








RESEARCH ARTICLE

Timing and magnitude of climate-driven range shifts in transboundary fish stocks challenge their management

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Funding information

Gordon and Betty Moore Foundation, Grant/Award Number: GBMF5668.02; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: PP00P2_198897; Swiss National Supercomputing Centre; David and Lucile Packard Foundation, Grant/Award Number: 2019-68336; Social Sciences and Humanities Research Council of Canada, Grant/Award Number: Partnership Grant; Horizon 2020 Framework Programme, Grant/Award Number: 724289 and 820989; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: Discovery Grant; Walton Family Foundation, Grant/Award Number: 2018-1371; Compute Canada (www.computecanada.ca)

Abstract

Climate change is shifting the distribution of shared fish stocks between neighboring countries' Exclusive Economic Zones (EEZs) and the high seas. The timescale of these transboundary shifts determines how climate change will affect international fisheries governance. Here, we explore this timescale by coupling a large ensemble simulation of an Earth system model under a high emission climate change scenario to a dynamic population model. We show that by 2030, 23% of transboundary stocks will have shifted and 78% of the world's EEZs will have experienced at least one shifting stock. By the end of this century, projections show a total of 45% of stocks shifting globally and 81% of EEZs waters with at least one shifting stock. The magnitude of such shifts is reflected in changes in catch proportion between EEZs sharing a transboundary stock. By 2030, global EEZs are projected to experience an average change of 59% in catch proportion of transboundary stocks. Many countries that are highly dependent on fisheries for livelihood and food security emerge as hotspots for transboundary shifts. These hotspots are characterized by early shifts in the distribution of an important number of transboundary stocks. Existing international fisheries agreements need to be assessed for their capacity to address the social-ecological implications of climate-change-driven transboundary shifts. Some of these agreements will need to be adjusted to limit potential conflict between the parties of interest. Meanwhile, new agreements will need to be anticipatory and consider these concerns and their associated uncertainties to be resilient to global change.

KEYWORDS

climate change, fisheries management, shared fisheries, species on the move, time of emergence

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1 | INTRODUCTION

Over the past century, human activities have dramatically altered the physical and biogeochemical conditions of the ocean, resulting in warmer, more acidic and less oxygenated waters (IPCC, 2019). Marine species' distributions reflect species' preferences for discrete environmental conditions (Hutchinson, 1957). As a result of changing ocean conditions, many marine species are shifting their distributions poleward or to deeper waters to remain within their optimal environmental niche (Dulvy et al., 2008; Poloczanska et al., 2016). The biogeography of marine species is projected to continue to shift as ocean conditions change (Cheung et al., 2010), impacting fish catchability, fisheries production, and dependent livelihoods and economies (Sumaila et al., 2019). These impacts are compromising our capacity to reach international sustainability goals under the United Nations (UN) 2030 Agenda for Sustainable Development, such as Goals 14 ("life below water") and 17 ("partnerships for the Goals") (Pecl et al., 2017; Singh et al., 2017; United Nations, 2018). The projected risks and impacts can be reduced by improving the effectiveness of current governance and fisheries management frameworks, including for species that cross international borders, also known as "shared stocks" (Miller et al., 2013; Pinsky et al., 2018).

The concept of shared stocks was developed following the ratification of the UN Convention on the Law of the Sea (UNCLOS) and the claiming of Exclusive Economic Zones (EEZs) by Coastal States (United Nations, 1986). As defined by the UN's Food and Agriculture Organization, shared stocks can be classified into four non-exclusive categories: (i) transboundary stocks, which cross neighboring EEZs; (ii) straddling stocks that, in addition to neighboring EEZs, also visit the adjacent high seas (i.e., areas beyond national jurisdiction); (iii) highly migratory stocks, mainly tunas and bill-fishes, that migrate across vast oceanic regions including both the high seas and EEZs; and (iv) discrete stocks that are only present on the high seas (Munro et al., 2004). This study focuses on transboundary stocks exploited by fisheries operating within EEZs only. Under UNCLOS, countries are responsible for the management of stocks within their EEZs and encouraged to cooperate when stocks are shared (United Nations, 1986). A recent study estimates that there are 633 exploited transboundary marine species globally, representing 67% of identified harvested taxa (Palacios-Abrantes, Reygondeau et al., 2020). Between 2005 and 2010, these species yielded an annual average of 48 million tons of catch and USD 78 billion in fishing revenue (Palacios-Abrantes, Reygondeau et al., 2020). Recent work also highlights that the exploitation status of marine species is largely worse when a stock is shared than when it is contained within a single EEZ (Liu & Molina, 2021).

The effectiveness of fisheries management for transboundary species is challenged by shifts in stocks' distribution under climate change (Oremus et al., 2020; Pinsky & Mantua, 2014; Pinsky et al., 2018, 2020). In most cases, catch or effort-based fishing quotas for transboundary stocks are based on historical records and do not necessarily consider the full distribution range of the stock (Baudron et al., 2020), nor the effects of a changing climate on fish stocks and associated fisheries (Palacios-Abrantes, Sumaila et al., 2020; Sumbly

et al., 2021). While many transboundary stocks experience natural seasonal variations in their distribution (e.g., migration, reproductive cycle), misalignment between fisheries resources' allocation and distributional shifts beyond such natural variation has previously resulted in unsustainable fishing levels and international disputes (Miller et al., 2013; Ortuño-Crespo et al., 2020; Spijkers & Boonstra, 2017). Continuing climate change is expected to exacerbate such patterns (Pinsky et al., 2018; Sumaila et al., 2011). Recent studies have looked at future global gains (Pinsky et al., 2018) and losses (Oremus et al., 2020) of transboundary stocks within the world's EEZs as well as regional sharing dynamics between neighboring countries (Palacios-Abrantes, Sumaila et al., 2020; Sumaila et al., 2020) because of climate change. However, previous studies have failed to identify changes in the distribution of current transboundary stocks at the global level, including the actual timeline of shifts in shared stocks, or the intensity of such shifts. Understanding when climate change will affect the sharing dynamics of transboundary stocks and the intensity of the resulting impacts is important for developing climate resilient international ocean governance and achieving the goals set out under the 2030 Agenda (Link et al., 2010; Pinsky et al., 2018; Sumaila et al., 2020; United Nations, 2018).

Here, we apply a mechanistic population dynamic model, driven by outputs from a comprehensive Earth system model with 10 ensemble members, to project transboundary stocks' distribution from 1951 to 2100 across 280 EEZs of 198 coastal countries/political entities under a high greenhouse gas emissions scenario (Methods). We develop a Transboundary Shift Index (TSI) to evaluate range shifts in the shared distribution of transboundary stocks. The index is based on estimated changes in the distance of the stock's abundance centroid and that of the EEZs that share a given stock (Figure 1). Furthermore, we apply the Game Theory concept of *threat point* (Munro, 1979, for its application to fisheries, see Sumaila et al., 2013) to quantify the intensity of changes in the shared distribution of transboundary stocks between neighboring EEZs (Methods). Finally, we discuss the implications of our projection results for the resilient management of transboundary fisheries worldwide.

2 | MATERIALS AND METHODS

2.1 | Databases and species selection

The analyses detailed herein are based on 633 exploited marine transboundary species that account for 80% of the catch taken from the world's EEZs between 2005 and 2014 (Palacios-Abrantes, Reygondeau et al., 2020). We defined a (transboundary) "stock" unit as a species shared between neighboring EEZs (Palacios-Abrantes, Reygondeau et al., 2020; Teh & Sumaila, 2015), resulting in a total of 9132 transboundary stocks. Let us consider the transboundary species Atlantic cod (*Gadus morhua*) as an example to illustrate our approach. Atlantic cod's distribution in the Northwest Atlantic ranges from the United States to Greenland. Based on our definition of a transboundary stock, the United States and Canada share a stock of Atlantic cod, and Canada

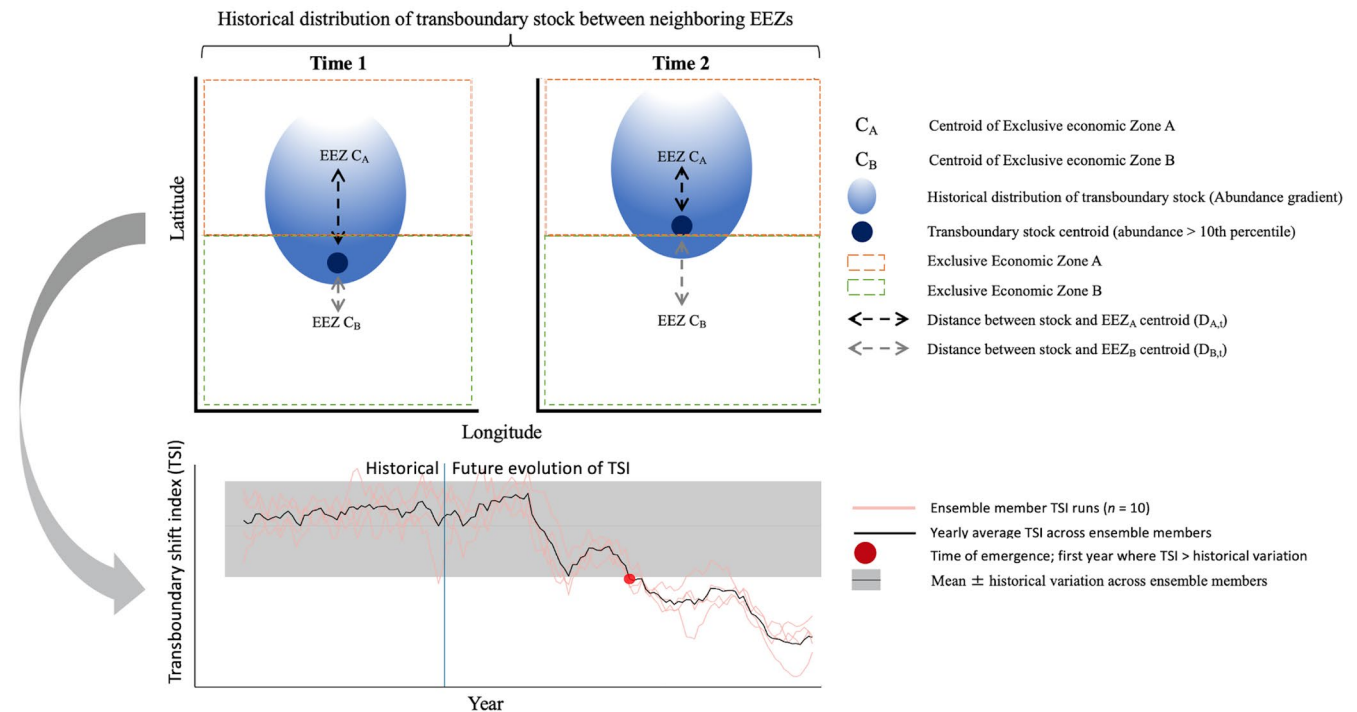


FIGURE 1 Schematic diagram of the transboundary index (TSI) to determine the time of emergence of transboundary stocks from one Exclusive Economic Zone (EEZ) to another. The large blue oval represents the hypothetical distribution range and shape of a shared stock. The index is based on the distance between the distributional centroid of the transboundary stock and the centroid of the neighboring EEZs sharing the stock (Top panel). Time of emergence is defined as the first year when the ensemble mean TSI overshoots historical natural internal variability (Bottom panel). Only showing a subset of ensemble members for clarity in the bottom panel

and Greenland share a separate stock of Atlantic cod, but the United States and Greenland do not share a stock as they do not have juxtaposing EEZs. We defined the boundaries of the world's EEZs using the Sea Around Us spatial division (updated 1 July 2015; <http://www.searoundsus.org>), noting that it subdivides the EEZs of 198 coastal states into 280 regions (Figure S1), including island territories. We determined the intersections between polygons using the R package *sf* (Pebesma, 2018). Each EEZ was categorized by geopolitical region according to the United Nations (<https://population.un.org/wpp/DefinitionOfRegions/>). The habitat preference of each species was determined following FishBase (<http://www.fishbase.org>) for fish species and SeaLifeBase (<https://www.sealifebase.org>) for invertebrates (Table S1). For each stock and EEZ, we used Sea Around Us data to estimate catch and fishing revenue from fishing activities (Sumaila et al., 2015; Tai et al., 2017; Zeller et al., 2016). We report both average catch and revenue for the last available decade (2005–2014).

2.2 | Projecting species distributions under climate change

We projected the future distribution of transboundary stocks using a dynamic bioclimatic envelope model (hereafter called DBEM). The DBEM determines the environmental space a species occupies based on physiology, habitat suitability, depth and latitudinal ranges,

and spatial population dynamics as well as preferences for sea temperature, salinity, oxygen content, bathymetry, and for polar species, sea ice. The DBEM then estimates species' abundance and maximum catch potential (a proxy for maximum sustainable yield) over a regular spatial grid of 0.5° of latitude \times 0.5° of longitude. While we provide an overall description of the model in the followings, further details are provided in Cheung et al. (2009, 2010, 2016, 2021). Importantly, Cheung et al. (2016, 2021) show that the DBEM is able to project catches by EEZ that are consistent with the spatial pattern and interannual variations of observational-based estimates of catch from 1950 to 2016.

For each species, the DBEM uses the Sea Around Us distributional data and environmental variables from 1970 to 2000 to estimate the current distribution and environmental profile of each species. It also projects the future habitat suitability (H_s) in each grid cell (i) according to the following:

$$H_s = P(T_i, TPP) * P(Ba_i, Min_D, Max_D) * P(Hab_{i,u}, Hab_{Assoc}) * (Sal_i, Sal_{Assoc}) * P(Ice_i, Ice_p)$$

where T is the seawater temperature, TPP is the species' temperature profile, Ba_i is the bathymetry, Min_D and Max_D are the species' minimum and maximum depth limits, Hab_i is the proportion of area of the habitat type u relative to the total seawater area of the cell i , Hab_{Assoc} is a habitat association index, Sal is the salinity class of cell i , and Sal_{Assoc} is a salinity

class association index. Finally, for polar regions species, I_{ce} is sea ice extent, and I_{ce_p} is association to sea ice. For pelagic species, the model uses environmental variables at the surface, whereas demersal and benthic species' distributions are driven by ocean bottom variables.

The DBEM also integrates each species' preference profile with physiological principles and population dynamics to project relative biomass, assuming that spatiotemporal dynamics are determined by intrinsic growth rate, larval dispersion, and adult migration:

$$\frac{dA}{dt} = \sum_{j=1}^n (L_{ji} + Ad_{ji} + G_i)$$

where L_{ji} is the settled larvae from surrounding cells (j) to i , Ad_{ji} is the adult migration from gridcell j to i , and G_i is the intrinsic population growth. Larval dispersal through ocean currents is modeled by means of an advection–diffusion–reaction model (O'Connor et al., 2007). G_i estimates intrinsic growth following a logistic equation and the intrinsic rate of population increase (r):

$$G_i = r * A_i * \left(1 - \frac{A_i}{K_i}\right)$$

where K is the carrying capacity of cell i , which varies positively with habitat suitability.

Finally, the DBEM projects maximum catch potential by setting fishing mortality to half of the intrinsic population growth rate of a given target species ($f = r/2$).

In our study, the DBEM was driven by simulated ocean conditions from a 10-ensemble member simulation of the Geophysical Fluid Dynamics Laboratory Earth system model (GFDL-ESM2M) to project the distributions of the 633 species from 1951 to 2100 (Dunne et al., 2012, 2013; Rodgers et al., 2015). The GFDL-ESM2M was run under historical forcing until 2005 and follows a high greenhouse gas emissions scenario, Representative Concentration Pathway 8.5 (RCP 8.5) over the 2006–2100 period (Riahi et al., 2011). Because the main approach of this paper relied on understanding the spatial and temporal variation of a stock's distribution, we sought to understand distribution variability during both historical and future periods, to infer differences between time frames. To this end, each of the 10 GFDL-ESM2M ensembles were started from infinitesimally small differences in Earth system initial conditions in 1951, resulting in a unique atmosphere and ocean state at each point in time after about 3 years for surface and 8 years for subsurface waters (Frölicher et al., 2020). By design, variations among ensemble members are then solely due to natural internal variability (e.g., different phases of the El Niño Southern Oscillation–ENSO).

2.3 | Calculating an index of transboundary range shift

We developed a Transboundary Shift Index (TSI) to evaluate range shifts in the shared distribution of transboundary stocks under

climate change. This index represents the shift in the distribution centroid of a transboundary stock relative to the centroid of the neighboring EEZs that share this stock (Figure 1). The centroid of a transboundary stock (ts) was determined by the average (μ) latitude (lat_{ts}) and longitude (lon_{ts}) across the high abundance grid cells (see below) of the neighboring EEZs sharing the stock. Therefore,

$$lat_{ts} = \mu(lat_{per}); lon_{ts} = \mu(lon_{per})$$

where lat_{per} and lon_{per} are the latitudes and longitudes, respectively, of the grid cells holding a given percentile (per^{th}) of the projected transboundary stock abundance in the historical time period (th). Fish stocks are not evenly distributed across their entire range, and we focused on areas where transboundary stocks are more abundant and consequently fishing activities more likely to take place. Thus, we estimated the centroid of a stock by only including grid cells where the projected stock abundance across neighboring EEZs sharing the stock was above the 95th percentile. A sensitivity analysis using a subset of species ($n = 34$) for all EEZs to examine the effects of different thresholds ($per = 20^{th}, 50^{th},$ and 90^{th} percentiles) on the calculated index value showed no apparent difference across percentiles (Figure S2). The centroid of each EEZ was estimated using the `st` package in R (Figure S1). For each ensemble member, neighboring EEZs, and transboundary stock, we computed the distance between centroids (i.e., distance between the fixed centroid of the EEZs and the mobile centroid of the transboundary stock; D_{ens}) using the `geosphere` package in R (Hijmans, 2021), assuming the Earth is a perfect sphere and ignoring geographic barriers:

$$D_{ens} = \text{acos}(\sin(lat_{eez}) * \sin(lat_{ts}) + \cos(lat_{eez}) * \cos(lat_{ts}) * \cos(lon_{eez} - lon_{ts}))$$

where lat_{eez} and lat_{ts} are the latitudes of the EEZ and transboundary stock centroids, respectively, and lon_{eez} and lon_{ts} are associated longitudes. Then, for each year between 1951 and 2100 and for each ensemble member, we calculated the transboundary index (TSI) as follows:

$$TSI = \left(\frac{D_{A,t}}{sd(D_{A,th})} - \frac{D_{B,t}}{sd(D_{B,th})} \right)^2$$

where D_A and D_B represent the distance between the distribution centroids of a stock and the centroid of the neighboring EEZs (A and B) sharing the stock for each time step from 2006 to 2100 (t); and SD is the standard deviation of the historical (th , 1951–2005) centroid distribution for D_A and D_B . The TSI was smoothed to a 10-year average to reduce interannual variability (Frölicher et al., 2016) and to match transboundary fisheries management that tends to operate over longer timeframes.

2.4 | Calculating shifts in the shared distribution of transboundary stocks

Knowing the point in time at which the distribution of a shared stock will diverge from historical natural variability is important to inform

decision-makers by when, ideally, climate adaptation plans will need to have been implemented (Link et al., 2010). To that end, we adopted the concept of time of emergence (ToE), commonly applied to multiple oceanic physical and biogeochemical variables (Frölicher et al., 2016; Henson et al., 2017; Keller et al., 2014; Rodgers et al., 2015; Schlunegger et al., 2019, 2020; Trisos et al., 2020) and defined as the moment in time when a signal (e.g., future anthropogenic trend) emerges from the background noise of natural variability (i.e., historical natural variability) (Hawkins & Sutton, 2012). The premise behind the time of emergence concept is that we can only be confident that a significant change has been detected when the signal of anthropogenic climate change is larger than the background noise of natural climate variability (Hawkins & Sutton, 2012). The TSI's historical natural variability was estimated from the ensemble members by first averaging the TSI from 1951 to 2005 (TSI_{μ}) and then estimating the variation (TSI_{σ}) across ensemble members. The TSI signal consisted in the average TSI across ensemble members from 2006 to 2100 ($TSI_{f,\mu}$). Additionally, we set a threshold (*thresh*) relative to TSI_{μ} and TSI_{σ} to define the time (t') of emergence of individual transboundary stocks (see Figure 1 for a graphical description):

$$\text{ToE} = TSI_{f,\mu} [t'] > \text{thresh}$$

This way we defined a shift in a stock's shared distribution (i.e., time of emergence) as the first year the $TSI_{f,\mu}$ "emerged" from historical natural variability (i.e., overshooting the *thresh*). It assumes that, from a fisheries' perspective, the first year a stock's distribution shifts from a 10-year average warrants caution. Two different arbitrary values of *thresh* were used. A conservative value ($\text{thresh} = TSI_{\mu} \pm 2TSI_{\sigma}$), representing a 95% probability that the index has emerged from historical natural variability and a more relaxed value ($\text{thresh} = TSI_{\mu} \pm TSI_{\sigma}$) for a 67% probability.

Since the ToE method was sensitive to the noise estimate (i.e., historical natural variability), we undertook a sensitivity analysis where we calculated the average across the 10 ensemble members for each year between 1951 and 2005 and the standard deviation from 1950 to 2005. Using this method, the historical natural variability was slightly larger resulting in a later overall time of emergence (average ToE = 2057 vs 2036 using the method described above). However, this alternative method projected 1139 more emerging stocks (5258 stocks vs 4119 using the original approach). The minimum and maximum ToE remained the same, and the number of EEZs with emerging stocks increased slightly under the alternative method. Further research looking into different approaches to estimate natural internal variability could help reduce the uncertainty around the estimation of time of emergence of transboundary stocks.

2.5 | Quantifying the intensity of transboundary stocks' range shift

Here, we adopted the concept of threat point to quantify the intensity of changes in the shared distribution of transboundary stocks

between neighboring EEZs. The concept of threat point comes from Game Theory and has been widely used in shared fisheries management (Bailey et al., 2010; Clark & Munro, 1975; Munro, 1979; Sumaila, 2013; Sumaila et al., 2020). In a game theoretic model, a player's strategy (e.g., to act cooperatively or not) will have direct consequences for other players, which, in turn, will affect the overall outcome of the game (Bailey et al., 2010). Cooperation will often result in the maximization of benefits for the system rather than for individual players. However, for a cooperative strategy to work, the benefit a player gets must not be less than the benefit under a non-cooperative strategy. Thus, the "threat point" is defined as the minimum payoff a player is willing to receive to cooperate in a game-theoretic model (Nash, 1953). We defined the threat point as the minimum catch proportion a transboundary stock had over the historical natural variability period within an EEZ, assuming this was required for a country to engage in cooperative management with their stock-sharing neighbor (Palacios-Abrantes, Sumaila et al., 2020; Sumaila et al., 2020). Any proportion below the defined threat point would result in the unilateral management of the stock, assuming that no country would be willing to engage in cooperative management if the future catch proportion of the transboundary stock was lower than it had ever been.

For each transboundary stock, we first estimated the proportion of the catch (hereafter referred to as stock share ratio; SSR) within each neighboring EEZ for each year between 1951 and 2100. To this end, we aggregated the projected catch within the 0.5° of latitude \times 0.5° of longitude grid cells in which the stock was present across neighboring EEZs, and then calculated the proportion of the stock's catch held within each EEZ (Palacios-Abrantes, Sumaila et al., 2020). In other words, if Canada were to hold a 20% and the United States 80% SSR of a shared stock in any given year, this would mean that Canada holds 20% of the catch of the shared stock. Second, to reduce the effects of temporal variability, we averaged the calculated proportion of stock occupying a given EEZ into three time periods: the historical time period (SSR_{th}) from 1951 to 2005, and two future periods, the early 21st century, between 2021 and 2040 (SSR_{te}), and mid 21st century, defined as the average of 2041 to 2060 (SSR_{tm}). These future time periods were chosen to correspond to the challenges of achieving fisheries-relevant UN-SDGs by 2030 (i.e., the 2030 Agenda), such as "SDG 14.4 (end overfishing), SDG 2.4 (ensure sustainable food production systems), and SDG 1.2 (poverty reduction)" (Singh et al., 2017; United Nations, 2020). The analysis was replicated for projected stock distributions from each of the 10 ensemble members and results were averaged across ensemble members. Third, we defined a threat point for each EEZ's stock as $SSR_{th} \pm 2\sigma$, where σ represents the standard deviation of SSR_{th} . Thus, a change in the SSR beyond an EEZ's threat point happens when the future SSR exceeds two standard deviations of historical natural variability in SSR (i.e., when $SSR_{te} \geq (SSR_{th} + 2\sigma)$ or $SSR_{te} \leq (SSR_{th} - 2\sigma)$). Finally, we estimated the percentage change in SSR (ΔSSR) of each future time period (SSR_{tf}) relative to the historic time period SSR_{th} for each stock whose share ratio exceeded the threat point (s) according to the following (Palacios-Abrantes, Reygondeau et al., 2020):

$$\Delta SSR_s = \frac{(SSR_{tf} - SSR_{th})}{SSR_{th}} * 100$$

A list of acronyms used in the equations and their definitions is shown in Table S2.

2.6 | Statistical analysis

We tested results for normality (e.g., skewness, kurtosis) and performed two nonparametric Kruskal–Wallis tests by ranks (Hollander & Wolfe, 2013) to investigate geopolitical and ecological differences in the range shift of transboundary stocks. Specifically, we tested whether the habitat preference of transboundary species and the geographic location of EEZs would have any effect on the distributional range shift of transboundary stocks. In both cases, our null hypothesis was that there would be no significant differences in the year of shift across habitat associations or EEZs' geographic location. All analyses were run using the statistical software R (R Core Team, 2021) versions 3.5.2 (2018-12-20; Eggshell Igloo) and 4.1.0 (2021-05-18; Camp Pontanezen) with the packages cowplot (Wilke, 2019), data.table (Dowle et al., 2019), ggrepel (Slowikowski, 2020), gmt (Magnusson, 2017), janitor (Firke et al., 2018), moments (Komsta & Novomestky, 2015), pgirmess (Giraudoux, 2018), rfishbase (Boettiger et al., 2019), sp (Pebesma et al., 2019), tidiverse (Wickham, 2017), tidytext (De Queiroz et al., 2019), viridis (Garnier, 2018), wesanderson (Ram & Wickham, 2018), zealot (Teetor, 2018), and zoo (Zeileis et al., 2019). Code and data are available at <https://github.com/jepa/EmergingFish>.

3 | RESULTS

3.1 | Identifying range shifts in the shared distribution of transboundary stocks

Our results suggest that 4119 transboundary stocks will experience a range shift beyond historical natural variability by 2100 (hereafter referred to as "shifts"; Figure 2a), using a two SD threshold (i.e., representing a probability of 95% that the stock has shifted). This corresponds to 45% of studied stocks (Figure 2c). Using a less conservative threshold (i.e., one SD representing a probability of 67% that the stock has shifted) results in 18% ($n = 5745$) more shifting stocks, that is, 63% of all studied stocks (Figure S3). In both cases, our projections show the first shift to have occurred in 2006. The average year of shift in the shared distribution of these transboundary stocks across all EEZs analyzed is projected to be between 2029 ± 27 years (one SD threshold) and 2036 ± 28 years (two SD threshold). Findings also indicate that between 83% and 81% of the world's EEZs will experience at least one transboundary stock shift by 2100 with 80% to 77% of EEZs recording a distributional stock shift by the UN 2030 Agenda's deadline, under one and two thresholds, respectively (Figure 2c).

The median year in which transboundary stocks are projected to experience a range shift varied significantly according to species' habitat association (Methods; Kruskal–Wallis, $X^2 = 203.85$, $DF = 93$, $p < 0.001$; using the 2 SD threshold; Tables S1, S3 and Figure S4) and EEZs' geographic regions (Methods; Kruskal–Wallis, $X^2 = 242.11$, $DF = 93$, $p < 0.001$; using the 2 SD threshold; Table S4 and Figure 3a). Overall, most tropical EEZs and stocks are projected to see earlier

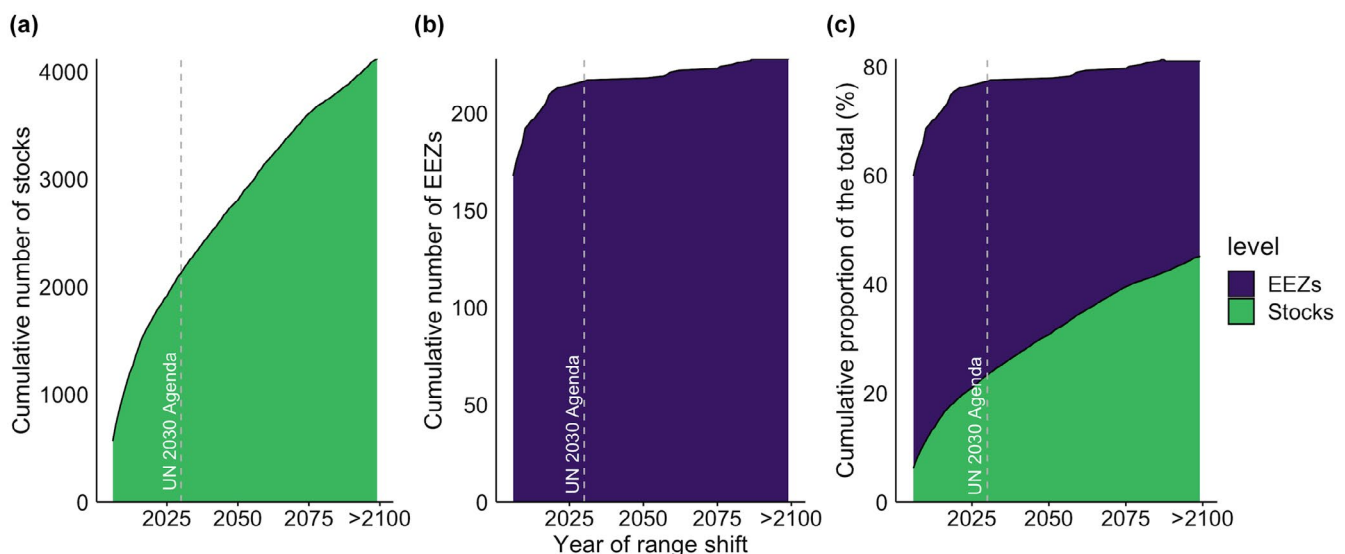


FIGURE 2 Timeline of projected shifts in transboundary shared stocks' distribution using a two SD threshold. (a) Number of stocks (cumulative) whose distribution centroids show shifts beyond historical natural variability over time (from 2006 to >2100), (b) Number of EEZs (cumulative) for which the distribution centroid of at least one stock that has shifted beyond historical natural variation between 2006 and >2100, and (c) proportion of total number of shifting stocks and EEZs with at least one stock shifting beyond historical natural variability. The dashed lines represent the year by which countries have committed to reach full implementation of the 2030 Agenda

shifts, with the EEZs of Latin America, the Caribbean, Melanesia, and Polynesia set to experience shifts significantly earlier ($p < 0.05$; Table S4) than almost any other region (Figure 3b, Figures S5 and S6). In contrast, EEZs and stocks located in temperate regions, like northern Europe and eastern Asia, are projected to experience later range shifts. Stocks in some EEZs, like Brazil's, are projected to experience no range shifts beyond the historical natural variability by the end of this century (Figure 3a), while others, like New Zealand's, are

only projected to have shifting stocks under the one SD threshold (Figure 3a and Figure S3).

We estimated the proportion of shifting transboundary stocks between neighboring EEZs relative to the total revenue derived from all transboundary stocks within each EEZ. Findings show that, on average, shifting transboundary stocks represent 27% to 23% (one and two SD thresholds) of annual revenue from fisheries targeting transboundary stocks across the world's EEZs (Figure 3a and Figure

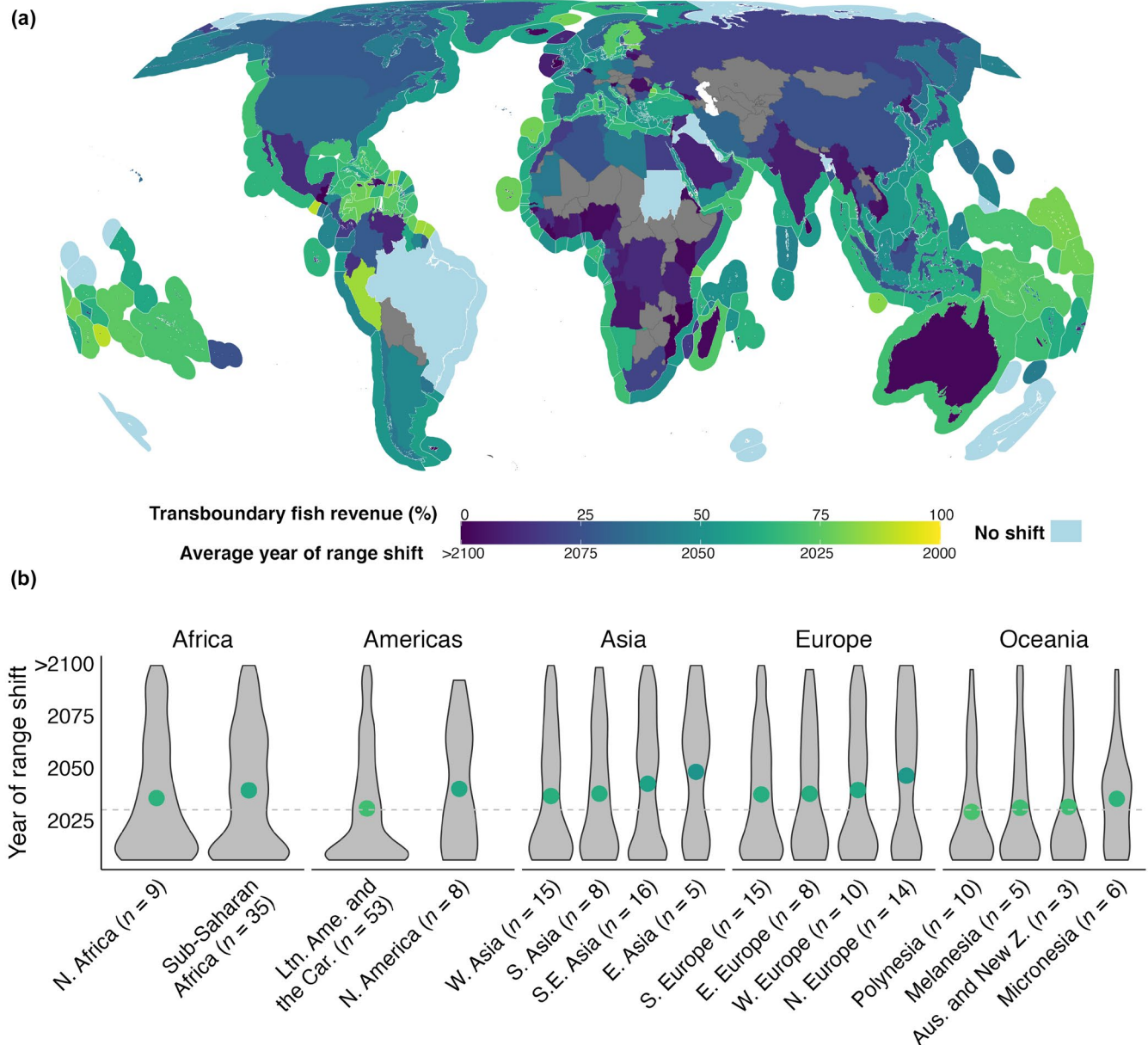


FIGURE 3 Mean year of change in the shared distribution of 4119 transboundary stocks using a two SD threshold. (a) Land polygons show the contribution of shifting stocks to a country or territory's total fishing revenue from transboundary stocks. Exclusive Economic Zone polygons display mean year of range shifts within them. Warm colors are indicative of an early shift/high fishing revenue contribution from transboundary stocks, while cool colors represent a late shift/low fishing revenue. EEZs with no distributional shifts between 2006 and 2100 are represented in pale blue. See Figure S5. for a figure highlighting results for land and EEZs separately and Figure S6 for an enlarged view of the Caribbean and Pacific Islands. (b) Mean year of range shifts in the distribution of shared stocks by UN sub-regions. Points are color coded by the mean year for all shifting stocks in each region. The horizontal dashed line represents the year by which countries have committed to reach full implementation of the 2030 Agenda. N = North, S = South, W = West and E = East. Ltn. Ame. and the Car. = Latin America and the Caribbean. Aus. and New Z. = Australia and New Zealand

S4). However, large variations exist, with shifting stocks accounting for less than 1% of fishing revenue in some countries (e.g., Ireland) and over 90% in others (e.g., Marshall Islands). Moreover, in some EEZs, while few transboundary stocks are projected to shift beyond historical natural variability, they still represent a large proportion of revenue derived from fisheries within that EEZ (e.g., Peru).

While the total number of shifting stocks is important for fisheries management, having more valuable stocks shifting sooner could represent a much bigger concern than having many low-value stocks shifting their distribution. Thus, we looked at the year of range shift of the top five most valuable transboundary stocks for each country (Figure 4). On average, countries are projected to see a range shift of the top five most valuable stocks by 2038 ± 25 years under a two SD threshold (2028 ± 22 years under a one SD threshold). Moreover, our projections suggest that some of these high-value stocks are already shifting in 129 (66%) coastal nations' EEZs under a two SD threshold ($n = 154$, 79% under a one SD threshold), with Latin America and the Caribbean ($n = 62$), Sub-Saharan Africa ($n = 36$), Polynesia ($n = 22$), and Southern Europe ($n = 19$) being home to the greatest number of shifting high-value stocks (and together accounting for 50% of shifting high-value stocks around the world).

3.2 | Shifting intensity of transboundary stocks

We estimated the intensity of the distributional shift of transboundary stocks in terms of changes in catch proportion by 2030 (2020–2040) and 2050 (2040–2060), relative to the historic time period (1951–2005) (see Methods). Projections show that by 2030, $59\% \pm 17\%$ of the yearly catch from transboundary stocks will have changed beyond

the historical natural variability experienced within an EEZ (Figure 5). Moreover, 85% ($n = 239$) of the world's EEZs will have experienced changes in catch proportion of transboundary stocks by 2030. By 2050, the number of EEZs with changing stocks, as well as the number of stocks experiencing changes in catch proportion and the magnitude of that change, will have increased (Figures S7 and S8). The direction and intensity of shifts in transboundary stocks are largely related to regional changes in biogeography and the geometry of EEZs (Figure 5 and Figure S9). For example, along the Atlantic and Pacific coasts of Northern and Southern America and the Atlantic coast of Southern Africa, shifts in stocks are expected to benefit poleward EEZs. However, shifts along the coasts of Pacific Central America and West Africa occur in an equatorial direction.

Most EEZs are expected to see a relatively small number of stocks shifting in their SSR (Figure 5). We project an average $16\% \pm 10\%$ of transboundary stocks to registering changes in their SSR between EEZs by 2030, with that number increasing by 2050. However, this result masks large variations in changes across EEZs. By 2030, the EEZs of French Guiana (54%), South Africa (59%), Islas Malvinas (Falkland Isl.) (61%), Brazil (75%), as well as Kerguelen and Pitcairn Islands (both 100%) are projected to see changes in SSR of over 50% in their transboundary stocks. On the other hand, some island territories such as Anguilla are projected to see changes in as low as 2% of their transboundary stocks.

Shifts in the SSR of the top five most valuable transboundary stocks of each country are projected to reach $65\% \pm 21\%$ by 2030 and $78\% \pm 18\%$ by 2050 in 77% of the world's EEZs (Figure S10). In some cases, the SSR of one EEZ is projected to more than double relative to neighboring EEZs (e.g., from 10% to 30% SSR). Examples include Guatemala gaining in SSR from Mexico in the Pacific, Mozambique from Madagascar, and Russia from Norway and Japan in the Barents Sea (Figure S10).

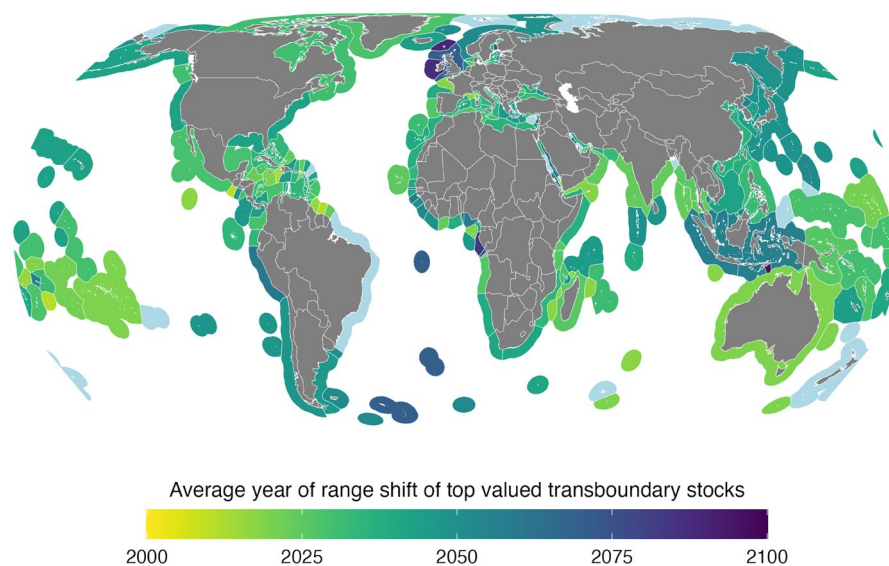


FIGURE 4 Mean year of change in the shared distribution of individual countries' top five most valuable transboundary stocks, using a two SD threshold. Warm colors are indicative of an early shift, while cool colors represent a late shift. EEZs with no distributional shift between 2006 and 2100 are represented in pale blue

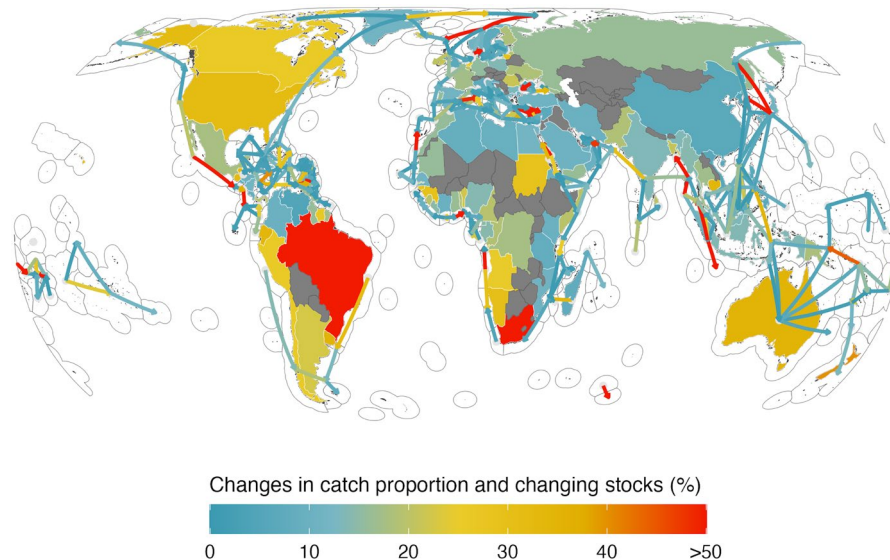


FIGURE 5 Changes in stock proportion of neighboring Exclusive Economic Zones by 2030 (2021–2040) relative to 1951–2005. Lines represent the average change in transboundary stock share ratio (SSR; Methods) with arrows going from EEZs with projected decreases in stock share (point) to those gaining shares (arrowhead). Land polygons depict the percentage of stocks that are projected to change their stock share ratio beyond the identified threat point (i.e., over two standard deviations from historical catch proportions). For both lines and land polygons, warmer colors denote higher gains

4 | DISCUSSION

4.1 | High present-day climate risk for transboundary fisheries

Our findings highlighting early shifts in the shared distribution of transboundary stocks concur with previous studies that have detected changes in marine catch composition and attributed these to climate change (e.g. Cheung et al., 2013; Frainer et al., 2017; Last et al., 2011). For example, in the early 2000s, Humboldt squid (*Dosidicus gigas*) substantially expanded its geographic range poleward, reaching the coast of Washington state (US), in response to climatic, and associated oceanographic and ecological changes (Zeidberg & Robison, 2007). A new fishery targeting Humboldt squid quickly developed on the heels of the species' range expansion (Pinsky & Mantua, 2014). In the northeast Atlantic, fisheries on Atlantic mackerel (*Scomber scombrus*) are multilaterally managed by the European Union (EU), Norway, Iceland, Russia, and Denmark (on behalf of the Faroe Islands and Greenland) through the North-East Atlantic Fisheries Commission (NEAFC). However, a range expansion due to environmental variations of Atlantic mackerel into Icelandic waters in 2007 resulted in Iceland capturing 6% of the fishery's total allowable catch and a further 18% in 2008, without consultation with NEAFC, threatening the sustainability of the stock (Spijkers & Boonstra, 2017). These changes resulted in disputes between Iceland and the Faroe Islands, as well as among NEAFC member states (Spijkers & Boonstra, 2017). Other documented cases of early range expansions across international jurisdictions have also been documented for multiple stocks along the European Union's regulatory areas (Baudron et al., 2020), the Benguela Current (Potts et al., 2014; Yemane et al., 2014), and the southwest South Atlantic Ocean

(Franco et al., 2020). Despite these documented cases, broadly speaking, there is a lack of information and data regarding which and how many transboundary stocks are shifting, where they are shifting to and whether they are jointly managed. Such knowledge is particularly important to inform international fisheries management, as modeling exercises project that climate change will continue to alter the distribution of transboundary stocks to the point that some tropical EEZs stand to lose them completely (Oremus et al., 2020) while other EEZs, mainly at higher latitudes, will win new stocks (Pinsky et al., 2018).

4.2 | Climate risk hotspots for transboundary fisheries management

The SDG target 17.16 (“Enhance the global partnership for sustainable development”) calls for multi-stakeholder partnerships to support the achievement of the SDGs in all countries, with a particular focus on developing countries (United Nations, 2020). Such collaborations, which include the mobilization and sharing of knowledge, expertise, technologies, and financial resources will be critical if we are to sustainably manage transboundary fisheries under climate change (Miller et al., 2013; Oremus et al., 2020; Pinsky et al., 2018). Our results identify regional “hotspots” of climate risk for transboundary fisheries management that will require the prompt adaptation of collaborative management plans (Figures 3a and 5). Regions such as the Caribbean are characterized by high levels of warming relative to historical natural variability (Hawkins & Sutton, 2012; IPCC, 2019) and species' high vulnerability to warming waters (CRFM, 2019; IPCC, 2019). Moreover, such regions encompass a large number of relatively small EEZs that border multiple

countries. Game theory predicts that the greater the number of negotiating parties, the harder it is for parties to reach an agreement (Gronbaek et al., 2020). Thus, coordinating the management of shifting transboundary stocks for countries in these regions will be particularly challenging (Gentner, 2016), yet necessary. Hopeful examples of what is possible include current arrangements under multistate groups such as the Parties to the Nauru Agreement (PNA), the EU Common Fisheries Policy (EU-CFP) and the numerous Regional Fisheries Management Organizations that are currently active.

Most management plans that are not designed or prepared to respond to range and abundance shifts will be less resilient to climate change (Bryndum-Buchholz et al., 2021; Koubrak & VanderZwaag, 2020; Miller et al., 2013; Sumbly et al., 2021). Focusing on identified “hotspots” will help anticipate any potential increases in and avert fisheries conflicts in coming years. Identified strategies to adapt to changes in the shared proportion of transboundary stocks include strengthening of current cooperative mechanisms and the consideration of side payments (including non-monetary arrangements) (Miller et al., 2013; Tunca, 2019), strengthened international cooperation (Mendenhall et al., 2020) and management rules that capture distributional shifts (Palacios-Abrantes, Reygondeau et al., 2020; Pinsky et al., 2018). Examples of existing agreements that have adapted some of these strategies include the following: the Pacific Salmon Treaty between Canada and the United States to manage Pacific salmon (*Oncorhynchus* sp.) and which has a conservation fund functioning as a side payment (Miller et al., 2013; PSC, 2020), the International Pacific Halibut Commission between Canada and the United States, which as the name implies manages Pacific halibut (*Hippoglossus stenolepis*) and allocates quota based on the stock's yearly distribution (IPHC, 2019; Palacios-Abrantes, Reygondeau et al., 2020); and the Parties to the Nauru Agreement (PNA), an agreement among 8 Pacific Island countries and Tokelau, which collectively manage the largest tuna fishery in the world (Aqorau, 2015; PNA, 2019, 2021), controlling around 50% of the global supply of skipjack tuna (*Katsuwonus pelamis*). Specifically, the PNA manages fishing effort under the so-called Vessel Day Scheme, an adaptive and equitable system which accounts for shifts in stocks and catches as a result of climate variability (Aqorau et al., 2018; Bahri et al., 2021). Quota allocation methods based on a stock's current distribution and/or according to fixed-historical proportions like that of the EU-CFP need to evolve to be more agile (Baudron et al., 2020) and potentially move toward a dynamic method or a combination of both (Palacios-Abrantes, Reygondeau et al., 2020; Sumaila et al., 2020). Such transition will require revision of current frameworks and negotiations between stakeholders to determine a new allocation formula from a full distribution-based system—such as for Pacific halibut—or a combination of both—as suggested for cod in the Gulf of Maine (IPHC, 2019; TRAC, 2016). In some cases, rules will need to be implemented to deal with newcomers or to establish management boundaries. However, the transition from historic to dynamic allocations can encounter strong resistance

from stakeholders “losing” benefits from a fishery they have historically been entitled to. Further research and documentation on how to move toward inclusive dynamic management (i.e., allocation formula, conflict management) is key to adapt and build resilience in transboundary fisheries management to shifting stocks.

Yet, even management plans that take into consideration such strategies might not be fully prepared for the consequences of shifting transboundary stocks (Engler, 2020; Koubrak & VanderZwaag, 2020; Pinsky et al., 2018). For example, species' shifts within the PNA area will likely also have to deal with stocks expanding to new jurisdictions, an issue that the NEAFC is currently facing regarding Atlantic mackerel (Pinsky et al., 2018; Spijkers & Boonstra, 2017). Moreover, changes in policy can be sluggish (e.g., it took the Pacific Salmon Treaty about 10 years to agree on a conservation fund) compared to the timeframe over which species shift (Pinsky & Fogarty, 2012). This point is all the more salient given that in many cases we lack standardized data to track shifts of species across international jurisdictions (Maureaud et al., 2021) and that these might already be happening. Recent efforts looking at 127 international fisheries plans found that most were not species specific, and that all lacked direct actions to address topics of climate change or species' range shifts across jurisdictions (Oremus et al., 2020). Having a better understanding of what stocks are managed as transboundary and under what rules would be an important complement to our study and an important step toward the sustainability of international stocks.

4.3 | Potential drivers of shifts and managing an uncertain future

Projected range shifts by 2030 of a large number of transboundary stocks can be partially attributed to the parallel global emergence of several ocean variables from historical natural variability. For example, sea surface temperature (SST) is projected to increase beyond historical natural variability by 2030 across 50%–70% of the global ocean (Frölicher et al., 2016; Mahlstein et al., 2011; Rodgers et al., 2015). Results from multiple marine ecosystem models show that SST and primary production (NPP) are the main indicators of species' distributional changes across ocean basins (Bryndum-Buchholz et al., 2019; Lotze et al., 2019). Specifically, in the species distribution model used here (see methods), SST is the main environmental driver of biomass changes in polar, tropical, and upwelling ecosystems, while NPP drives temperate regions' results (Heneghan et al., 2021). The combination of the SST emergence pattern and model characteristics could be partially responsible for the early distributional shift of transboundary stocks in the tropics, where marine species live close to their thermal tolerance, making them highly vulnerable to warming waters (IPCC, 2019), while also explaining the later, and sometimes non-existent, shifts at higher latitudes (Figure 3b).

Different levels of uncertainty exist around the projected emergence of environmental variables that are mainly related

to (i) climate change scenarios and (ii) model structure (Frölicher et al., 2016). First, our analysis is based on a high emissions climate change scenario (RCP 8.5), which translates into an “extreme” case of shifts in the shared distribution of transboundary stocks. Thus, mitigation efforts could result in substantial delays in projected distribution shifts as environmental signals are responsive to mitigation, at least after the middle of the 21st century (Frölicher et al., 2016). Second, a substantial source of uncertainty is related to model selection for both climate change and fish distribution. This is specifically important for early time periods (e.g., 2016–2035) where the uncertainty related to ESM selection, including the parameterization of poorly understood processes that regulate NPP changes, is often larger than the uncertainty stemming from the climate change scenario (Frölicher et al., 2016). While such uncertainty could potentially be reduced by incorporating ensemble simulations from a range of different ESMs, these are computationally expensive simulations (Frölicher et al., 2009, 2016; Rodgers et al., 2015) that are only just becoming available (Deser et al., 2020) and cannot address limitations of process-level understanding. It is unlikely that these complex uncertainties will adequately be addressed in the coming decade. Therefore, decision-makers are confronted with the challenge of having to take action in the face of an uncertain future. One strategy to address some of this uncertainty is to adapt and integrate scenario planning into fisheries management (Frens & Morrison, 2020). In developing a response using such an approach to adapt to expected shifts in stock distribution by 2036 ± 28 years (Figure 2), managers might want to consider, for example, a scenario based around where stocks are currently shifting and another that integrates where they are projected to shift in 20 years. Scenario planning can also be used to estimate potential losses in revenue when adaptation to climate change is not developed cooperatively (Miller et al., 2013; Sumaila et al., 2020). This is critical for the tropics, where the shared distribution of transboundary stocks is expected to shift first, and the response of the base of the food web to climate change is most uncertain (Kwiatkowski et al., 2020; Tagliabue et al., 2020).

These uncertainties also affect projections of species' distributions (Bryndum-Buchholz et al., 2019; Heneghan et al., 2021; Lotze et al., 2019). Overall, multiple upper trophic level models present broad agreement in terms of directional change in fish biomass, but there is considerable variability in the magnitude of that change (Lotze et al., 2019). Further research that reduces uncertainty in the NPP response at the base of ocean food webs, alongside large ensemble simulations of multiple species distribution models could lead to smaller structural uncertainty of fish and fisheries models (Bryndum-Buchholz et al., 2019). Another important source of uncertainty in this study is the utilization of political boundaries (EEZs) to define stocks, rather than biologically defined populations. While such an approach might define some stocks that do not necessarily align with biologically defined sub-populations within an EEZ, in many EEZs, fisheries are often managed at the species level (e.g., MAP, 2017) and sub-populations

are potentially interconnected (Ramesh et al., 2019), providing additional ecological ground for our analysis (Dunn et al., 2019). Moreover, the population structure of most exploited species in the world are poorly defined or undefined (Begg et al., 1999; Moore et al., 2020). Future studies that focus on particular shared stocks might want to use a more specific unit stock definition. Reproducing our analysis regionally, where spatially explicit stock data are available, would generate better constrained results and potentially identify different types of shared stock shifts at a meta-population level (Archambault et al., 2016; Link et al., 2010). Addressing these uncertainties systematically can serve as a roadmap for future studies to provide additional information to inform policy toward sustainable and equitable international fisheries management under climate change.

5 | CONCLUSION

The global community has set the ambitious goal of managing all fisheries sustainably (SDG 14—“Life below water”) by 2030. Achieving this goal would have clear benefits for several other societal goals (Singh et al., 2017; United Nations, 2018). Developing anticipatory policies to deal with shifting transboundary stocks is key to achieving the SDGs and ensuring effective governance of the world's fisheries (Oremus et al., 2020; Pecl et al., 2017; Pinsky et al., 2018). Here, we developed an approach to inform the sustainable management and governance of transboundary fisheries in a changing world. First, we identified the transboundary stocks that would likely see shifts in their shared distribution compared to their historical natural variability and the year in which such shifts would occur. Second, we estimated the intensity of such change. While future studies, specifically at more localized scales, will provide valuable nuance in designing effective policies, our results offer an important baseline on which to build when preparing ocean governance for shifting transboundary stocks (Palacios-Abrantes, Sumaila et al., 2020; Pinsky et al., 2018). Our findings emphasize recent calls for the urgent adoption of measures in support of more adaptive, equitable and flexible fisheries management and ocean governance to support resilient fisheries and durable management systems (Oremus et al., 2020; Pinsky et al., 2018, 2020).

ACKNOWLEDGMENTS

We thank T. Clarke, L. Kwong, and A. Tidd for helpful comments on earlier versions of the manuscript as well as figures. We also thank M. Abas and I. da Mata Oliveira for helping with the translation of the Spanish and Portuguese abstracts.

DATA AVAILABILITY STATEMENT

All primary data generated by this project can be found at the Scholars Portal Dataverse (<https://doi.org/10.5683/SP3/TMPEHR>). Secondary data-sources and reproducibility code can be found on GitHub (<https://github.com/jepa/EmergingFish>).

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How to cite this article: Palacios-Abrantes, J., Frölicher, T. L., Reygondeau, G., Sumaila, U. R., Tagliabue, A., Wabnitz, C. C., & Cheung, W. W. L. (2022). Timing and magnitude of climate-driven range shifts in transboundary fish stocks challenge their management. *Global Change Biology*, 28, 2312–2326. <https://doi.org/10.1111/gcb.16058>