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Original Article

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

$$\frac{\mathrm{d}E_k}{\mathrm{d}t} = K_e \frac{\text{revenue}_k - \text{cost}_k}{E_k} \; \mathrm{e}^{-S} + \left(1 - \mathrm{e}^{-S}\right) \; K_s \; \left(E_{\text{targ},k} \; - \; E_k\right), \tag{1}$$

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

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

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 $F_{\mathrm{targ},k}$, 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, $t_{\mathrm{ro},k}$, as the time when catch declines below a certain fraction, θ_{ro}, of the observed maximum historical catch, $H_{\max,k}$. We here use $\theta_{\mathrm{ro}} = 0.75$, reflecting a relatively rapid reaction to declining catch. As long as the fishing mortality ($q_k E_k$) is larger than $F_{\mathrm{targ},k}$, regulation is initiated at time $t_{\mathrm{ro},k}$. This guarantees that regulation is only initiated after local overfishing has occurred:

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

Once initiated, regulation forces the nominal effort towards $E_{\mathrm{targ},k}$. 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 $F_{\mathrm{MSY,k}}$ (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. $0.3 \times F_{\mathrm{MSY}}$	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 homogenously across all grid cells.

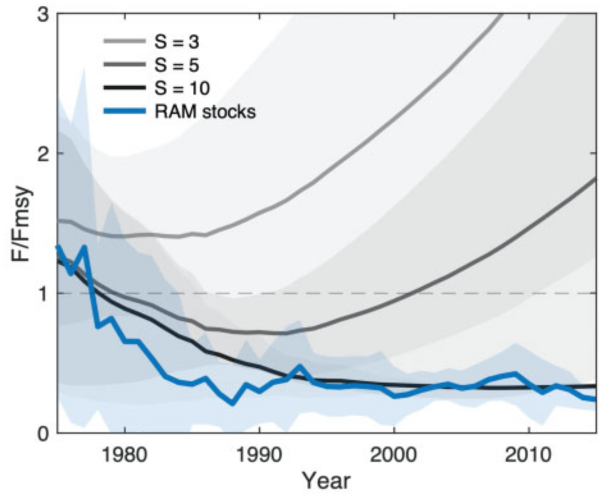

Figure 1. Modelled and empirical fisheries reference points in a well managed fishery. Lines show stock assessments (blue) and corresponding modelled fish populations in BOATS under different regulation effectiveness (grey) in US Alaska. If $S \geq 10$, the *F* is maintained at 30% of F_{MSY} over the 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

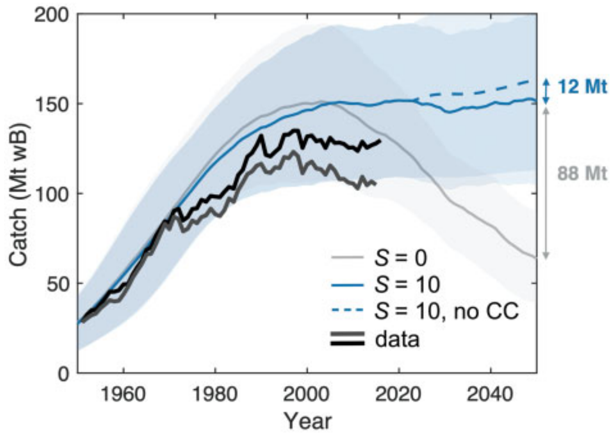

Figure 2. Simulated and empirical global catch (1950–2050). Two end-member scenarios with continued technological progress and either open access ($S = 0$, light grey) or strong regulation ($S = 10$, blue) are compared with historical catch data (1950–2014) from the SAUP (dark grey) and Watson and Tidd (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% year^{-1}, regulation plays a larger role than climate, indicated by the grey and blue arrows, respectively.

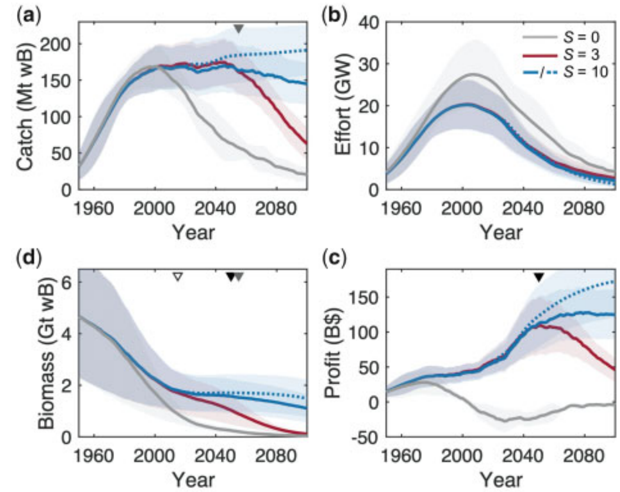

Figure 3. Simulated fisheries trajectories under continued technological progress. Aggregated global (a) catch, (b) effort, (c) profit (in year 2000 US\$), and (d) biomass under no ($S = 0$, dark grey), weak ($S = 3$, red), or strong ($S = 10$, blue) regulation. Weak regulation prolongs the period of 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.

stocks with an asymptotic size corresponding to that of the large fish size group modelled here (<8.5 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 (Kroodsma *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 globally strong enforcement ($S = 10$, solid blue line), the catch plateaus at 150 ± 50 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 ± 20 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 $F_{MSY,k}$ (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).

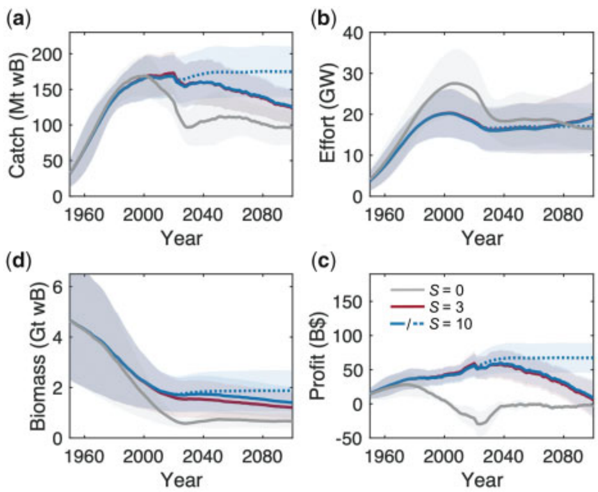

Figure 4. Simulated fisheries trajectories under stabilizing technology. Aggregated global (a) catch, (b) effort, (c) profit (in year 2000 US$), and (d) biomass under no ($S = 0$, dark grey), weak ($S = 3$, red), or strong ($S = 10$, blue) regulation. The importance of regulation strength is greatly 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

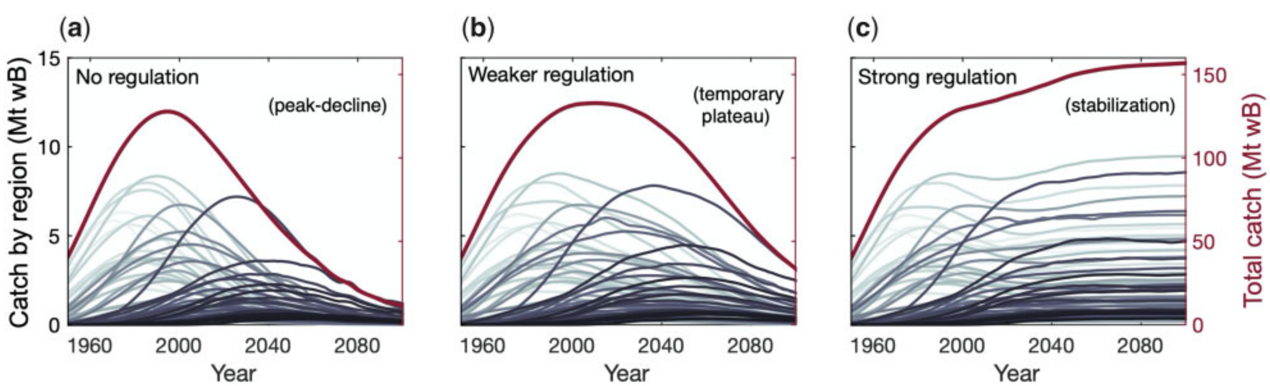

Figure 5. Illustration of the impact of regulation strength. Three types of global catch curves (thick red line) arise under different regulation strengths and continued catchability increase (5% year^{-1}). Grey lines show underlying catches in each of the world's large marine ecosystems, and shade 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 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 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.

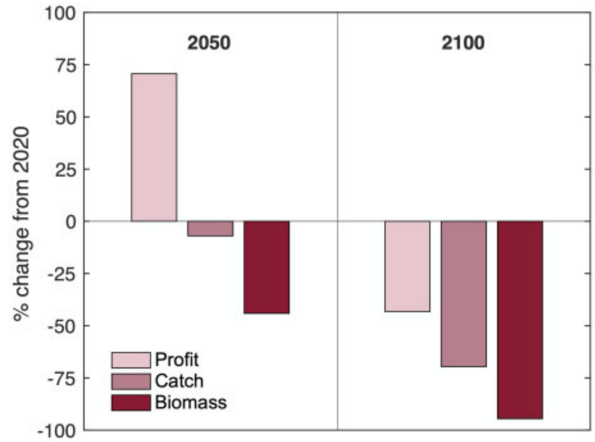

Figure 6. Hidden losses under weak regulation. The percent change in ensemble average global profit, catch, and biomass is shown for 2050 and 2100 relative to year 2020, for the simulation with weak regulation ($S = 3$), continued technological progress, and climate change. In year 2050, weak regulations 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.

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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