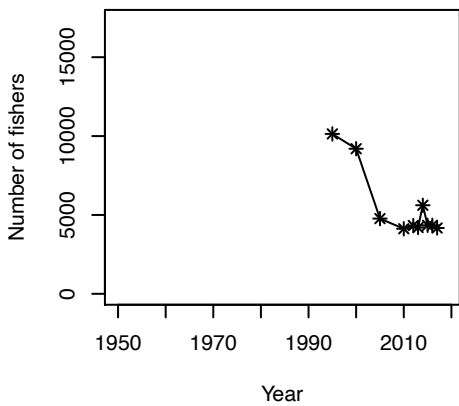
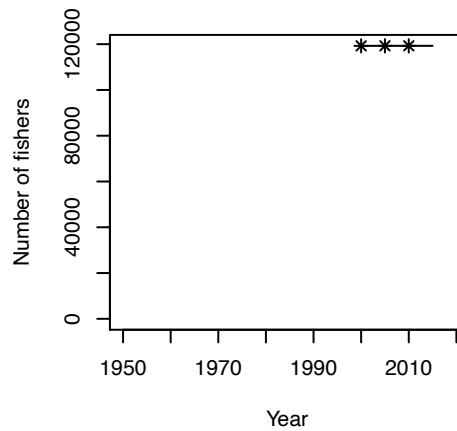
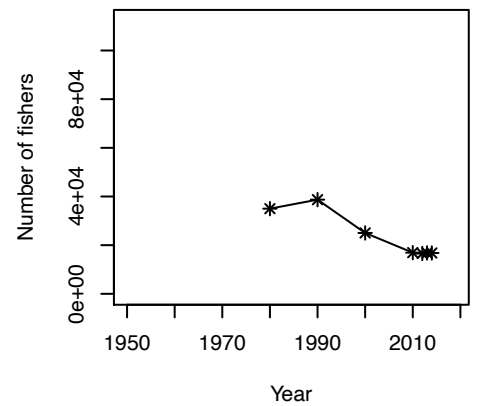
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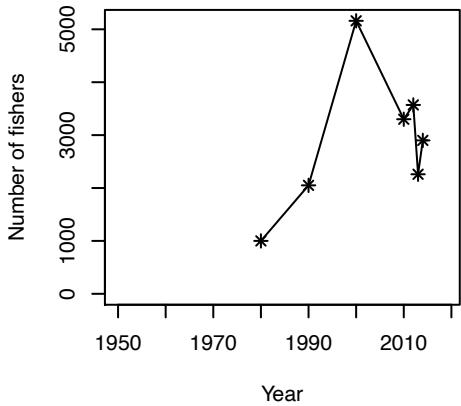
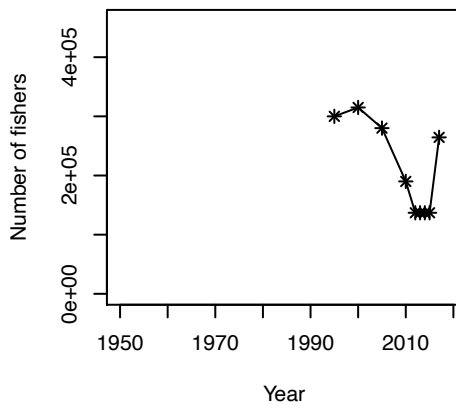
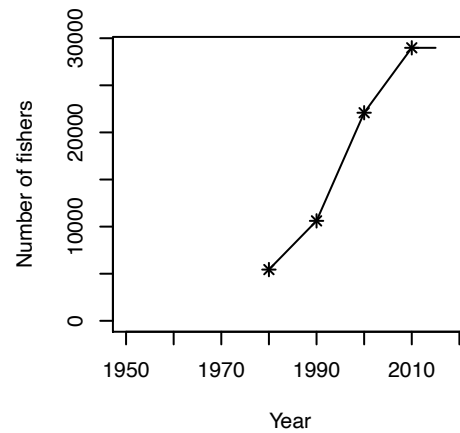
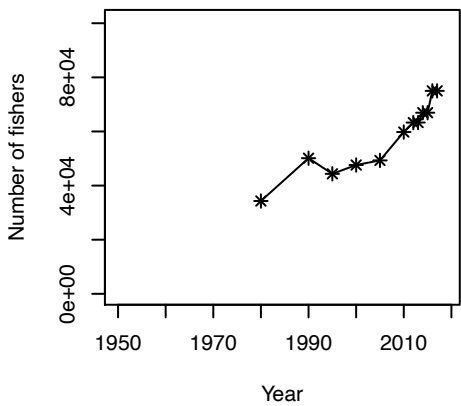
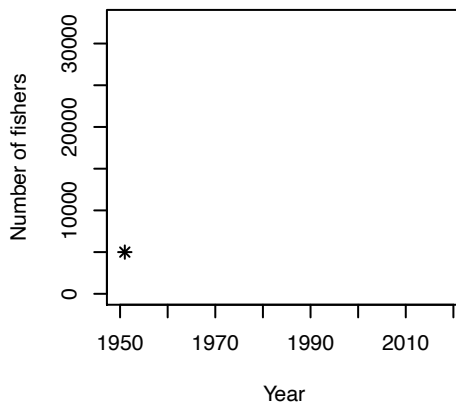
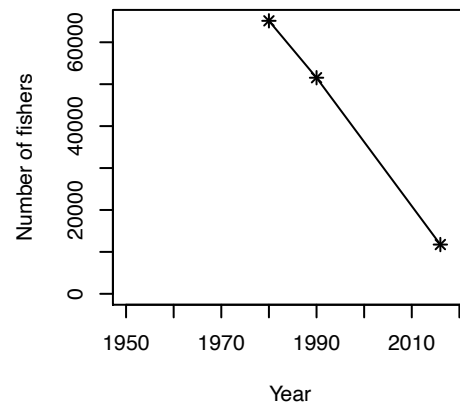
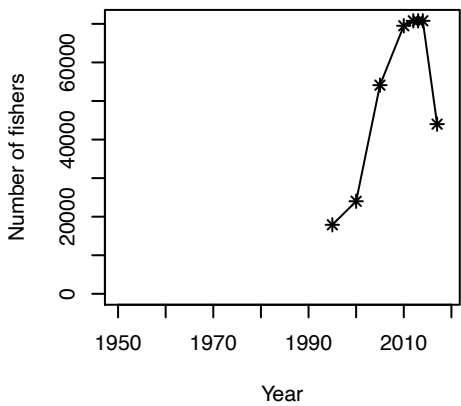
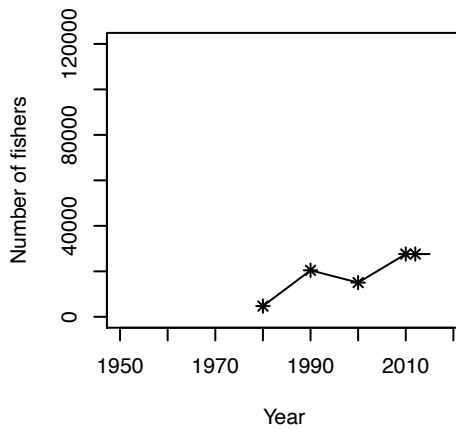
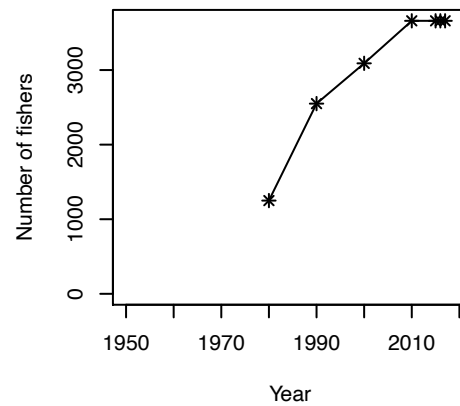
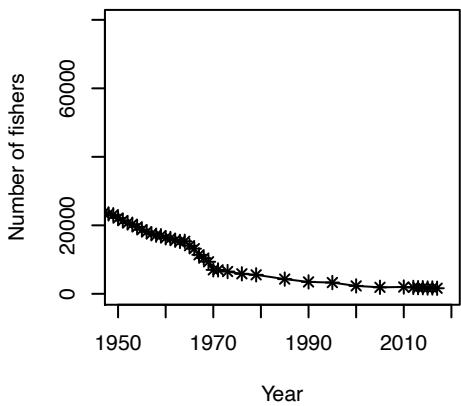
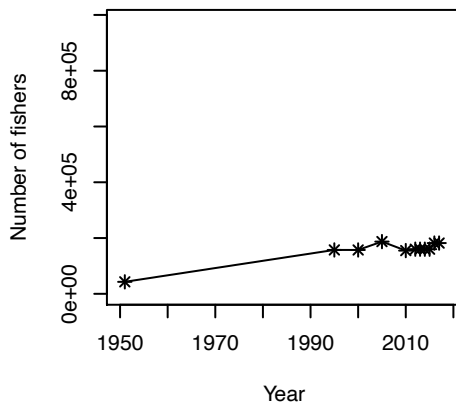
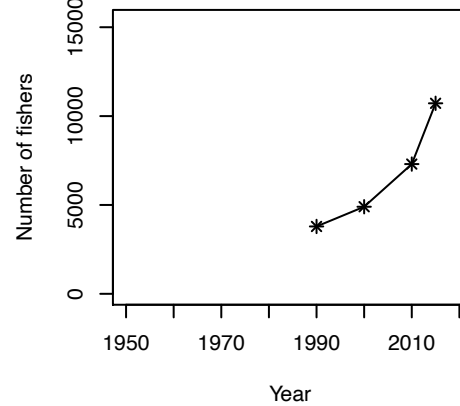
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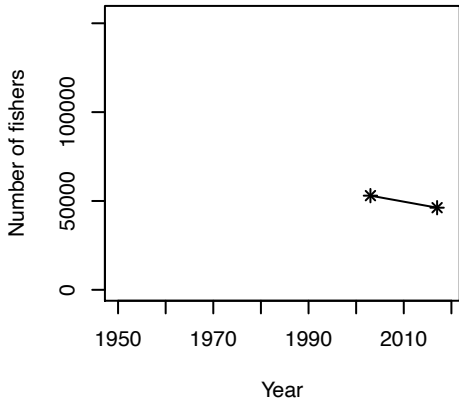
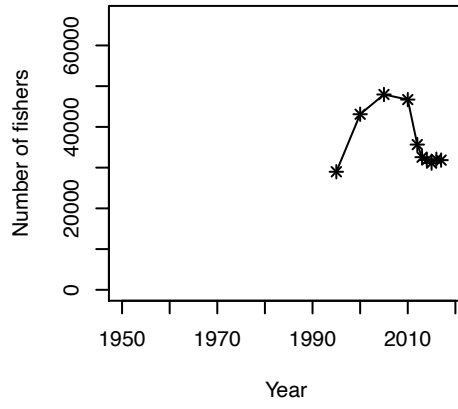
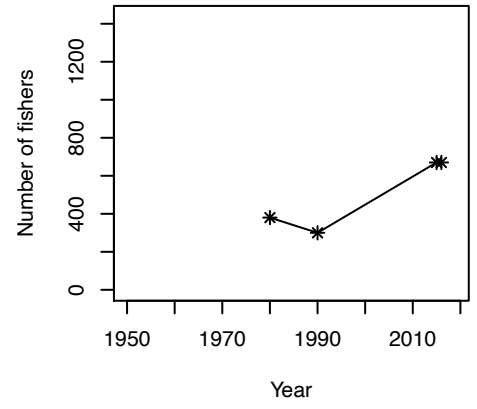
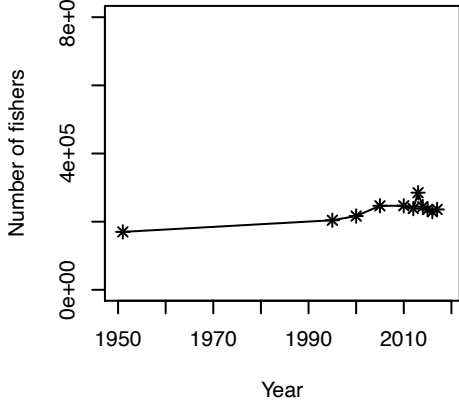
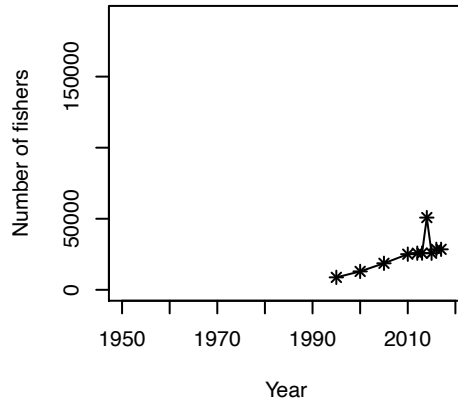
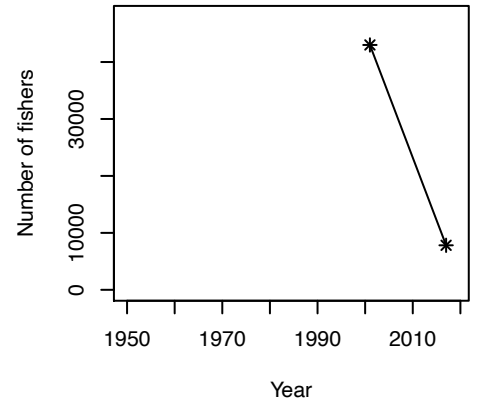
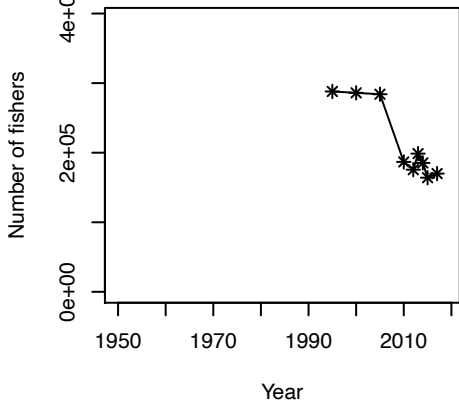
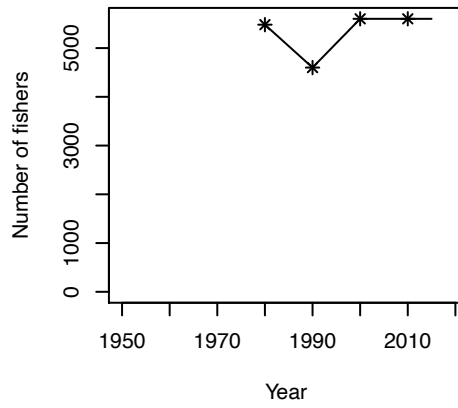
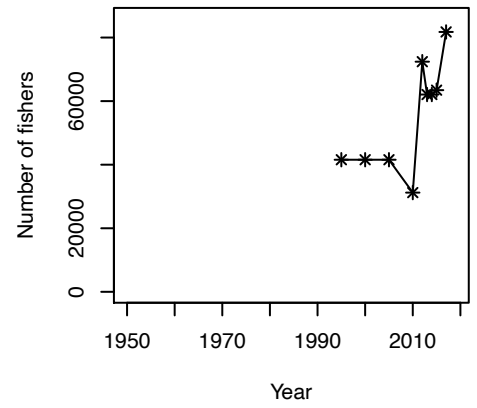
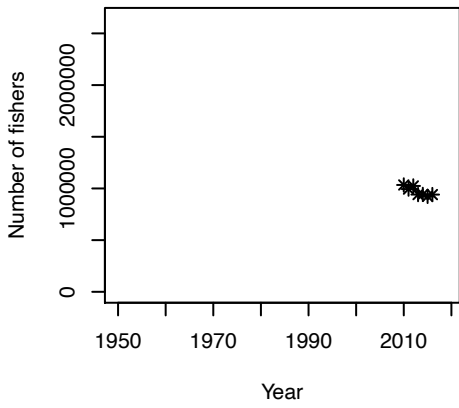
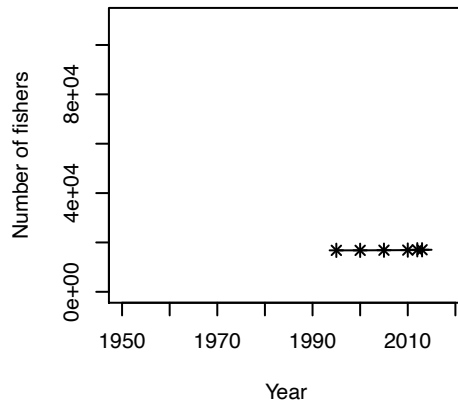
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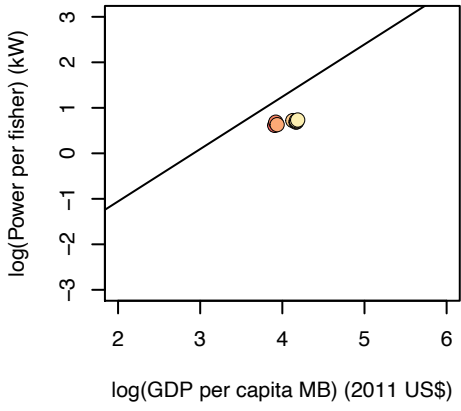
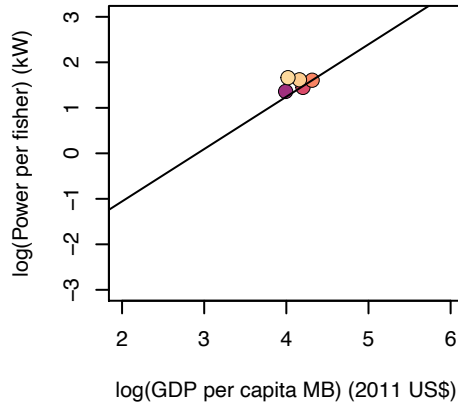
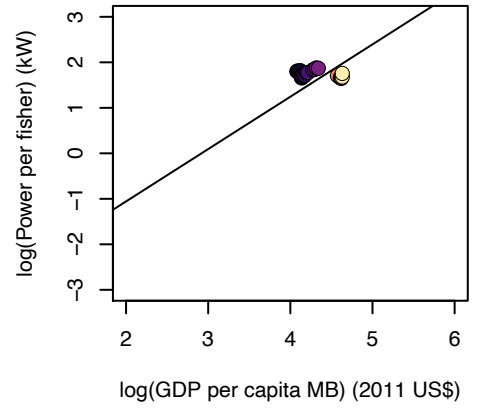
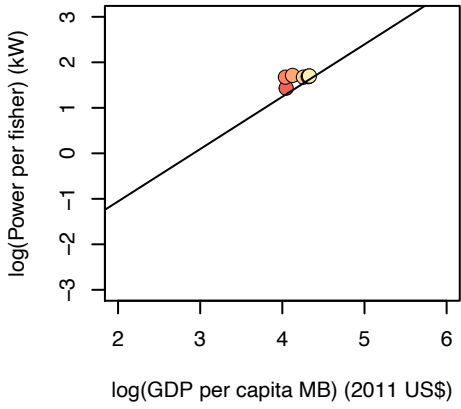
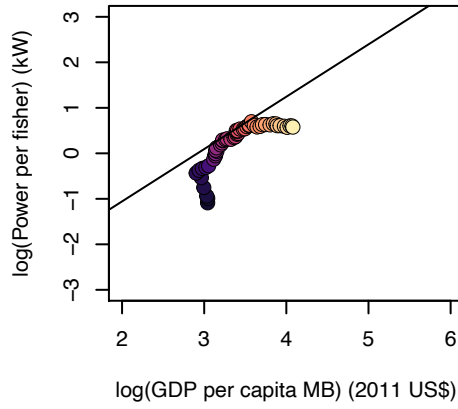
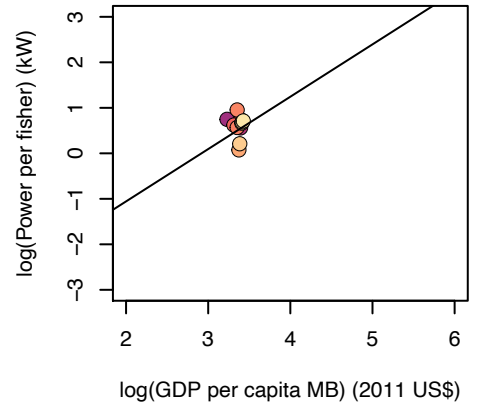
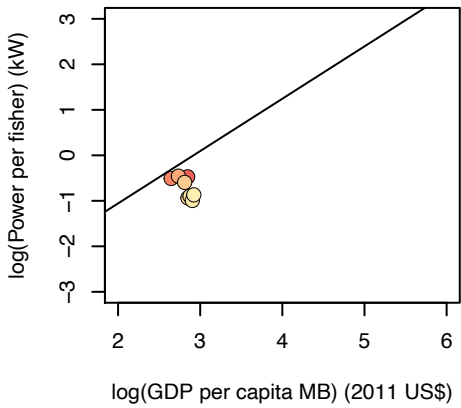
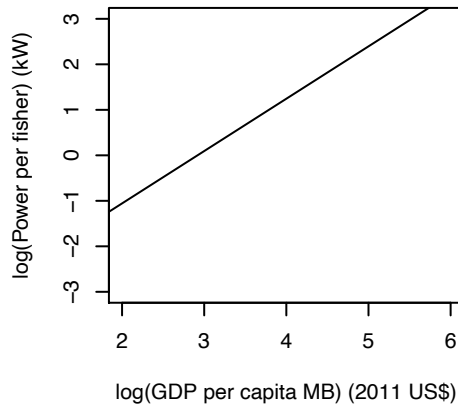
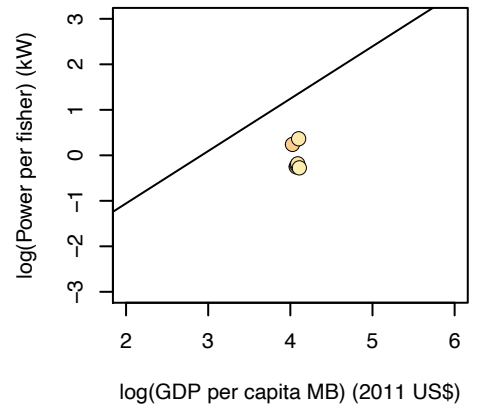
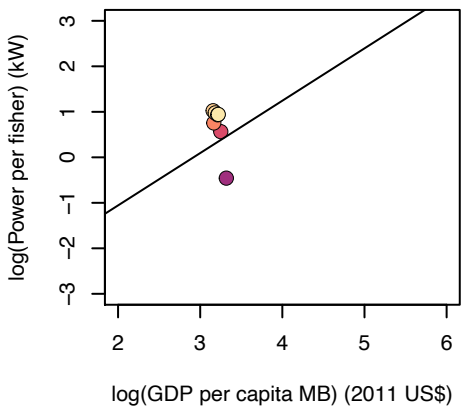
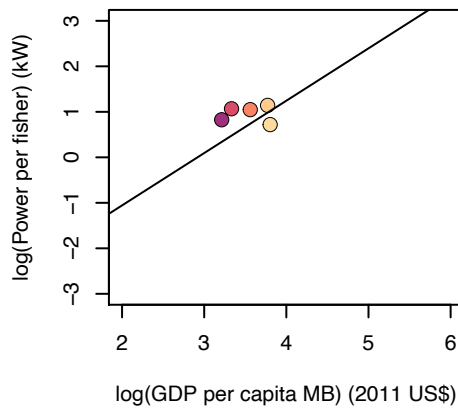
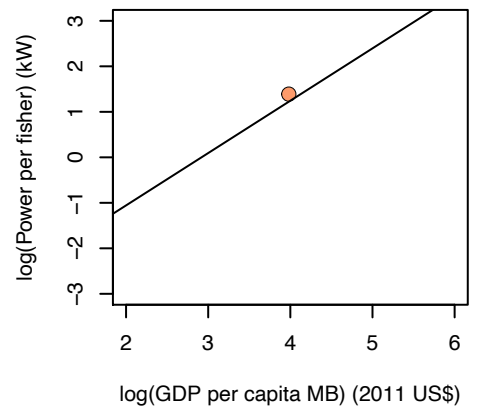
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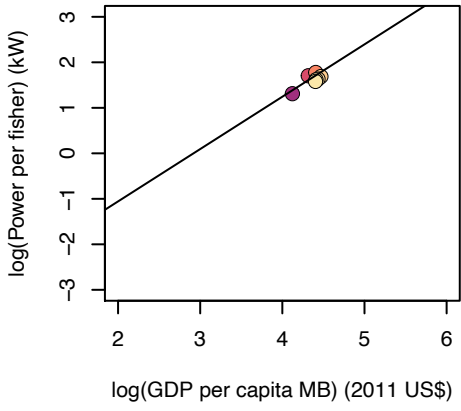
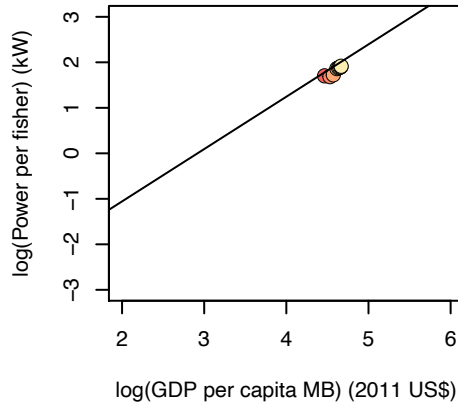
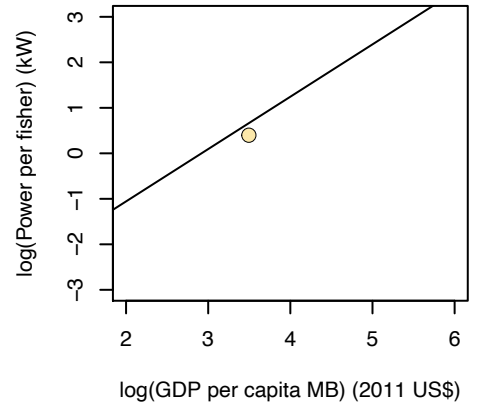
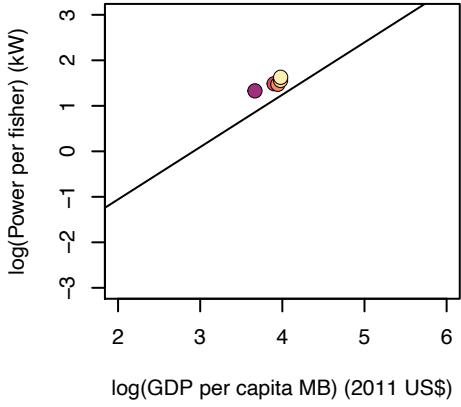
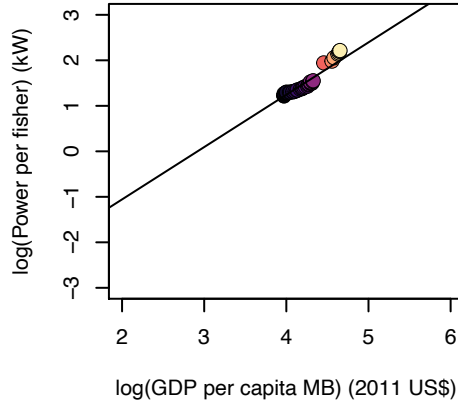
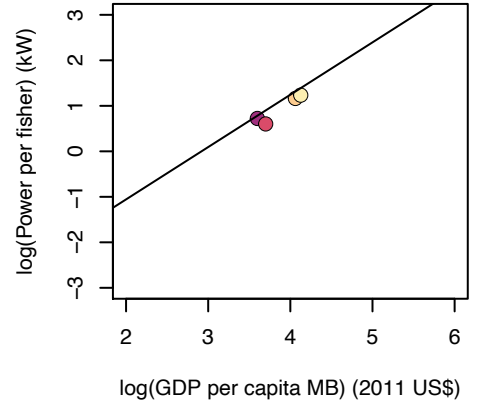
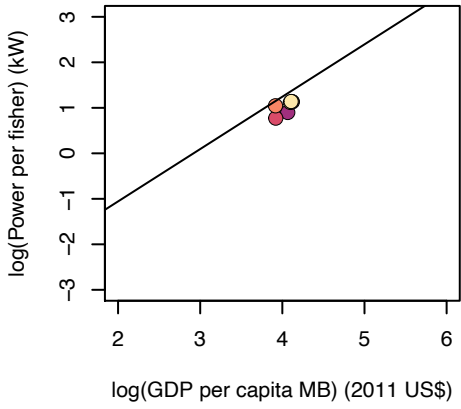
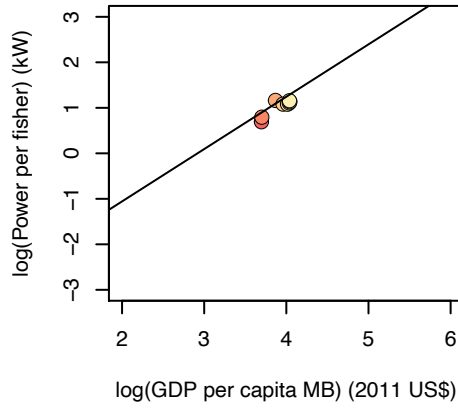
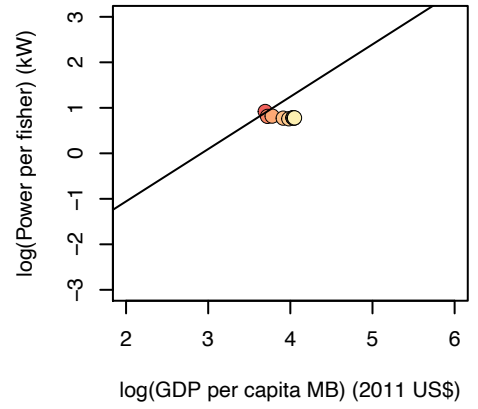
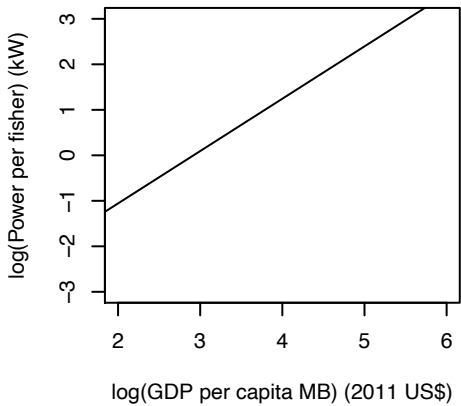
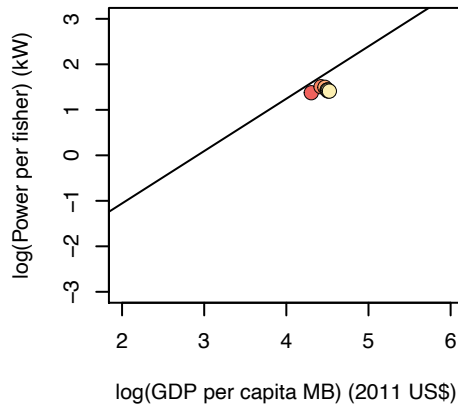
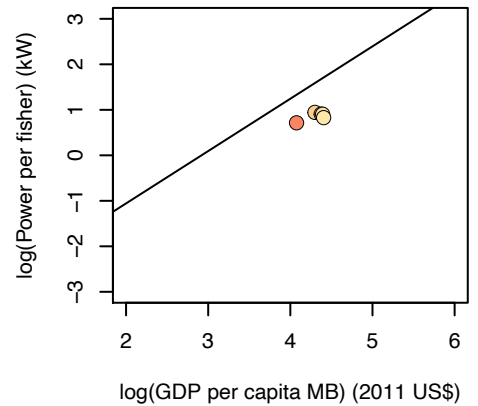
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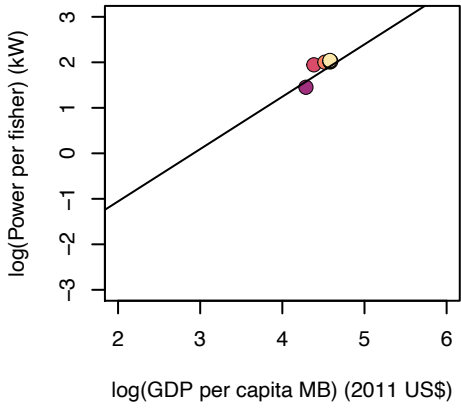
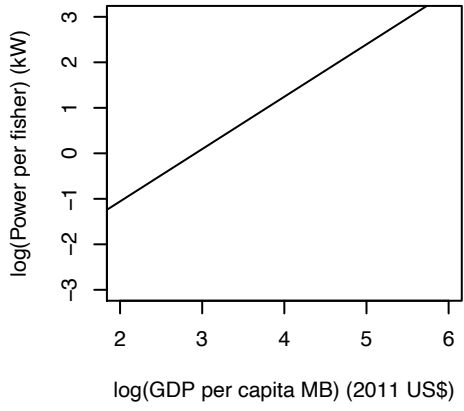
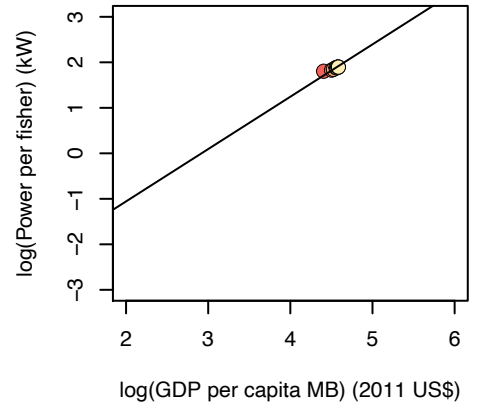
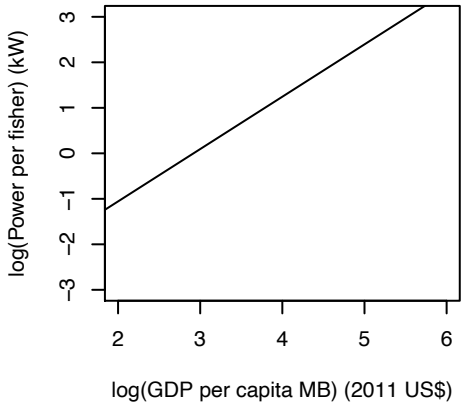
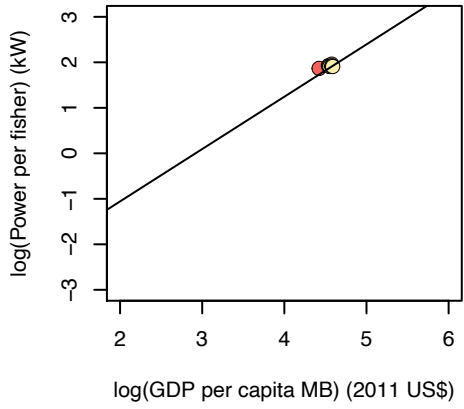
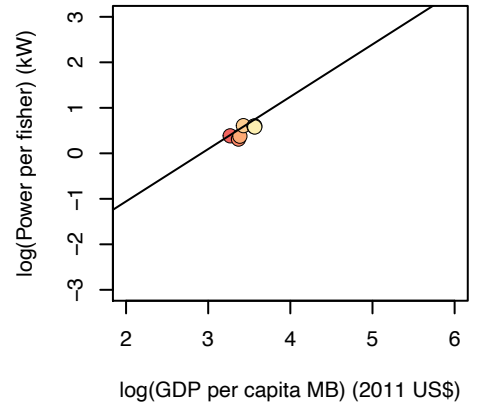
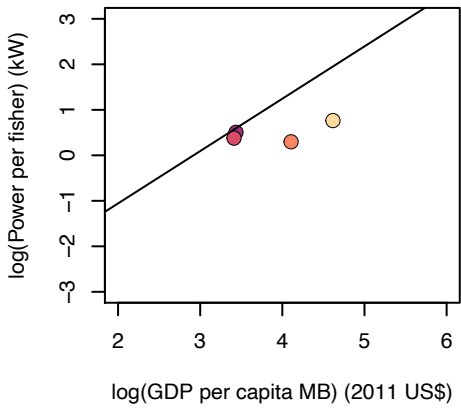
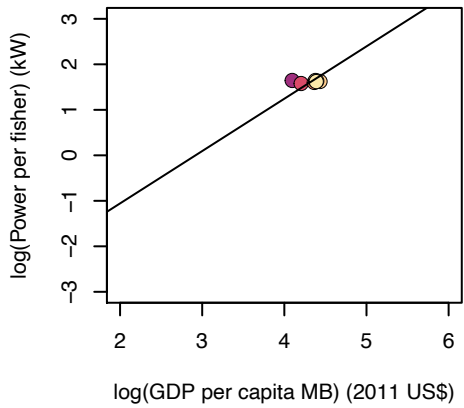
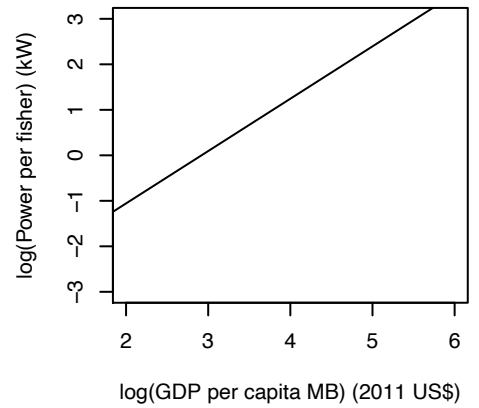
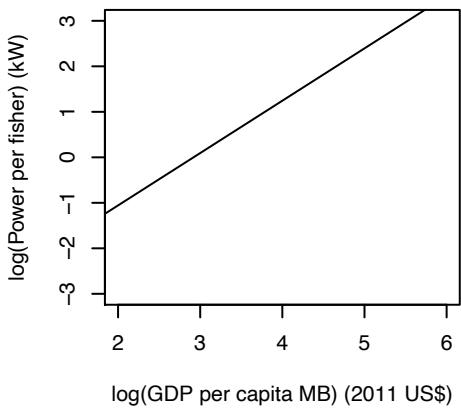
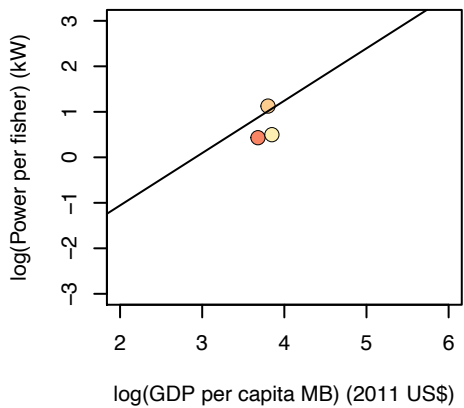
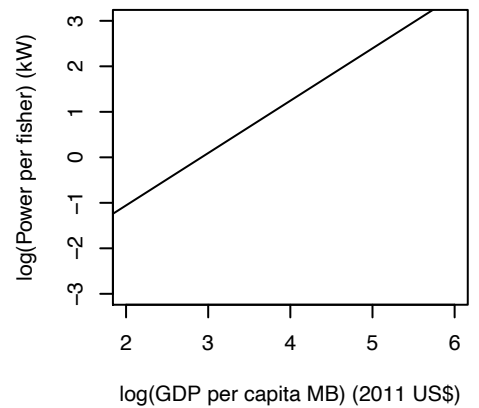
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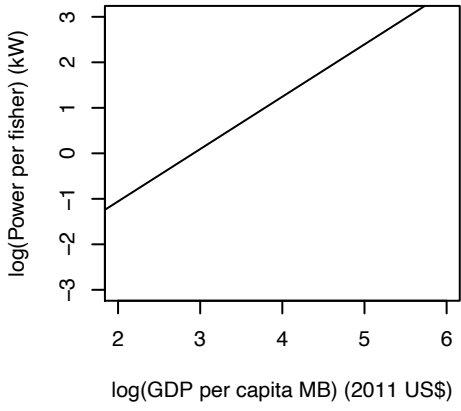
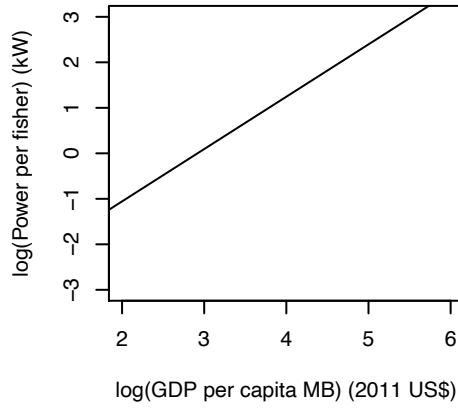
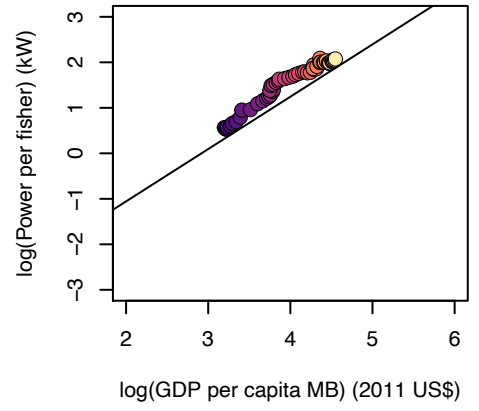
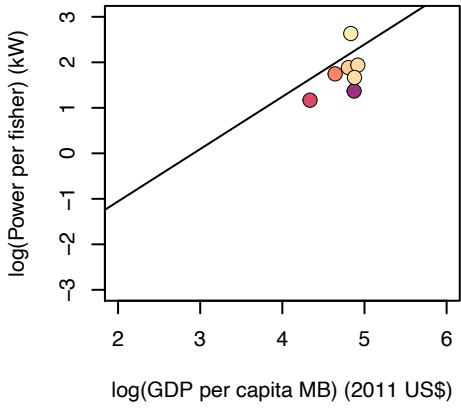
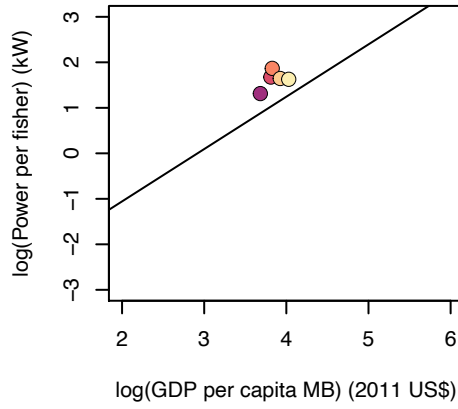
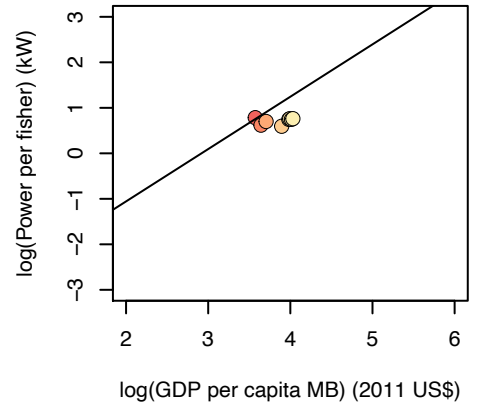
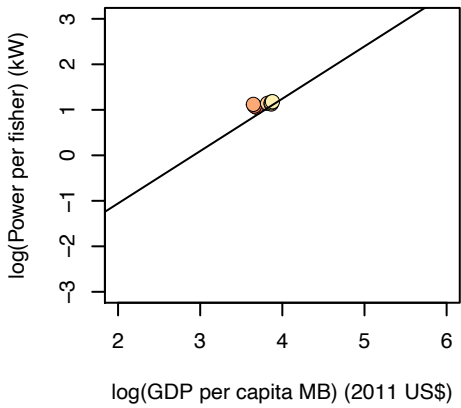
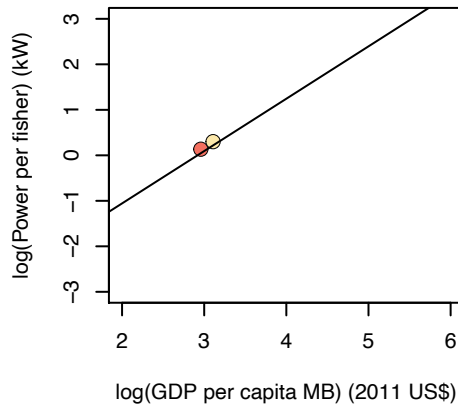
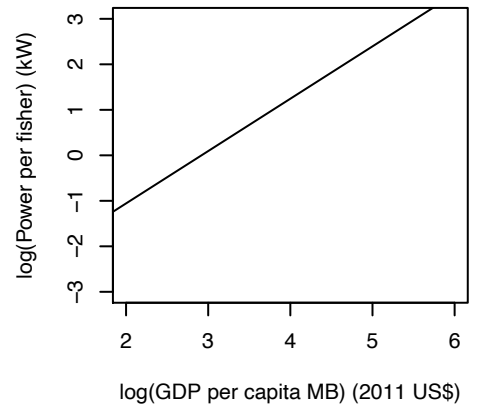
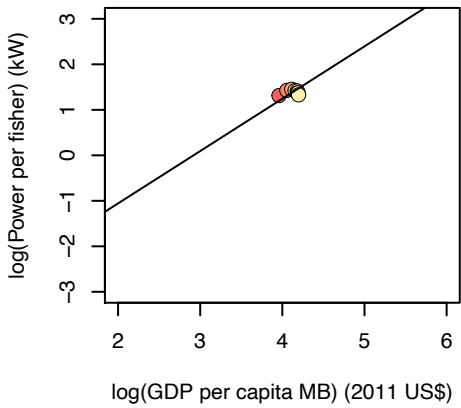
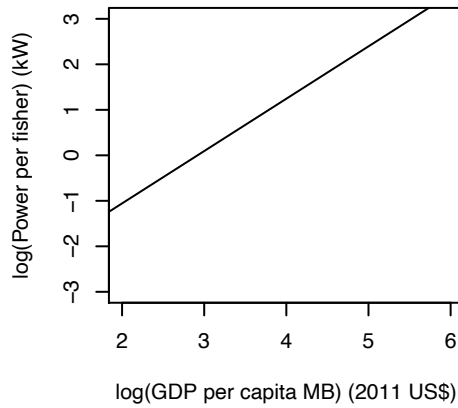
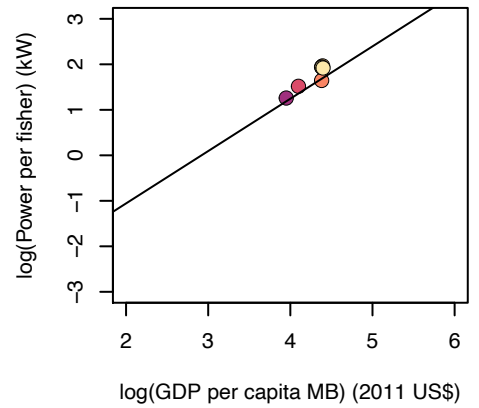
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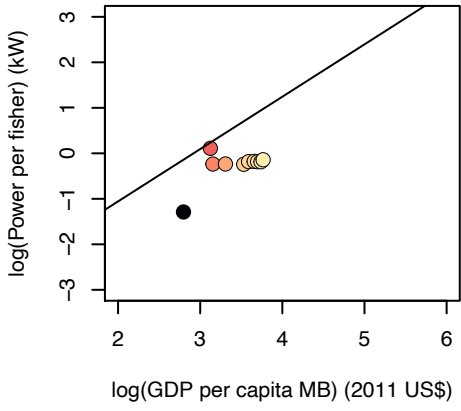
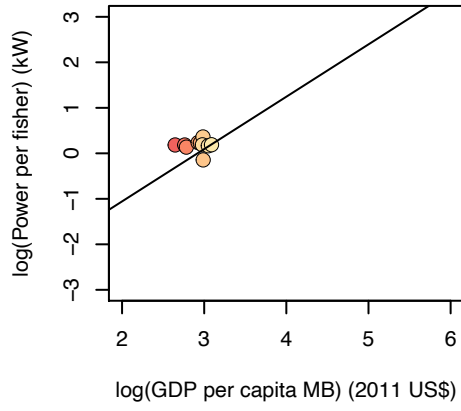
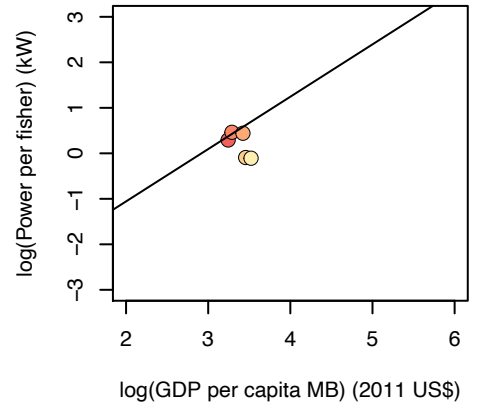
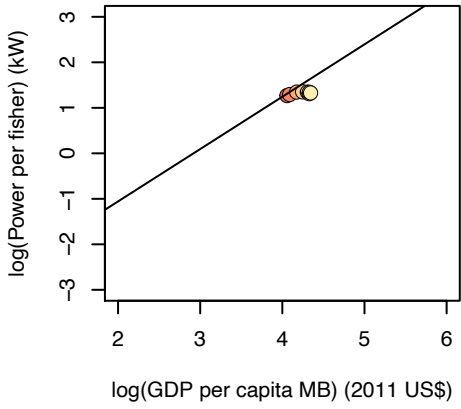
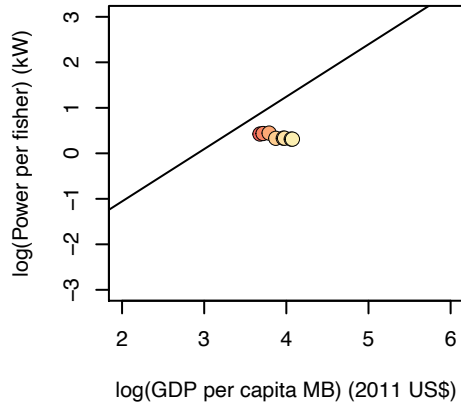
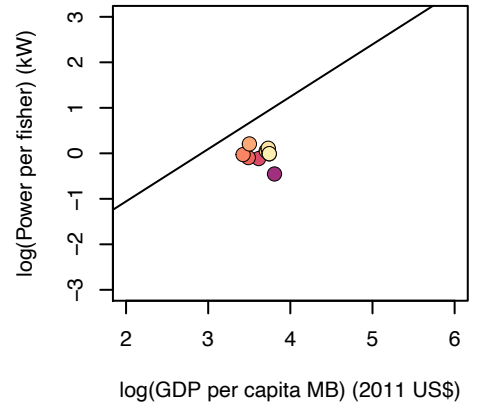
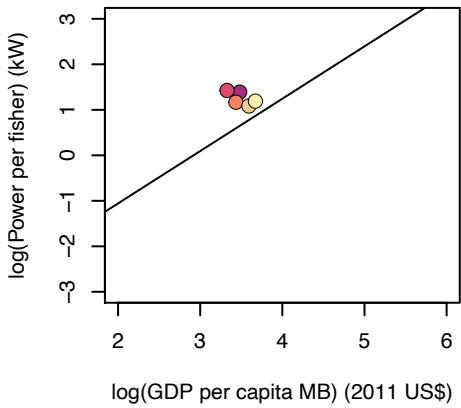
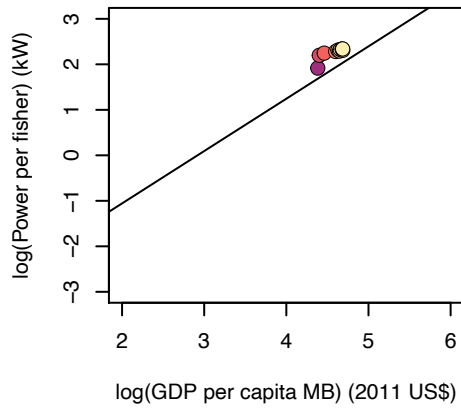
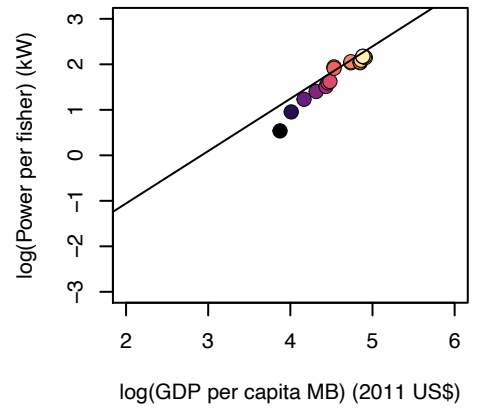
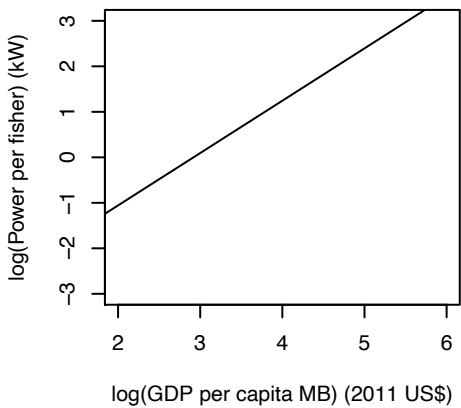
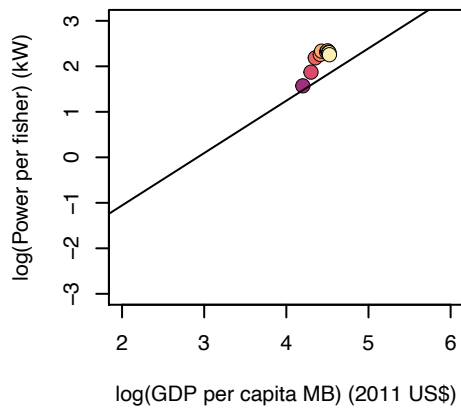
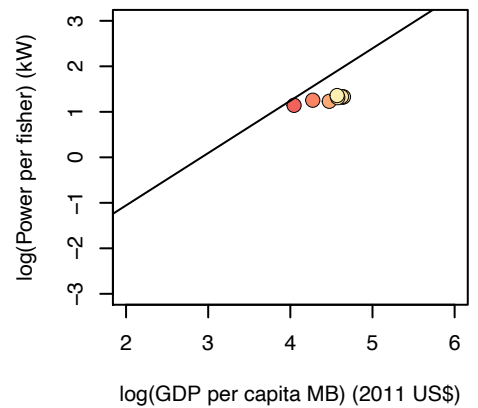
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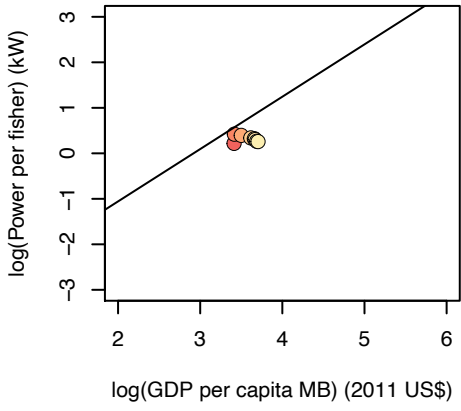
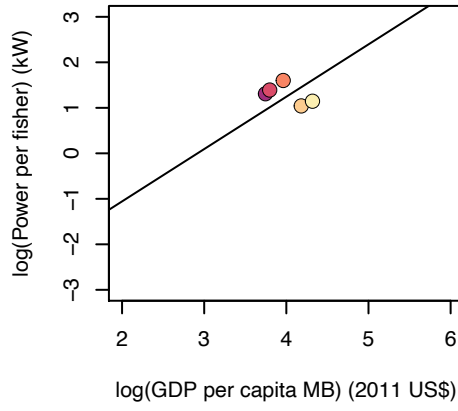
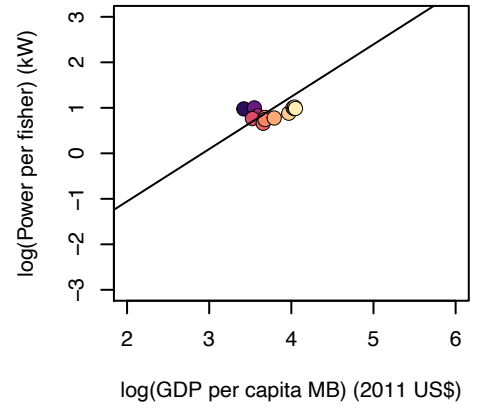
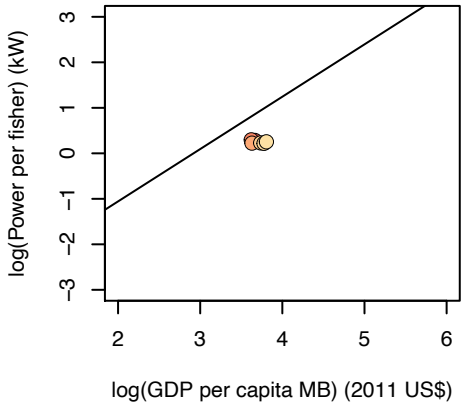
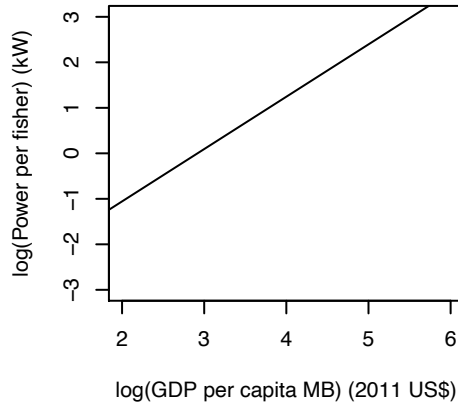
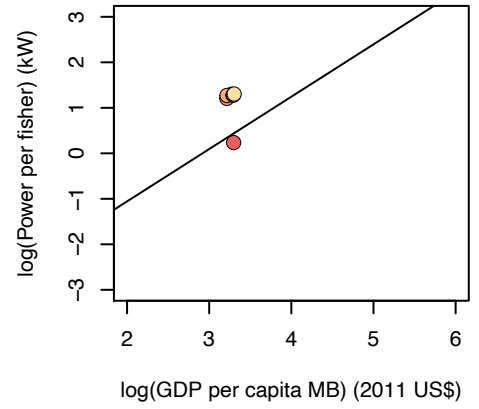
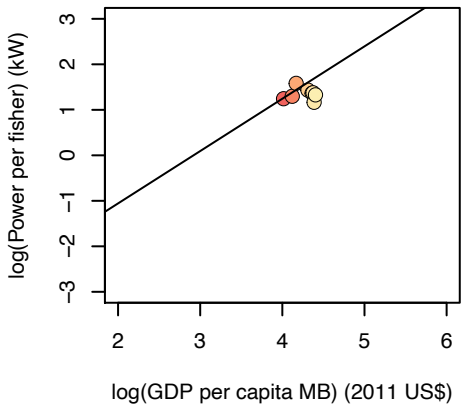
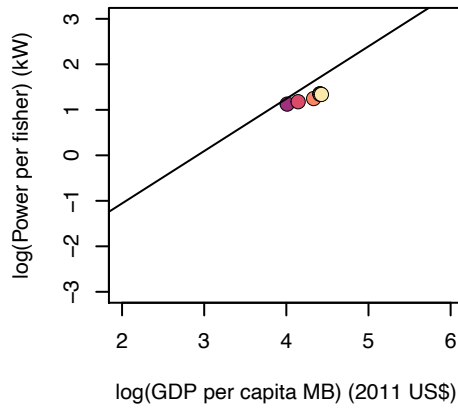
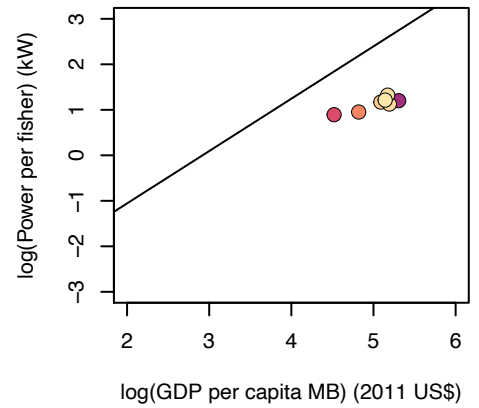
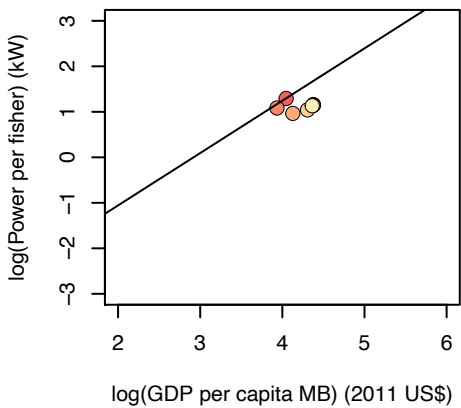
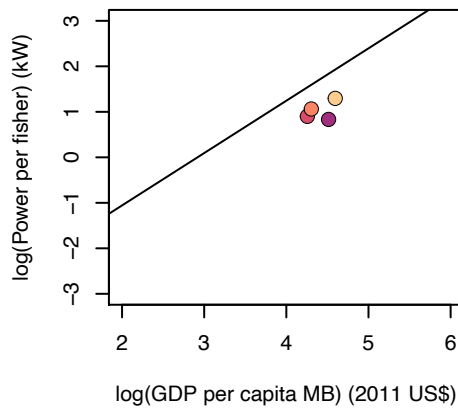
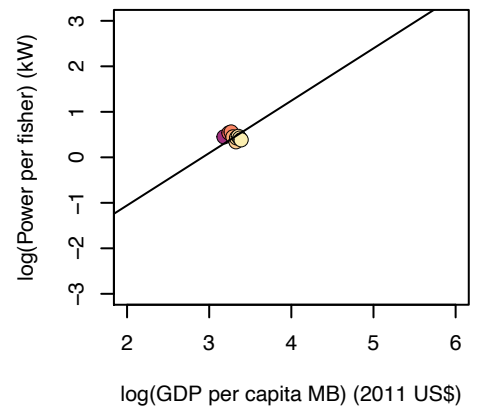
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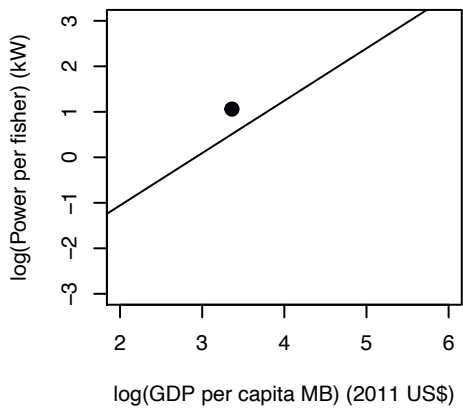
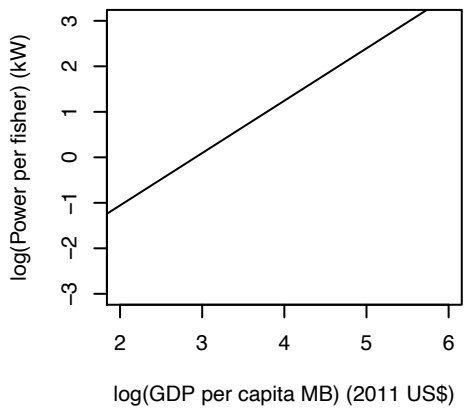
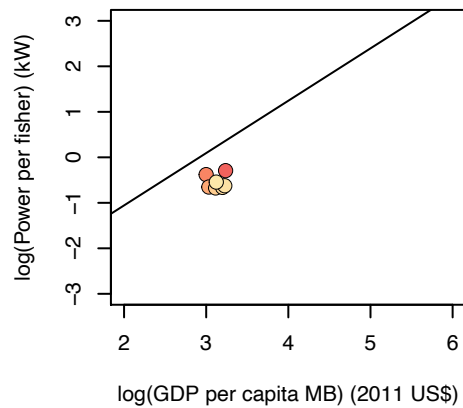
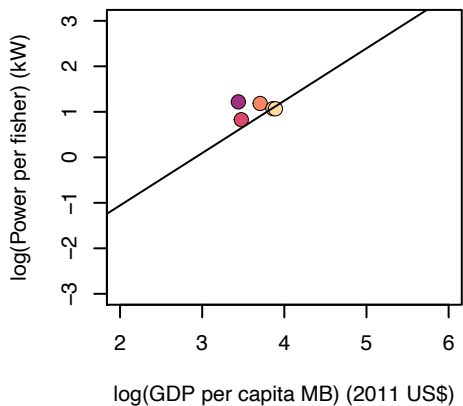
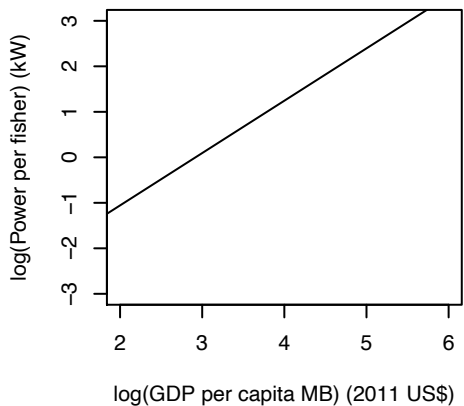
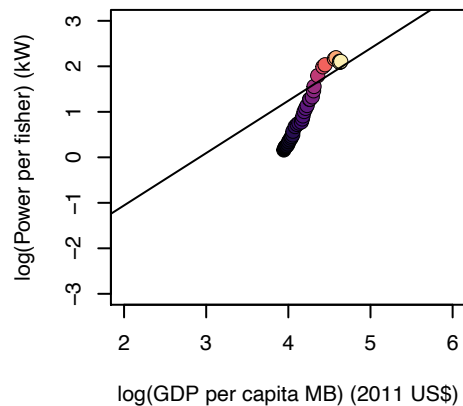
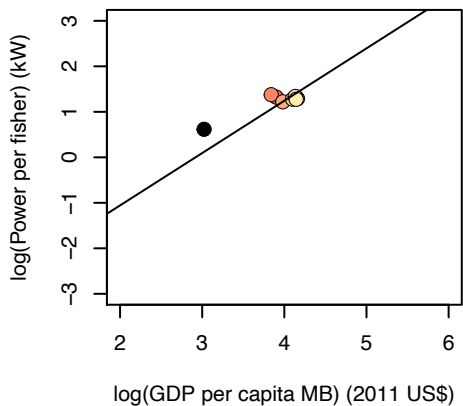
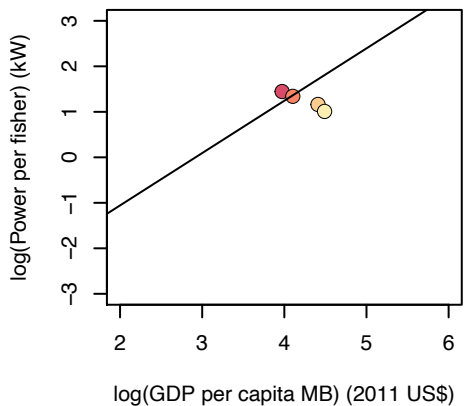
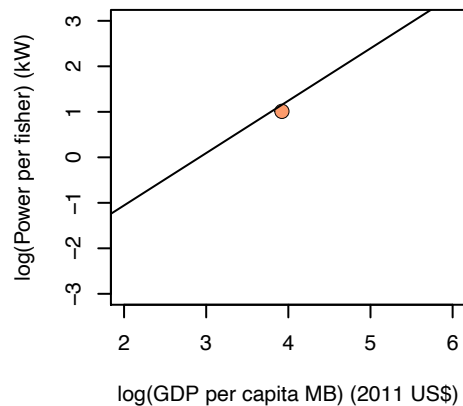
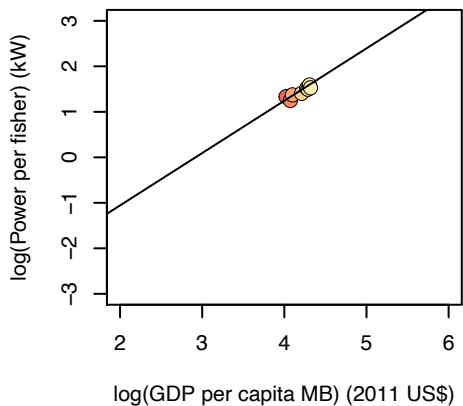
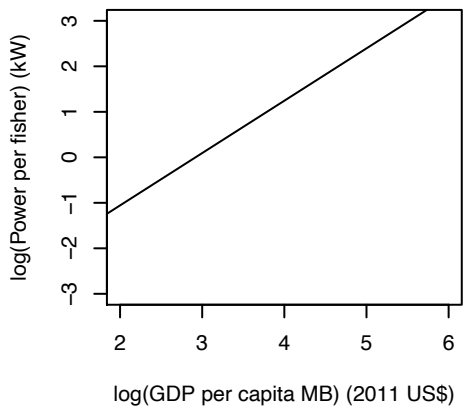
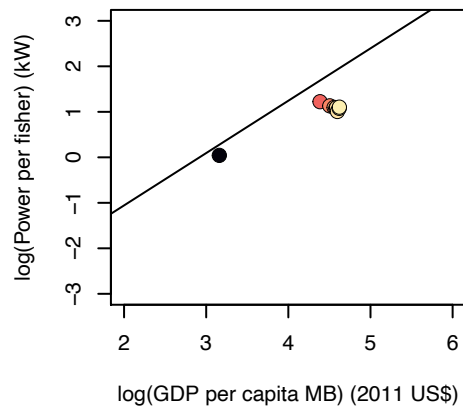
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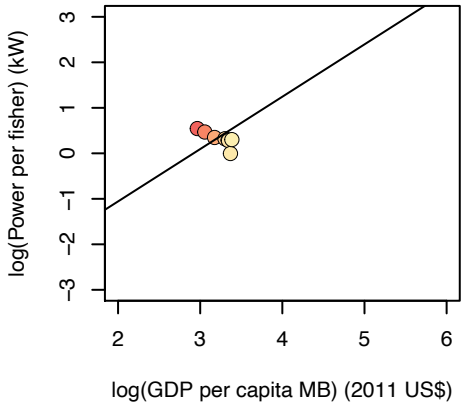
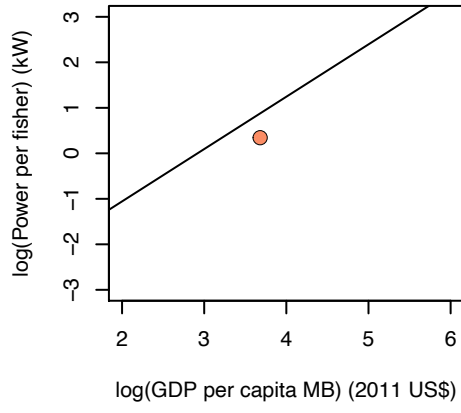
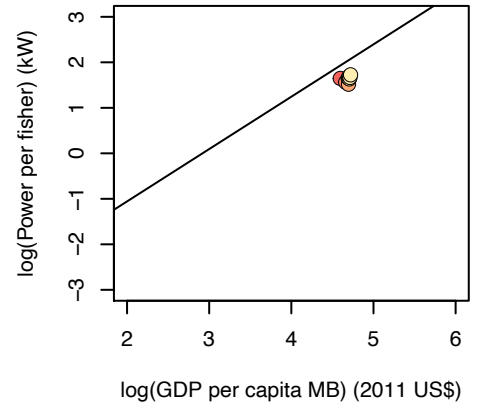
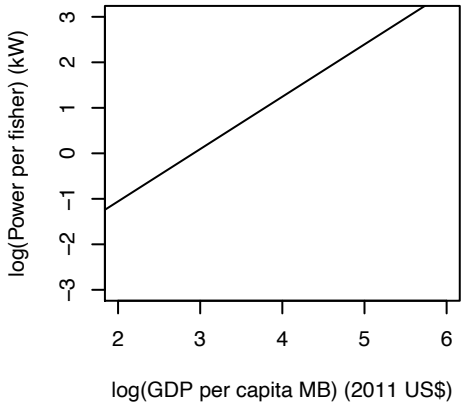
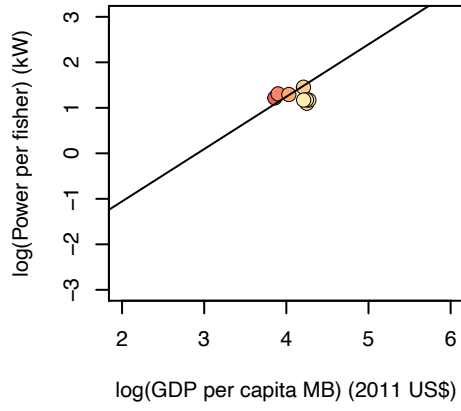
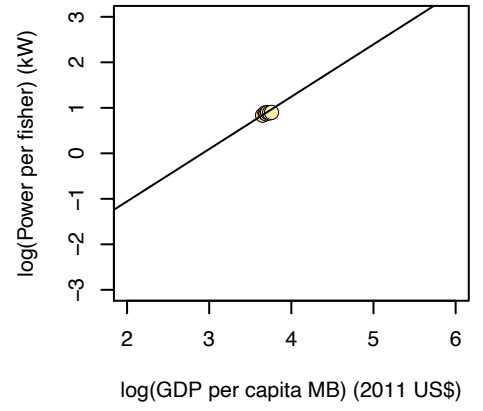
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