Ocean warming drives abrupt declines in fish productivity at global scale

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Abstract

Marine life is under multiple pressures, including climate change and overfishing. Environmental change and variability can threaten fishery sustainability, especially when it results in large, abrupt and persistent shifts in productivity of fish stocks. Reports of abrupt shifts in marine systems are not uncommon, but a global assessment of their occurrence and drivers is seriously lacking. Here, we systematically classified the temporal dynamics of fish stock productivity from agency-assessed fisheries worldwide. Among the 315 fish stocks with time series available, we detected at least one productivity abrupt shift for more than a quarter of the stocks. Using an integrative modeling approach including life history, environmental conditions, and fishing intensity variables, we showed that abrupt declines are over-represented in stocks where sea surface temperature increases have been larger during the period covered by fish stock monitoring, while abrupt increases are more likely under lower fishing intensity. We investigated the link between productivity abrupt shifts and stock collapses. We found that abrupt declines in productivity preceded stock collapses by ten to twenty years in 25% of the cases, suggesting that some major stock collapses could be anticipated if abrupt shift were more systematically detected and examined. Overall, our results highlight the importance of considering productivity abrupt shifts to prevent a pervasive risk of fish population collapse in warming oceans.

Significance Statement

Using the largest global stock assessment dataset for marine fisheries, we found a large proportion of abrupt shifts in the trajectories of productivity time series for 315 fish stocks. We evidenced that abrupt productivity declines were over-represented in marine regions with highest warming rates. We also demonstrate that abrupt productivity declines preceded stock collapses by about a decade in a quarter of the stocks that shifted. Our results shed light on a likely warming-related timeline to fisheries collapse and call for more systematic examination and early detection of abrupt shifts. This paper contributes to setting priorities in managing stocks that would be more likely to undergo strong and persistent shifts in their productivity.

Keywords: abrupt shift, fisheries, nonlinear dynamics, stock assessment, warming temperatures

Introduction

Marine ecosystems are facing intense anthropogenic pressure (Georgian et al., 2022; Halpern et al., 2008), putting the survival of marine species along with the food security and economies of many coastal human populations at risk (FAO, 2022). Although the capture of wild fish from the oceans has been maintained at high levels since its peak in the 1990s (Pauly and Zeller, 2016), it does not imply that all stocks are sustainably exploited (FAO, 2022). Indeed, despite the overall success of some management strategies (Frank and Oremus, 2023; Melnychuk et al., 2021), overexploitation and stock collapses are still major threats (Georgian et al., 2022) with no guarantee that recent improvements in fishery sustainability (Hilborn et al., 2020) can be maintained in the face of climate change.

One particular challenge for fisheries management is the ability to avoid abrupt, strong, and persistent declines of exploited stocks, which undermine sustainability goals (King et al., 2015; Levin and Möllmann, 2015). Even though the existence of such so-called “regime shifts” in fisheries has long been documented (deYoung et al., 2004; Hare and Mantua, 2000; Steele, 1998), such events have yet to be broadly integrated within stock assessment and management (Conversi et al., 2015; Sguotti et al., 2022). Regime shifts are usually considered at the ecosystem level involving the synchronous change in multiple variables from fish to phytoplankton (deYoung et al., 2008). But it has been argued that abrupt shifts at the level of fish populations could be indicative of putative regime shifts (Daskalov et al., 2007; Pedersen et al., 2020). In fisheries, examples of once plentiful stocks that crashed to very low levels are not uncommon, notably with the case of the Peruvian anchoveta (Idyll, 1973), North Atlantic cod (Myers et al., 1997), or Western Atlantic bluefin tuna (Safina and Klinger, 2008). However, beyond these emblematic examples the extent to which regime shifts in fisheries occurred in recent decades might be underestimated.

Accounting for regime shifts within fisheries management can be hindered by two major knowledge gaps. First, they are hard to detect. The search for regime shifts in time series often relies on the sole use of breakpoint detection algorithms without relevant alternative non-abrupt models (Spake et al., 2022), which can limit the confidence in the conclusions (Rudnick and Davis, 2003). Second, regime shifts are overlooked in most stock assessments,despite evidence that regime shift models are frequently a better descriptor of stock dynamics (Vert-pre et al., 2013). Attempts to account for regime shifts and non-stationarity remain

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scarce and insufficient to improve current practices (Levin and Möllmann, 2015; Sguotti et al., 2022). Instead, the usual standard for evaluating the sustainability of management strategies relies on fixed thresholds – related to biological reference points like minimal biomass or maximal fishing mortality – to trigger actions (Walters and Martell, 2004), despite recent efforts to introduce more dynamic reference points (Berger, 2019; Hodgdon et al., 2022).

Although the notions of regime shifts and stock collapses appear strongly connected, they are not equivalent. Regime shifts are usually characterized by an abrupt temporal trajectory with a final state potentially persistent in time (Bestelmeyer et al., 2011). In contrast, stock collapses relate to stock depletion based on fixed arbitrary thresholds related to stock size or catch (Yletyinen et al., 2018) that give no indication about the circumstances preceding the collapse nor the persistence of the collapse state. For instance, (Vert-pre et al., 2013) showed that abrupt shifts from high to low surplus production levels – a proxy for stock productivity corresponding to the change in abundance in the absence of fishing (Walters et al., 2008) – can happen quite regularly and were unrelated to abundance levels for a substantial proportion of stocks. Although this finding implies that abrupt shifts in productivity do not necessarily lead to stock collapse, the relationship between the two phenomena has not been systematically explored. In addition to not fully understanding the consequences of abrupt shifts in productivity, we also poorly understand what causes them. The relative contributions of climate and exploitation to stock collapse has been well investigated (Möllmann and Diekmann, 2012), but usually focused on a few data-rich stocks (Beaugrand et al., 2022; Pershing et al., 2015). Broader syntheses of stock collapse mostly focus on a single pressure at a time, either fishing intensity (Essington et al., 2015), climate change (Free et al., 2019), or life history (Pinsky et al., 2011) but rarely all pressures together (Pinsky and Byler, 2015). Overall, we lack a global overview of the prevalence of abrupt shifts in fisheries productivity, along with information on their drivers, and potential link with stock collapses.

The aim of this study is to identify potential regime shifts in fish stocks globally, by looking at abrupt shifts in productivity. Here, we systematically classify the dynamics of 315 productivity time series, estimated from assessments of marine fish stocks from around the world, to address the following questions: (i) How prevalent are productivity abrupt shifts (PAS) and how are they distributed in space and time? (ii) Are PAS

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related to species life history, environmental conditions or fishing pressure? (iii) Are PAS associated with stock collapses?

Results

Productivity Abrupt Shifts (PAS) prevalence and distribution

We classified 315 fish stock productivity time series into basic trajectory types based on shape and trend and found all types of trajectories over the period 1950–2020 (Fig. 1). Quality scores indicated that selected models, especially for abrupt and quadratic trajectories, performed well and were robust to the removal of individual data points (Fig. 1, Fig. S1). Still, the variance explained by the models remained low given the intrinsically high variability of productivity time series (Fig. S1). The full list of trajectories is available in the supplement (Table S1).

Globally, PAS were found for more than a quarter of stocks (25.7%, N=81), with roughly equal numbers of negative (13.3%, N=42) and positive (12.4%, N=39) PAS (Fig. 2A). The other types of trajectories (quadratic, linear, and no change) were found in similar proportions. Balanced proportions between different trajectory types were also found at the scale of FAO major fishing areas (Fig. 2B), with no significant difference across areas (Chi-square test, $p = 0.32$). The direction of shifts was however unevenly distributed in space (Chi-square test, $p = 0.02$), with regions like the North-West Atlantic and North-West Pacific comprising a higher proportion of negative PAS (30% and 29% respectively), whereas the region with most positive PAS (32%) was the South-West Pacific. Similar patterns were found using large marine ecosystems (LMEs) as grouping areas (Fig. S2). Considering taxonomic groups, we found significant differences in the proportions of PAS against non-abrupt trajectories across the five most numerous orders in number of stocks (Chi-square test, $p = 0.01$), with notably a higher proportion of positive PAS in Perciformes and of negative PAS in Clupeiformes (Fig. S3).

Over time, the occurrence of positive PAS were spread from the 1960’s to the 2010’s and the distribution did not differ significantly from the coverage of time series (Fig. 2C, Kolmogorov-Smirnov test, $p = 0.32$). However, the distribution of negative PAS differed from coverage (Kolmogorov-Smirnov test, $p = 0.04$) and tended to cluster during the 1980’s (Fig. 2D), before the maximum of time series available was reached

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between 1994 and 2000. The observation of PAS being less frequent after 2010 could arise from a lack of available data along with the difficulty of detecting very recent shifts.

Drivers of Productivity Abrupt Shifts (PAS)

We tested which drivers among life history, environment (sea surface temperature, SST), and fishing intensity (exploitation rate, ER) were more related to the occurrence of PAS using generalized additive mixed models to account for phylogeny and spatial location. We found that the main drivers of PAS differed between negative and positive PAS. Negative PAS were mostly influenced by environmental conditions like positive trends in SST occurring before the shift ($p = 0.005$, Fig. 3A) and marginally by lower average SST ($p = 0.054$, Fig. 3A) compared to other trajectories. Positive PAS were influenced by fishing intensity and life history and were associated with higher trends in ER ($p = 0.005$, Fig. 3B), higher age at maturity ($p = 0.048$, Fig. 3B), and marginally lower trends in SST ($p = 0.054$, Fig. 3B).

Clearly, as both models for negative and positive productivity abrupt shifts explained between 13% and 14% of the total variance, the occurrence of PAS was only partly explained by the variables selected. But the identity and relative importance of those variable is not a matter of model structure. Indeed, analysis of PAS using an entirely different method (hierarchical partitioning) identified the same significant predictors (Table S2–S3).

Productivity Abrupt Shifts PAS and stock collapse

We also tested the extent to which negative PAS were associated with stock collapse defined as being below 25% of the average stock biomass recorded to date following (Essington et al., 2015). While not all negative PAS led to stock collapse (only 11 out of 42 stocks did, 26%, Fig. 4A), among the stocks that did collapse, we found a higher proportion of negative PAS (23%, Fig. 4A) compared to those that did not collapse (12%, Fig. 4A). Collapsed stocks also tended to have more decreasing and fewer increasing productivity trajectories (Fig. 4A). On average, collapsed stocks experienced a stronger magnitude of negative PAS than stocks that did not collapse (t-test $p = 0.06$, Fig. 4B). Most of the negative PAS occurred between 4 to 12 years before the stock collapsed, while no such temporal lags were found for positive PAS (Fig. 4C).

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The influence of SST on PAS and collapse was further investigated at the scale of large marine ecosystems (LMEs). We evaluated the relationship between warming rate (SST change) between 1950 and 2020 and the proportion of stocks that underwent a PAS or a collapse. We found a significant positive linear relationship between negative PAS and warming rate ($p = 0.006$, Fig. 4D), meaning that LMEs with the most rapid warming rate were also those with the highest proportion of stocks that underwent negative PAS. However, we only found a not significant positive linear relationship between warming rate and the proportion of collapsed stocks ($p = 0.205$, Fig. 4F), even when using different definitions of collapse ($0.25 < p < 0.44$, Fig. S4). That is, the LMEs warming most rapidly had more frequent negative PAS, but this did not translate into more frequent collapse of stocks in these LMEs.

Discussion

In this work we distinguished productivity abrupt shifts (PAS) in fisheries time series from gradual productivity trajectories using a systematic classification of trajectory types based on shape and trend (no change, linear, quadratic, abrupt). We found that PAS were detected in more than 25% of stocks worldwide and that PAS occurrence varied in space and time. We provide evidence that large negative PAS frequently preceded stock collapses and were associated with a higher warming rate. Those findings could have critical implications for fisheries management in warming oceans.

Our results expand on the well-documented examples of regime shifts (e.g., (Blöcker et al., 2023; Möllmann et al., 2021)), giving a more complete picture of the prevalence of such shifts. Our classification aptly identifies stocks like Newfoundland cod (Myers et al., 1997), Baltic sea cod (Möllmann et al., 2021), or Japanese sardine (Watanabe et al., 1995), which underwent among the most prominent and rapid abrupt collapses previously characterized (full list available in Table S1). More importantly, we also identify others that were surprisingly not extensively treated in the literature (e.g., Greenland halibut off Labrador Shelf - Grand Banks in the 1990s). Assuming that retrospective analyses of productivity trajectories can give good insights into how stocks are likely to react in the future, our approach enables the identification of stocks that could be more prone to abrupt decline and thus require more careful management.

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The prevalence of abrupt shifts we found (25%) is somewhat below those from previous analyses (46% for (Sellinger et al., 2024), 39% for (Vert-pre et al., 2013)). The differences in prevalence could be explained by the set of stocks analyzed, the different relationships considered (stock-recruitment in (Sellinger et al., 2024)), the different models used (productivity-abundance relationship in (Vert-pre et al., 2013)), and perhaps most importantly because our classification involved the congruence of two independent models to confirm a trajectory as abrupt, making the attribution of abruptness more strict but also probably more reliable. Our trajectory classification without the confirmation step doubles the prevalence of abrupt shifts (51%, Fig. S5).

Among the life history, climate change, fishing intensity related factors that have been proposed to affect stock collapses either regionally or globally, we found that trend in SST to be the most significant variable related to the occurrence of negative PAS. Climate change, alone or in conjunction with other factors, had already been stated as one of the most prominent drivers of marine regime shifts (Rocha et al., 2015) and stock collapses (Pinsky and Byler, 2015). Interestingly, the large marine ecosystems that underwent the largest SST increases between 1982 and 2006 (> 1°C, (Belkin, 2009)) are also those for which we found the largest proportions of stocks with negative PAS during the same period, namely the Baltic and North Sea, the East China Sea and Sea of Japan, and Newfoundland - Labrador Shelf. As fishing intensity alone did not explain negative PAS, we did not explore potential interactions between fishing and temperature that have previously been examined for global (Pinsky and Byler, 2015) and regional (Rouyer et al., 2014) stock collapses. However, we found an effect of fishing intensity related to positive PAS. This effect might in fact correspond to the early stages of a fishery when the productivity of unfished stocks is usually low because the stock is assumed to be near carrying capacity. It corresponds to the basic principle of maximum sustainable yield, that productivity is maximized for intermediate levels of fish abundance corresponding to fishing mortality rates near those associated with maximum sustainable yield (F_{MSY}, (Walters and Martell, 2004)). No sign of abrupt recovery after collapse was found in the data, except for the herring in the North Sea, which recovered rapidly following reduction in fishing pressure - a result already documented by (Dickey-Collas et al., 2010).

We accounted for life history essentially through maturity related metrics and principal habitat, but in contrast with previous studies (Pinsky et al., 2011; Pinsky and Byler, 2015) we found no significant effect of those life

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history traits on negative shifts. Only the age at maturity (which is negatively correlated with somatic growth rate, Fig. S6A) tended to be positively associated with positive shifts, meaning that rapid productivity increases were more often found in slower growing, later maturing species. This pattern is consistent with the periodic life history strategy (Winemiller and Rose, 1992) where delayed maturation and consequent large numbers of eggs can result in occasional very large recruitment events when these eggs encounter favorable conditions for early life survival. These periodic strategists often exhibit years of minimal or even negative productivity punctuated by occasional large year classes that create a period of high productivity as the year class ages and grows.

We also found support for a link between negative PAS and subsequent stock collapse for a quarter of the stocks that shifted negatively. This sequence of events could be expected with productivity decline impacting stock abundance and biomass. However, collapse following negative PAS was far from inevitable, a fact likely explained by the high prevalence of harvest control rules, which reduced fishing pressure as abundance declines (Punt, 2010). Our results also suggest that gradual stock collapses were associated with lower levels of warming, while areas that underwent rapid warming were more likely to experience negative abrupt shifts. There is evidence for such warming-driven declines notably in the case of insufficient management adaptation (Pershing et al., 2015) but a more extensive coverage of stocks with lower warming rate would be necessary to confirm this. These results are all robust to different definitions of stock collapse (Fig. S7).

Additional analyses would be needed to ascertain whether the abrupt shifts in productivity of individual fish stocks that we detected here correspond with ecosystem-wide regime shifts. , Such analysis would require time series of other ecosystem components, many of which (e.g., zooplankton abundance) are unavailable at a global scale (deYoung et al., 2008; Lees et al., 2006). Still, the fact that abrupt shifts occur is meaningful, even in the absence of a broader regime shift, as they have serious implications for management regardless of the mechanisms driving such shifts (Beaugrand et al., 2022; Möllmann and Diekmann, 2012).

While the RAM Legacy database, on which this analysis was based, has broad geographic coverage, it does not reflect the actual distribution of fisheries worldwide and is biased towards intensively monitored stocks

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mostly from wealthy nations at temperate latitudes (Ricard et al., 2012). Fisheries from tropical latitudes are more often data limited or monitored for a lower amount of time, which limits reliable shift detection. Yet, the correlation we found between warming rate and negative PAS suggests that marine areas like the North-West and South Atlantic, or South Indian Oceans that are projected to be hotspots of rapid temperature increase in the next decades (Cheng et al., 2022) require careful monitoring and management. This is a challenging task since it has been suggested that regional fisheries agencies are still struggling to account effectively for climate change in their practices (Sumby et al., 2021). As our results contribute to the understanding of fish stock long-term dynamics, they could pave the way for advancing the anticipation of productivity abrupt shifts to improve effective fishing regulation in the face of rising global change pressures.

Materials and Methods

Fisheries data

Time series of catch and stock biomass were download from the freely available RAM Legacy Stock Assessment database (RAMLDB v4.61, (Ricard et al., 2012)). From those, we estimated stock productivity (or surplus production) time series, which is a biological variable particularly relevant to investigate putative regime shifts (Vert-pre et al., 2013). Abrupt shifts in productivity time series have been used as hallmark of regime shift in some particular fish stocks (Blöcker et al., 2023; Möllmann et al., 2021). Surplus production can be assimilated to stock productivity if it is independent to biomass, which has been suggested to be the case for most of the stocks (Vert-pre et al., 2013). We therefore refer to surplus production as productivity. The productivity $S(t)$ in the year t was estimated from catch and total biomass time series according to the following formula:

$$S(t) = B(t+1) - B(t) + C(t)$$

with $B(t)$ stock total biomass and $C(t)$ catch in the year t. While catch values are raw data, often assumed to be measured without error, biomass estimates are model outputs and concerns have been raised when considering model outputs as input data (Brooks and Deroba, 2015). Here, the greatest concern is that interannual smoothing of biomass time series by the assessment model could cause us to miss true abrupt

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shifts. This concern is minimized by the fact that most biomass time series in the database are from highly flexible statistical catch at age models that allow for substantial process error (e.g., internnual variation in reproductive output or recruitment, (Ricard et al., 2012; Thorson et al., 2014)). Our data filtering criteria (described below) removed a small number of stocks where smooth biomass trajectories were clearly a model artifact..

The RAMLDB includes stock assessments from several phyla including mollusks, crustaceans, and vertebrates (fishes). For consistency, we only focused on marine fish stocks including both ray-finned and cartilaginous fishes, and ignored data before 1950 that sometimes corresponded to model extrapolations. Fish productivity time series with no missing data points were estimated for 397 stocks but a total of 82 were discarded either because they had time series length below 25 years (68 stocks) or because biomass estimates were apparently generated from deterministic models which could only produce smooth changes (14 stocks). The classification was thus performed on 315 stocks corresponding to 161 taxa, among which 158 were at the species and 3 at the genus level. Median time series length was 41 years and the longest time series was 71 years. To allow for inter-stock comparisons, productivity was normalized by average stock biomass following (Essington et al., 2015).

Time series classification

Productivity time series were fitted with four different types of model – intercept-only (no change), linear trend, quadratic trend, and abrupt change – and Akaike Information Criterion corrected for small sample size (AICc) were computed for each model fit. The best trajectory was considered to be the model with lowest AICc and validated following (Pélissié et al., 2024). To validate abrupt trajectories, an independent breakpoint detection method (*asdetect*, (Boulton and Lenton, 2019)) was run and we checked whether both methods agreed on the shift date with a tolerance of five years. For quadratic and linear cases, we tested the significance of the higher order coefficient. We used the classification with default parameters for *asdetect* method (anomalous rate of change equal to three medians absolute deviations and detection threshold set to 0.15) that have been tested to be most reliable for time series of at least 25 time points (Pélissié et al., 2024). To avoid uncertain shifts, shifts less than five year from the start or the end of the time series were not considered. If the abrupt

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shift model and the *asdetect* method agreed that an abrupt shift occurred but disagreed on the year of the shift, the year identified by the abrupt shift model was used. We also computed three classification quality score to assess different aspects of model reliability, namely the relative support for each fitted model (AICc weight), model choice robustness to individual data point removal (Leave-One-Out cross validation), and the ratio between variation not explained by the model and the overall variation (normalized RMSE). This framework permits the identification of at most one shift in each time series, which is assumed to be the largest one if several might be present. The standardization by stock average biomass changes the absolute AICc values but does not affect model ranking or best model choice.

Spatial data

A stock represents a consistent population unit that is spatially bounded. Most stock polygons were extracted from the dataset used by (Free et al., 2019). An addition of 64 stock polygons to the dataset was made following Free's methodology either by combining fishing subareas or divisions, approximating polygons to already existing ones, or digitizing fishing areas based on individual assessment data. All added polygons were processed using QGIS v3.16. Stocks were grouped by FAO Major Fishing Areas as directly available from RAMLDB dataset. We also grouped stocks by Large Marine Ecosystems (LMEs) that represent biogeographically more relevant units. We assigned each stock to the LME with which stock polygons overlapped most, except for high seas fisheries for which they were assigned to main ocean areas.

Explanatory variables

Potential explanatory variables were gathered for each taxa or stock, spanning life history, environmental, and fishing-related pressure. To avoid missing data, we used imputed life history traits from the FishLife database (Thorson, 2020) and selected two relevant variables among the least correlated ones, namely age and length at maturity (Fig. S6A). Primary habitat was retrieved from FishBase (Froese and Pauly, 2023) with classes grouped as pelagic (pelagic-neritic, pelagic-oceanic, bathypelagic) and demersal (bathydemersal, benthopelagic, demersal, reef-associated). Sea surface temperature (SST) was used as the most relevant environmental variable using data from the Met Office HadISST1 dataset (Rayner et al., 2003) from 1870 to 2020 on a monthly basis (then averaged annually) and with one degree spatial resolution. Annual SST maps

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were clipped based on stock or LME boundaries and averaged to obtain a single SST time series per stock (Free et al., 2019). Exploitation rate (ER) was used as a proxy for fishing intensity and corresponds to the ratio of catch to total biomass in the same year. Exploitation rate relative to that at maximum sustainable yield U/Umsy may have been a better proxy since it accounts for intrinsic differences in productivity among stocks but was not available for 15% of the stocks. SST and ER means and trends were estimated from the start of productivity time series up to the shift if any was detected or to the latest year available otherwise. The absence of strong multicollinearity of explanatory variables was determined by performing pairwise Pearson correlation tests (Fig. S6B).

To test the association between stock collapse and PAS, we defined a stock as collapsed if biomass in a given year was below 25% of the average stock biomass recorded to date following the definition by (Essington et al., 2015) and if such threshold was crossed for at least two consecutive years to limit artifacts. We focused on whether a stock ever collapsed and the first year of collapse. We repeated the analyses that involved collapsed status with alternative definitions used by (Yletyinen et al., 2018), namely 10% of maximum biomass and 15%, and 50% of average biomass.

Statistical analyses

We assessed the homogeneity of trajectories found across regions and taxonomic orders separately using Chi-square test and computed p-values by Monte Carlo simulation using 10^5 replicates to deal with cases of low expected values.

We used logistic generalized additive mixed models (GAMM) to assess the effect of independent variables on the occurrence of productivity abrupt shifts using the *mgcv* package (Wood, 2011). Positive and negative shifts were considered separately as dependent variable against all other trajectories to contrast conditions of abrupt shifts against all conditions available. The effect of life history, environmental conditions, and fishing intensity were estimated as fixed effects by considering age at maturity, length at maturity, main habitat, average and trend in SST, and average and trend in ER altogether. Numerical variables were standardized to allow comparison. To account for space, stock centroid coordinates were considered as smooth terms. Taxonomic orders and families were treated as random effect to account for broad phylogenetic relationships.

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Two stocks from the Japanese Seto inland sea lacked SST data due to limited spatial resolution and were thus discarded for these analyses.

An alternative approach was also performed to assess the contribution of each predictor variable independently and in conjunction with the other predictors on the occurrence of abrupt shifts. This approach controls for the possible influence of unchecked multicollinearity among variables. We used the *hier.part* package (Nally and Walsh, 2004) to run hierarchical partitioning and randomization tests with 999 repetitions on positive and negative shift occurrence as binomial variables with a logit link function. Phylogeny was not used for these analyses because of excessive number of groups in each taxonomic level.

Sensitivity analyses

We also ran the classification without the step for abrupt shift confirmation to determine how frequently this step was eliminating potential abrupt shift classifications. Without the confirmation step, the proportion of stocks classified as PAS reached 51.4% with similar proportions of negative (26%) and positive (25.4%) shifts (Fig. S5). We also repeated the GAMM analysis of predictors of PAS with this less strict classification for PAS. In that case, we still found the effect of SST change ($p = 0.049$, Fig. S8A) for negative PAS, with average SST and ER also found as significant predictor ($p = 0.006$ and $p = 0.008$ respectively, Fig. S8A). For positive PAS, the effect of both average ($p < 0.001$) and trend in ER ($p = 0.013$) were found as well as a positive effect of average SST ($p = 0.034$, Fig. S8B).

We repeated the GAMM with fishing intensity relative to that at maximum sustainable yield (U/Umsy) instead of exploitation rate (ER). U/Umsy accounts for intrinsic species differences in withstanding fishing pressure but was available only for 269 stocks. Similar effects to the initial models in Fig. 3 were found in estimates although not significant for SST change ($p = 0.084$), probably due to the loss of many stocks with negative PAS (14 out of 42, among which 6 also collapsed), with in addition a significant positive effect of trend in U/Umsy ($p = 0.002$, Fig. S8C). Similar effects to the initial models in Fig. 3 were also found for positive PAS with age at maturity as the only significant variable ($p = 0.049$, Fig. S8D).

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We also tested the robustness of the results related to stock collapse by using different thresholds of collapse (10% of maximum stock biomass, 15% and 50% of the average stock biomass), which gave similar results in terms of relationship with negative PAS (Fig. S7) and warming rate (Fig. S4).

Author Contributions

All authors designed research; M.P. performed empirical analyses; M.P. analyzed the data and all authors contributed to writing the paper.

Data availability

All analyses were conducted using R software (version 4.3.3). The R script to replicate all analyses is available on Github (https://anonymous.4open.science/r/ocean_warming_fisheries).

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Figures and Tables

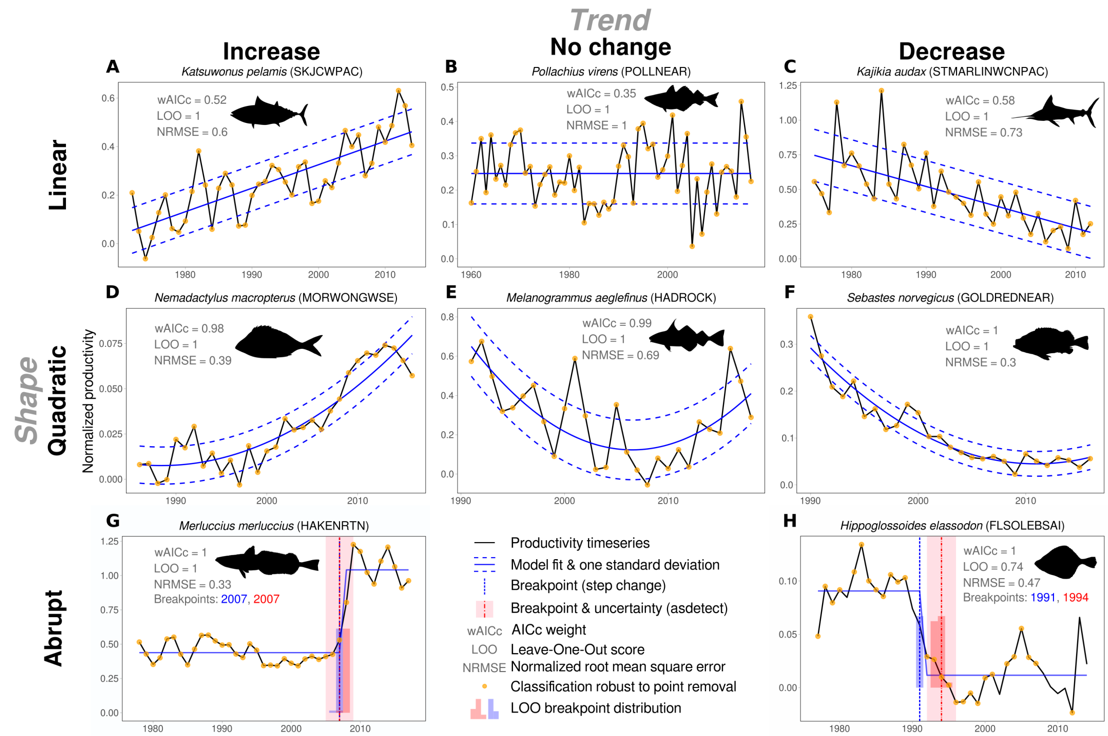

Figure 1. Examples of productivity time series classified into trajectory types based on shape and trend. Some time series were best described by either linear (A-C), quadratic (D-F), or abrupt trajectories (G, H), and overall trend either positive (A, D, G), or negative (C, F, H). No change is a types of shape that corresponds to a trajectory without trend (B, E). Each panel shows fish stock productivity time series normalized by the average stock biomass (black line) with the best model fit (solid blue line) and standard deviation (dashed lines) following the classification procedure detailed in the methods. Three classification quality scores are specified for each time series: AICc weight (wAICc), leave-one-out score (LOO), and normalized root mean square error (NRMSE). Timepoints that if removed in the LOO process would result in the same shape are highlighted by orange dots. For abrupt trajectories (G, H), the location of breakpoints is indicated by vertical lines, the pink background corresponds to the breakpoint uncertainty for the *asdetect* method, and the distribution of breakpoint locations from LOO time series are represented by color bars. Note that scales are not the same for the different panels. Species name and (stock ID) are also displayed. Fish silhouettes come from https://www.phylopic.org/.

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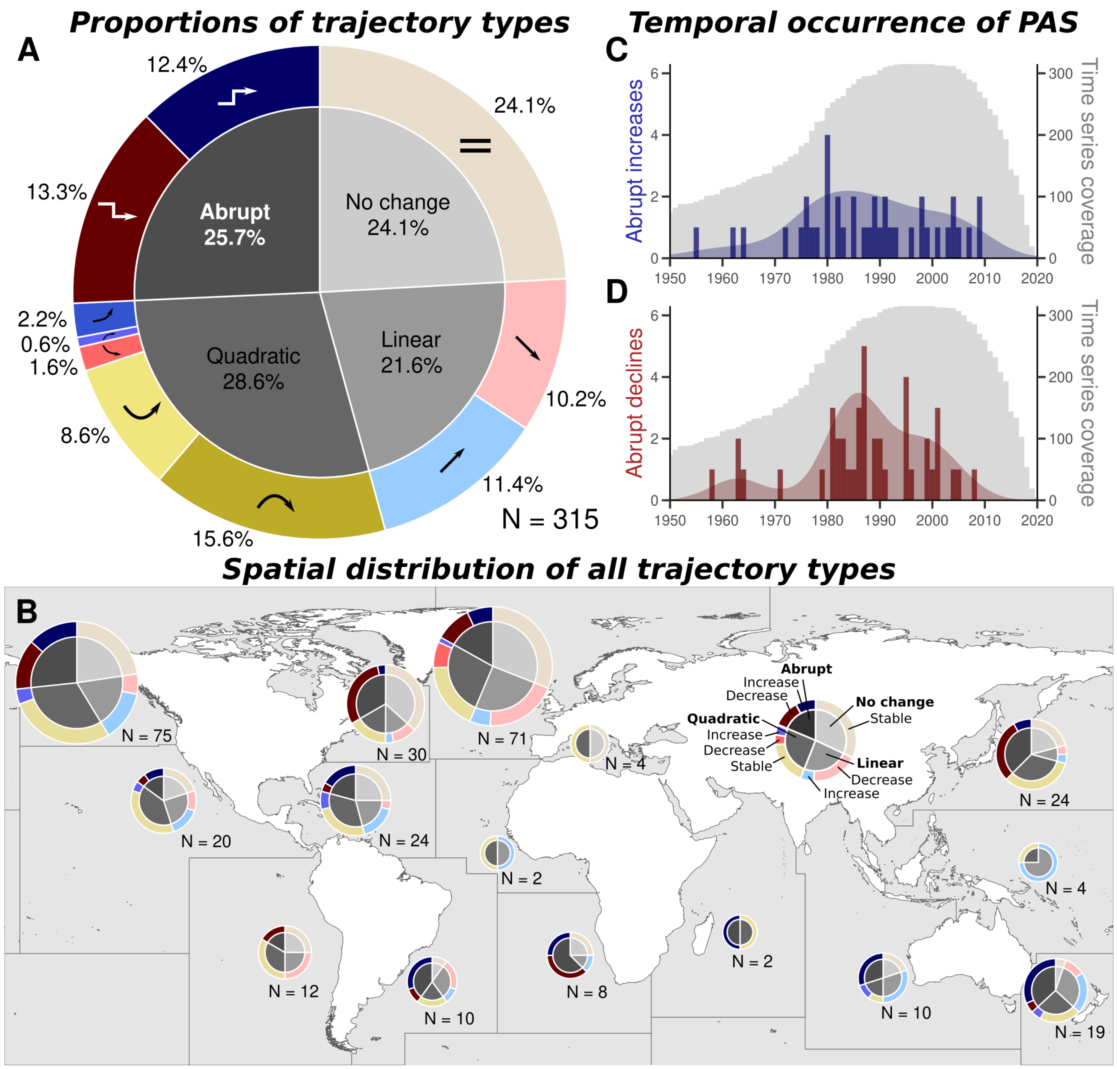

Figure 2. Overview and spatial distribution of all productivity trajectory types alongside the temporal distribution of productivity abrupt shifts (PAS). (A) Overall proportion of all productivity trajectory types, with the inner pie chart indicating trajectory shape and the outer layer specifying the trend. (B) Spatial distribution of all trajectory types by FAO major fishing areas. The size of the charts is indicative of the number of stocks, which are also displayed. (C-D) Temporal distribution of positive (C) and negative PAS (D) (color bars and density) with in gray the coverage (i.e., number of stocks with data available in each year) of the time series classified.

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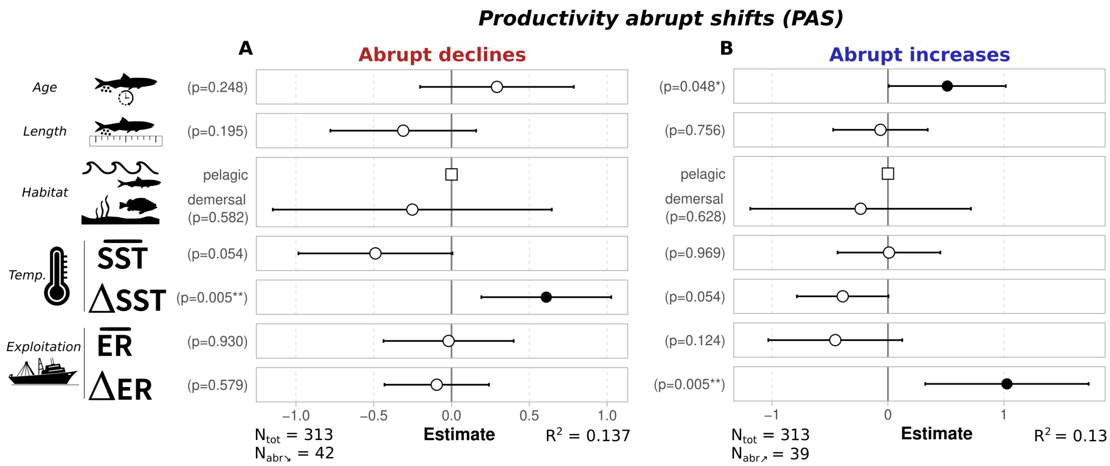

Figure 3. Generalized additive mixed model (GAMM) coefficient estimates for models accounting for negative (A) and positive (B) PAS against all other trajectories. Positive estimates mean that PAS are more often found for larger values of the variable and conversely. Dependent variables are arranged from top to bottom with age at maturity, length at maturity, main habitat (pelagic as reference category), mean (SSTbar) and linear trend (deltaSST) in sea surface temperature, mean (ERbar) and linear trend (deltaER) in exploitation rate. Mean and trend in SST and ER were computed from the first year of productivity available up to the shift if any was detected. Model estimates (circles) with confidence intervals at 95% (horizontal bars) are presented and significant estimates are indicated with filled circles. All numeric variables were standardized.

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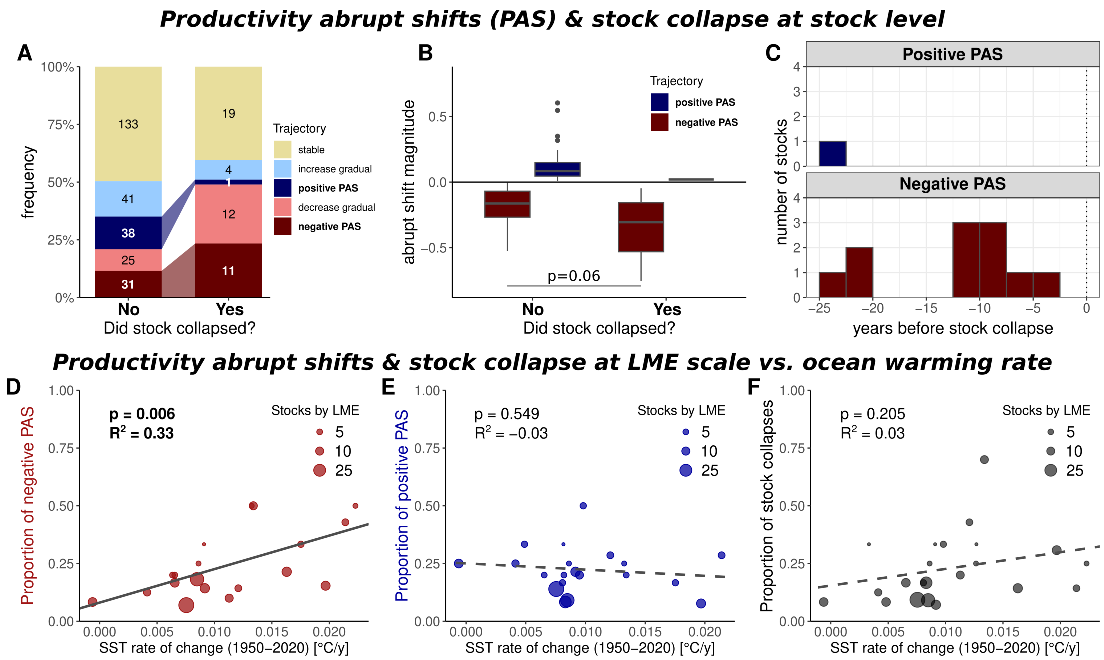

Figure 4. Relationship between PAS and stock collapse at stock level (A-C) and at the scale of Large Marine Ecosystems (LMEs) related to ocean warming rate (D-F). (A) Proportion of trajectories depending on whether stocks ever reached collapsed state (defined as 25% of the mean biomass) with actual number of stocks indicated. (B) Standardized PAS magnitude for negative (dark red) and positive (dark blue) shifts and collapsed state. (C) Distribution of PAS location relative to the first year as collapsed (vertical dotted line), with positive PAS (top panel in blue) and negative PAS (bottom panel in blue). (D-F) Relationship between the proportion of PAS (D, E) or stock collapse (F) within LMEs and Sea surface temperature (SST) rate of change between 1950 and 2020. LMEs with less than two stocks were not included. Significant linear regression are drawn with a solid line, and dashed line otherwise.