Global hotspots of coherent marine fishery catches

JOYCE J. L. ONG [iD],[1,5,6] JONATHAN A. WALTER [iD],[2] OLAF P. JENSEN,[3,4] AND MALIN L. PINSKY[1]

[1]*Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, New Jersey 08901 USA*
[2]*Department of Environmental Sciences, University of Virginia, 291 McCormick Road, Charlottesville, Virginia 22903 USA*
[3]*Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey 08901 USA*
[4]*Center for Limnology, University of Wisconsin-Madison, 680 N Park Street, Madison, Wisconsin 53706 USA*

Abstract. Although different fisheries can be tightly linked to each other by human and ecosystem processes, they are often managed independently. Synchronous fluctuations among fish populations or fishery catches can destabilize ecosystems and economies, respectively, but the degree of synchrony around the world remains unclear. We analyzed 1,092 marine fisheries catch time series over 60 yr to test for the presence of coherence, a form of synchrony that allows for phase-lagged relationships. We found that nearly every fishery was coherent with at least one other fishery catch time series globally and that coherence was strongest in the northeast Atlantic, western central Pacific, and eastern Indian Ocean. Analysis of fish biomass and fishing mortality time series from these hotspots revealed that coherence in biomass or fishing mortality were both possible, though biomass coherence was more common. Most of these relationships were synchronous with no time lags, and across catches in all regions, synchrony was a better predictor of regional catch portfolio effects than catch diversity. Regions with higher synchrony had lower stability in aggregate fishery catches, which can have negative consequences for food security and economic wealth.

Key words: fishery catches; global hotspots; marine fisheries; phase relationships; portfolio effects; synchrony; wavelet coherence.

INTRODUCTION

Marine fisheries contribute substantially to food security, nutrition, livelihoods and foreign trade of many countries (FAO 2018). Hence, the stability of marine resources is of substantial interest. Although research has shown that anthropogenic and environmental changes have led to variable and sometimes decreasing fishery catches, the consequences for food production and livelihoods depend not only on the magnitude of the variation but also on whether decreases in one fishery are offset by increases in another (Hilborn et al. 2003, Moore et al. 2010, Schindler et al. 2010). In contrast, synchronous fluctuations across multiple fisheries reduce the stability of marine food production and can depress regional fishing economies (Laevastu and Marasco 1982). Although synchrony between particular marine species has been observed (Lluch-Belda et al. 1992, Tsikliras et al. 2018, Zimmermann et al. 2019), we currently know little about the prevalence of synchrony in fisheries across large spatial and temporal scales.

Synchrony results when the dynamics of multiple system components are similar through time, which reduces the effective diversity of the system and leads to greater volatility and greater potential for collapse of yields (Schindler et al. 2010, Thibaut and Connolly 2013). In contrast, asynchronous fluctuations have a stabilizing role, also termed the portfolio effect (Figge 2004, Schindler et al. 2010). Portfolio effects describe the degree to which the dynamics of the aggregate system are less variable than the individual components, a concept that is analogous to financial portfolios (Figge 2004). The concept of portfolio effects has been widely applied to provide a framework for understanding the relationship between diversity at one level and stability at a more aggregated level, including to studies of fishery catch diversity and stability (Schindler et al. 2010, 2015, Kasperski and Holland 2013). These variability estimates are typically dependent on the number of species (taxonomic richness) or populations, where higher diversity leads to stronger portfolio effects (Thibaut and Connolly 2013). Synchronous fluctuations within a system increase variability and weaken portfolio effects (Moore et al. 2010, Schindler et al. 2010). However, the relative importance of the number of components in the system vs. synchrony among the components in determining the strength of portfolio effects is currently unclear for many systems.

Synchrony is typically considered in one of two forms, either between numbers of the same system component

in different places (i.e., spatial synchrony) or between numbers of different system components in the same place (i.e., community synchrony). For example, studies of community synchrony have predominantly focused on relatively small geographic scales and on groups of species that are closely taxonomically related or that share similar life history strategies (Cheal et al. 2007, Buttay et al. 2017). Fishery catches of certain pelagic fish species exhibit greater community than spatial synchrony (Corbineau et al. 2008, 2010). Other studies of community synchrony have found that Lepidoptera with similar feeding strategies (Raimondo et al. 2004) and taxonomically related seabirds have synchronous fluctuations (Robinson et al. 2013). From these prior studies, it remains unclear whether community synchrony is strongly structured by taxonomy or by life history strategies at global scales.

Most studies on synchrony have focused only on synchronous and anti-synchronous fluctuations, and mostly with climate as a driver of synchrony (Grenfell et al. 1998, Haynes et al. 2013, Sheppard et al. 2016). The Moran effect, for example, describes spatial synchrony of population fluctuations driven by exposure to shared climate fluctuations (Moran 1953). However, human behavior can also exert strong effects on populations of harvested species, especially in coupled social-ecological systems like marine fisheries. For example, commercial exploitation was found to be a strong driver of synchronous fluctuations among cod stocks in the North Atlantic (Frank et al. 2016). Furthermore, trophic or competitive relationships can also drive community synchrony (Huitu et al. 2004, Loreau and de Mazancourt 2008). The nature of fluctuations (e.g., synchronous, anti-synchronous, lagged) can help point to likely drivers, yet attributing causality to patterns in synchronicity among marine fisheries time series is still debated (Lluch-Belda et al. 1992, Schwartzlose et al. 1999, Sugihara et al. 2012, Izquierdo-Peña et al. 2019).

Controversy over the nature and mechanisms of synchrony in many systems still exist, in part because different mechanisms produce patterns that are indistinguishable using common analytical approaches like cross-correlation (Sugihara et al. 2012, Defriez and Reuman 2017). Wavelet coherence, however, can help resolve relationships when time lags confound correlation (Fig. 1; Sheppard et al. 2016). Two variables are coherent if they exhibit correlated oscillations and consistent phase differences through time, even if the variables are phase-lagged or anti-phase (Sheppard et al. 2016, Sheppard et al. 2017). Consistency of phase differences is important because it is more likely to imply a causal relationship that is not due to chance. Furthermore, identification of the type of phase relationships can help inform the potential drivers. Like other wavelet approaches, wavelet coherence also accommodates complex temporal autocorrelation structures, another common property of fisheries time series that confound correlation tests.
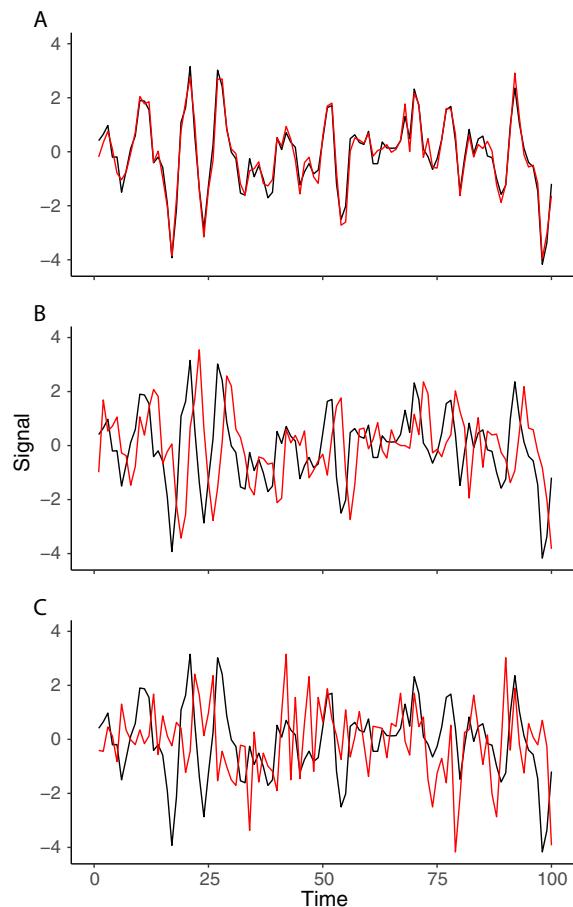

Fig. 1. Illustration of coherence and phase relationships comparing wavelet approaches and Pearson's correlation tests. (A) Two time series with an in-phase relationship that shows both coherence ($P = 0.001$) and correlation ($P = 2.2 \times 10^{-16}$). (B) Two time series with a phase-lagged relationship that shows coherence ($P = 0.001$) but statistically nonsignificant correlation ($P = 0.662$). (C) Two time series with no significant coherence ($P = 0.437$) or correlation ($P = 0.648$). Units for signal and time are arbitrary.

Here, we make use of long-term, global, fisheries catch records to test for coherence in marine fisheries on a global scale. We use wavelet analysis to ask, (1) Are marine fishery catches globally coherent, and if so, with what phase relationships? (2) Are fishery catches in the same region or from taxonomically related species more likely to be coherent? (3) Are there global hotspots of coherence? (4) Where and to what extent does coherence influence portfolio effects among fishery catches? We aim to describe the nature of coherent marine fishery catches and how coherence relates to portfolio effects that stabilize ecosystems and fishing economies. We focus on catch data and not abundance or catch per unit effort (CPUE) indices due to the availability of long and consistent catch time series, and we do not assume that catch fluctuations represent changes in population

abundances (Branch et al. 2011, Pauly et al. 2013). However, we also use available biomass and fishing mortality data from global coherence hotspots to directly examine the relative strength of coherence in biomass and fishing mortality time series.

MATERIALS AND METHODS

Data compilation and processing

We examined publicly available FAO catch data (Food and Agriculture Organization of the United Nations)[7] from fish, crustaceans and molluscs. We filtered the data to select only time series that had a median of more than 10 metric tons harvested per year and for which more than three-quarters of the values were non-zero. After filtering, we had 1,092 time series that each represented a unique species-location across 15 FAO regions. These 1,092 time series spanned the years 1955–2014 (60 yr) and consisted of 510 unique taxa from 132 taxonomic families (Appendix S1: Table S1). The majority (76%) of these time series were species- or genera-level stocks. An additional 19% were family-level stocks, and the remaining were classified under Orders or Subclasses. None of the "miscellaneous", "unidentified", or "not elsewhere included" groups were included. As is standard for coherence analysis, all time series data were linearly detrended separately for each stock, optimally Box-Cox transformed to normalize marginal distributions (Sheppard et al. 2016), and standardized by dividing each time series by its standard deviation prior to analyses.

Additional information on reconstructed population biomass and fishing mortality were included from the RAM Legacy Stock Assessment database (Ricard et al. 2012; version 4.491) for three regions identified as having high coherence in catches. Time series for stocks in these regions were compiled for 1950–2018. We examined total biomass of each stock, though only for years in which total catch was greater than zero to remove stock assessment spin-up periods. We also examined reported exploitation rate or, where this was unavailable (20% of populations), instantaneous fishing mortality rate, hereafter referred to as fishing mortality. The longest possible period for each pair of stocks in each of the identified regions with <10% missing values was used. These restrictions resulted in 4–59 stocks spanning 46–57 yr (Appendix S1: Tables S2, S3). All time series data went through the same linear detrending and transformation process as the catch data, and all subsequent results reflect coherence in the fluctuations (anomalies) of each time series.

Wavelet coherence statistical analyses

We used wavelet coherence analyses to determine whether marine fishery catches were coherent at global

and regional scales, and to determine the distribution of phase relationships between fishery catches (questions 1 and 2). We computed pairwise wavelet coherences among all 1,092 species-location combinations, averaging over the study period (1955–2014) and across all timescales from 2 yr (the shortest fluctuations that can be resolved from annual time series) to 20 yr (one-third of the full time series length of 60 yr). Wavelet coherence is a complex quantity with (1) a phase representing the phase difference between oscillations in two time series and (2) a magnitude representing the tendency for the time series to have consistent phase differences and correlated magnitudes of oscillations through time (Cazelles et al. 2008). Coherence values range from 0 (not coherent) to 1 (strongly coherent) and can be interpreted like a correlation coefficient. Significance testing was performed for each pair-wise comparison using 1,000 Fourier surrogates that preserved spectral properties of the time series but randomized their phase relationships. Therefore, these surrogates represented an appropriate null hypothesis of no coherence because they break coherence while holding constant the other statistical properties of the time series that would affect coherence between the two variables (see Sheppard et al. 2017 for detailed methods). To account for multiple testing (almost 600,000 pairwise comparisons), we set a false discovery rate (FDR) of <20% (Benjamini and Hochberg 1995). Alternative values of FDR were also tested and compared to balance the potential number of false positives and false negatives. All coherence analyses used the continuous complex Morlet wavelet transform (Torrence and Compo 1998).

To test for evidence of coherence on a global scale (question 1), we compared the number of significantly coherent relationships observed in the empirical data to the number of significantly coherent relationships expected under a null model. Our null model was composed from random red noise time series with lag-1 autocorrelation of 0.7, which was the mean value for the 1,092 empirical catch time series. We produced 100 simulations of 1,092 time series each. Each simulation was then analysed for significant coherence in the same way as the empirical data. The number of significantly coherent relationships was tallied for each null simulation for comparison against the empirical data. We also developed an alternative null model using 100 simulations of random red noise time series with lag-1 autocorrelation values drawn at random from the distribution of lag-1 autocorrelation values calculated from the empirical time series. Results of both null models were compared to test the robustness of our choice of lag-1 autocorrelation values.

To test for clustering of coherence within ocean basins, FAO regions, and taxonomic groupings of Order and Family (question 2 and 3), a second set of null models were constructed using randomization testing for each of the four clustering levels. We randomly resampled the cluster assignment (ocean basin, FAO region,

Order, and Family) for every pairwise coherence result (595,686 observations) 1,000 times and compared the observed test statistics against the distributions from these randomizations. Our test statistics included the average coherence value and the number of coherent relationships within ocean basins, FAO regions, Order, or Family (taxonomic groupings). P values were calculated using $P = (r + 1)/(n + 1)$, where r was the number of randomizations that produced a test statistic greater than or equal to the value calculated from the observed data, and n was the number of randomizations (North et al. 2002). The null models enabled us to test if the clustered coherence (at the four different levels) was greater than expected from a null model without clustering.

The number of each type of phase relationship was calculated for the previously identified statistically significant (FDR < 20%) relationships globally, within ocean basins or within each FAO region (questions 1 and 2). Further significance testing ($P < 0.05$) was performed for specific timescale bands of 2–4, 4–8, 8–12, and 12–16 yr, chosen from exploratory analyses of wavelet phasor mean field and power plots (Appendix S1: Fig. S1). The analysis enabled us to calculate a P value for the aggregate significance of coherence and the average phase relationship across each specified timescale band. The number of significant relationships within each FAO region and across all timescale bands were calculated for in-phase ($-\pi/4 <$ mean phase $< \pi/4$), phase-lagged ($-3\pi/4 <$ mean phase $< -\pi/4$ or $\pi/4 <$ mean phase $< 3\pi/4$), and anti-phase (mean phase $< -3\pi/4$ or mean phase $> 3\pi/4$) relationships. Percentages of each type of phase relationship were computed from the total number of significant phase relationships within the three spatial scales (global, ocean basin, or FAO region).

Pairwise wavelet coherences were also computed for the biomass and fishing mortality time series within each of the three identified regions of high coherence. Significance testing used 1,000 Fourier surrogates and FDR < 20%, similar to the method described earlier for catch data. The percentages of significant pairwise coherences were calculated for each of the biomass and fishing mortality time series from each region.

Portfolio effects statistical analyses

We measured the strength of portfolio effects (question 4) in each FAO region as the percent reduction in the coefficient of variation (CV; standard deviation divided by mean) of the aggregate catch time series attributable to variation among individual taxa. Therefore, $\text{PE} = (\overline{\text{CV}_{\text{ind}}} - \text{CV}_{\text{agg}})/\text{CV}_{\text{agg}} \times 100$, where CV_{ind} and CV_{agg} were the CVs of individual and aggregate time series, and the overbar indicates taking the average (Carlson and Satterthwaite 2011). The aggregate time series is the sum of the catch from all individual taxa and therefore represents fluctuation through time at the system level. Hence, the higher the percent reduction in CV

from individual to aggregate scales, the stronger the portfolio effect in fishery catches. We used multiple linear regression with multi-model inference to assess how portfolio strength was influenced by taxonomic richness (species number) and by the percentage of statistically significant in-phase and anti-phase relationships. Exploratory analyses revealed that the percentage of phase-lagged relationships were highly correlated with in-phase relationships and not related to portfolio effects, so phase-lagged relationships were not included as explanatory variables in the model selection process. We conducted model selection with second-order Akaike Information Criterion (AIC_c; Burnham and Anderson 2004). Due to the low number of observations, we limited all models to a single explanatory variable. The most parsimonious model was chosen using the difference in AIC_c values (ΔAIC_c).

Computation

All analyses were carried out in R (R Core Team 2018). Wavelet coherence analyses were performed using the Reumannplatz (Zhao et al. 2018) and wsyn (Reuman et al. 2018) R packages. Model selection was done using the R package MuMIn (Barton 2015).

RESULTS

Evidence for coherence

Catches from nearly every fishery (96%) were coherent with at least one other fishery globally, which was significantly higher than the expected 69% from null models ($P = 0.010$; Appendix S1: Fig. S2). We found 3,382 pairs of fishery catches globally that were significantly coherent at a false discovery rate (FDR) of 20% (see Appendix S1: Fig. S3 for alternative FDRs), which was five times greater than expected from red noise null models ($P = 0.010$; Fig. 2A and Appendix S1: Fig. S4). The average strength of coherence between pairs was not higher than expected from a null model ($P = 0.970$; Fig. 2B), but the significantly coherent fisheries were more likely to fluctuate in-phase as compared to other types of phase relationships (Fig. 2C). In-phase coherence tends to amplify fluctuations in total catch across all fisheries and tends to weaken portfolio effects.

Based on a resampling test, we also found that coherent pairs of fishery catches were significantly more likely to be clustered within ocean basins ($n = 1,427$ coherent pairs within basins), both in terms of the number of coherent relationships within basins ($P = 0.002$, Fig. 2 D) and in terms of the average coherence value within basins ($P = 0.031$; Fig. 2E). A third of the significantly coherent fisheries within ocean basins fluctuated in-phase (35%, Fig. 2F). At the narrower spatial scale of Food and Agriculture Organization (FAO) fishery regions (Fig. 3A), coherent fishery catches were also significantly more clustered ($n = 382$ coherent pairs within
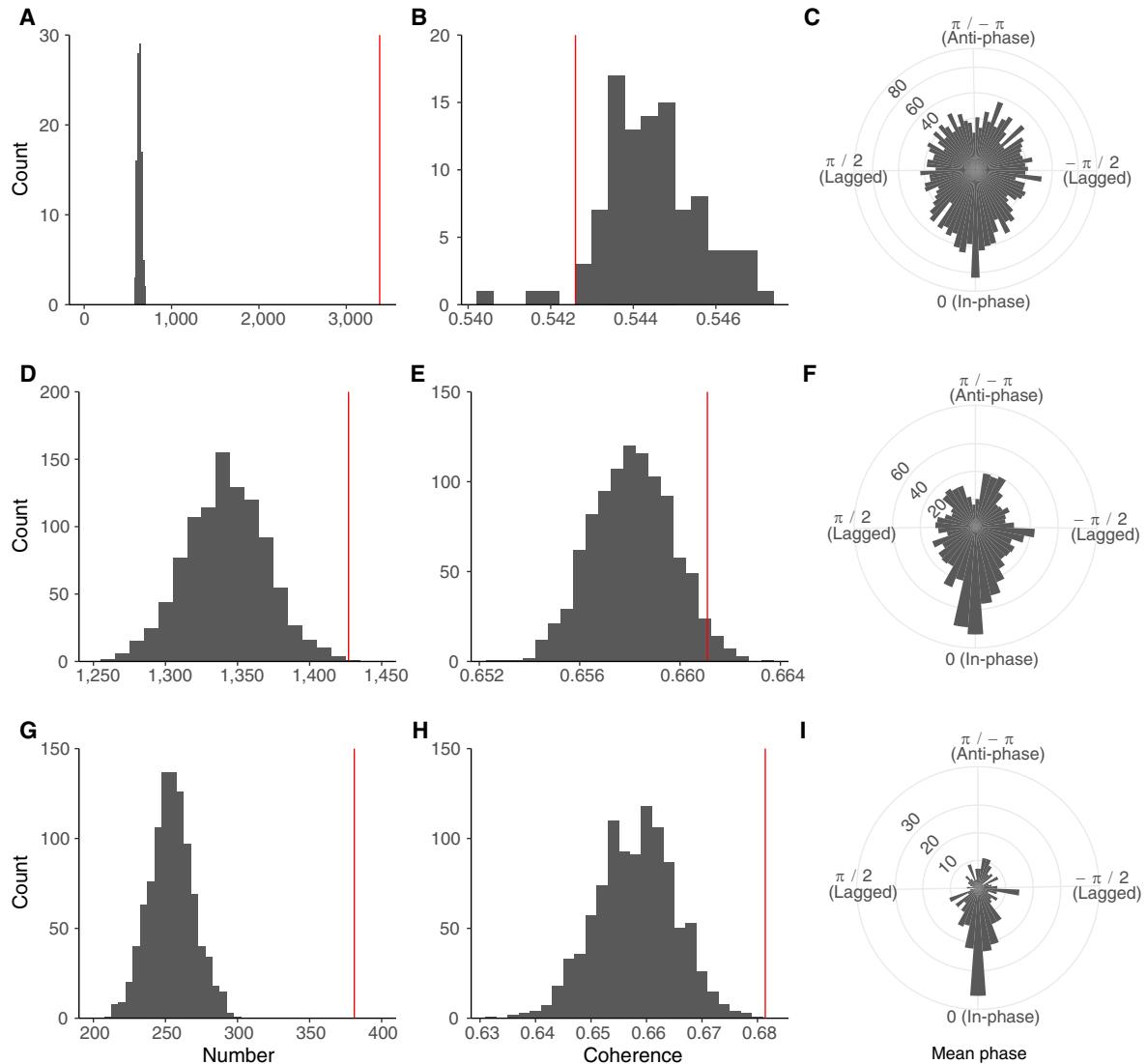
Fig. 2. Histograms of coherent relationships in fishery catches across spatial scales. (A, D, and G) Number of significant coherent relationships (count) observed (red line) and expected from a null model (gray histogram) globally (A), within ocean basins (D), and within FAO regions (G). (B, E, and H) Average coherence values observed (red line) and expected from a null model (gray histogram) globally (B), within ocean basins (E), and within FAO regions (H). (C, F, and I) Circular histogram of average phase relationships among the significant, coherent relationships globally (C), within ocean basins (F), and within FAO regions (I). For all plots, significance was defined with a false discovery rate of <20%. See Appendix S1: Fig. S2 for an alternative null model.

regions) compared to null models for the number of coherent relationships ($P = 0.001$; Fig. 2G) or for the average coherence value ($P = 0.001$; Fig. 2H). On average, more than one out of every three fisheries (38%) were coherent with at least one other fishery within the same region, significantly greater than the expected 9% from null models ($P = 0.010$; Appendix S1: Fig. S2). Almost half of the significantly coherent fisheries within FAO regions fluctuated in-phase (49%, Fig. 2I; see Appendix S1: Fig. S5 for individual regions).

Resampling tests on taxonomic groups showed that coherent pairs of fishery catches were significantly clustered within the same Order ($n = 1,023$ coherent pairs in

the same Order, $P = 0.031$) and same Family ($n = 131$ coherent pairs in the same Family, $P = 0.014$; Appendix S1: Fig. S6). However, the average coherence values for coherent pairs were not higher than expected from a null model at both taxonomic levels of Order and Family (Appendix S1: Fig. S6). Additional resampling tests on taxonomic groups within and across FAO regions (Appendix S1: Fig. S7) showed that the coherent pairs of taxonomically similar fishery catches were primarily pairs within the same region ($P = 0.001$ for Order and $P = 0.003$ for Family) rather than across regions ($P = 0.172$ for Order and $P = 0.093$ for Family). A majority of the significantly coherent relationships
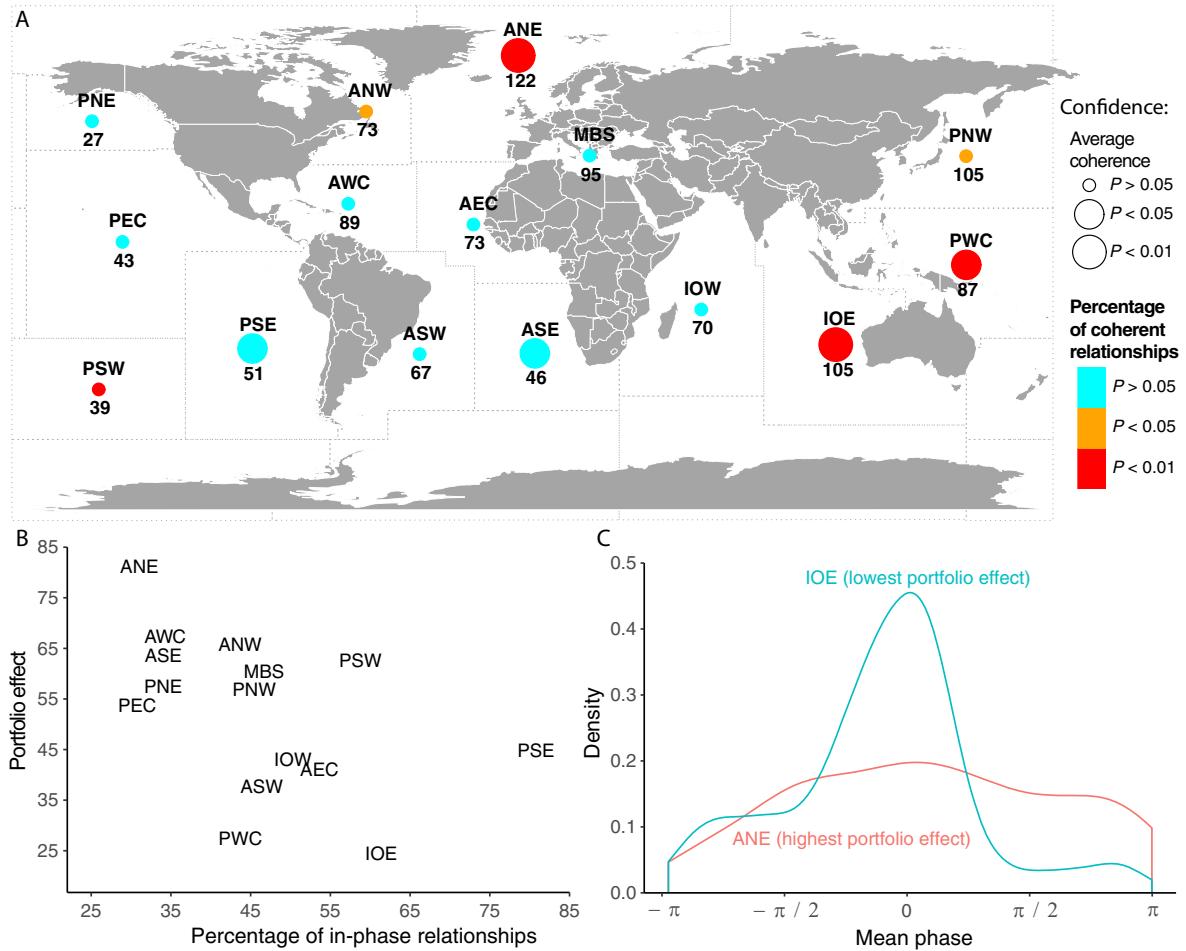
FIG. 3. Global coherence hotspots and relationship to portfolio effects for fishery catches. (A) Map of FAO regions ranked by confidence (*P*) that the observed coherence (in terms of average coherence values or the percentage of coherent relationships) is greater than that expected from the null model. Larger sizes and warmer colors represent regions with stronger evidence for coherence. The number of fisheries in each region is written below each dot. (B) Scatterplot showing that the strength of the portfolio effect is weaker (*y*-axis) in FAO regions with a higher percentage of in-phase relationships (*x*-axis). (C) Density plot of mean phase relationships within eastern Indian Ocean (IOE) and the northeast Atlantic (ANE), the two regions with the lowest and the highest portfolio effect, respectively. A, Atlantic; P, Pacific; IO, Indian Ocean; MBS, Mediterranean and Black Sea; N, S, E, W are North, South, East, West, respectively; C, central.

within or across regions were species from the Order Perciformes (perch-like fishes), which was the dominant Order within the fisheries catch time series (Appendix S1: Table S1 and Fig. S8). Species from the Family Scombridae (tunas) were the most common Family for coherent relationships both within and across regions, again the dominant Family within the fisheries catch time series (Appendix S1: Table S1), followed by those from the Family Istiophoridae (marlins; Appendix S1: Table S1 and Fig. S8).

Global hotspots of coherence

Our analysis identified a subset of FAO regions with particularly strong coherence; the northeast Atlantic, western central Pacific, and eastern Indian Ocean (Fig. 3 A, Appendix S1: Figs. S9, S10). The strongest coherent

relationships in the northeast Atlantic were dominated by benthic fishes (e.g., pollock, sparids, and hake) and prawns; those in the western central Pacific had a mix of pelagic fishes (e.g., barracuda, marlin, and Indian scad) and benthic fishes (e.g., threadfins, lizardfish, and flatfish); and those in the eastern Indian Ocean were dominated by pelagic species such as sharks, tunas, and mackerels. These coherent relationships had a mix of in-phase (e.g., skipjack tuna and blue shark from eastern Indian Ocean), anti-phase (e.g., lizardfish and threadfin from western central Pacific) and phase-lagged (e.g., prawn and pollock from northeast Atlantic) relationships (Appendix S1: Fig. S11). Additionally, the fishery catches were commonly coherent at fluctuation timescales of <8 yr (e.g., Appendix S1: Fig. S11).

For these three hotspots of coherence, we additionally examined time series of biomass and fishing mortality

(Appendix S1: Table S2). Strong coherences were generally more common among fish biomass (69.39% of stocks) time series than among fishing mortality (2.67% of stocks), but coherent fishing mortality did occur in the eastern Indian Ocean (Appendix S1: Figs. S12, S13).

None of the sardine and anchovy fishery catches had significant coherence within (Appendix S1: Fig. S14) or between FAO regions. This suggests that sardine and anchovy catches have not had consistently related dynamics at the timescales considered by this study. However, the Pearson's correlation between sardine and anchovy in the northwest Pacific was statistically significant, likely due to trends or cycles at timescales longer than those considered herein (Appendix S1: Fig. S14).

Portfolio effects

Across regions, the eastern Indian Ocean had the weakest portfolio effect in fishery catches and northeast Atlantic had the strongest portfolio effect (Fig. 3B). Both regions were hotspots for coherence in catches (Fig. 3A), but a majority of the coherent relationships in the eastern Indian Ocean were in-phase, while few relationships in the northeast Atlantic were in-phase (Fig. 3 C). Hence, the phase relationships between fisheries were linked to the strength of portfolio effects. The best predictor of the strength of portfolio effects was the percentage of in-phase relationships at timescales of 8–12 yr. The second-best predictor was the percentage of anti-phase relationships at timescales of 12–16 yr (Table 1). The number of taxa was not an important contributor ($\Delta AIC_c = 5.4$) to variation in the strength of portfolio effects across regions (Table 1).

Discussion

We found evidence for significantly coherent fluctuations among marine fishery catches globally. Nearly all marine fishery catch time series (96%) have been fluctuating persistently and with consistent phase relationships with at least one other fishery, usually among different species within the same taxonomic group and same geographic region, since at least the 1950s. This finding indicates the presence of community synchrony within fishery catches. The northeast Atlantic, eastern Indian Ocean, and western central Pacific in particular stood out as geographic hotspots of coherence. Most of the statistically significant coherence relationships were in-phase, which tended to create weaker portfolio effects among fishery catches. Regions where anti-phase and phase-lagged relationships were more common displayed the strongest portfolio effects. Contrary to expectations, the number of stocks had little influence on the strength of portfolio effects. The use of wavelet coherence to examine phase relationships and consistent relationships over the entire time period (as opposed to ephemeral relationships) are a unique feature of this approach to understanding synchrony and portfolio effects.

There was strong evidence that coherence among fishery catches was clustered geographically. Coherence within taxonomic groups was also driven by coherent pairs of fishery catches within rather than across regions. Our results are consistent with earlier studies on catches of pelagic species (tuna, billfish, and swordfish) in both the Indian and Atlantic oceans, where variability in catches were structured geographically within the two ocean basins (Corbineau et al. 2008, Rouyer et al. 2008). However, our study has greatly extended the spatial scales of analysis and the number of species (510 unique taxa) compared to earlier studies with less than 10 species, emphasizing the global prevalence of coherence among fishery catches. Taken together, the previous and current results suggest that regional rather than species-specific or global factors are important drivers of synchronous fluctuations in fish populations and fishery catches (Alheit and Bakun 2010, Corbineau et al. 2010, Tsikliras et al. 2018).

Across the multiple spatial scales of this study, we found that most of the coherent relationships among

TABLE 1. Model selection results comparing 10 models for portfolio effects.

Rank	Variable	Coefficient	Intercept	R^2	df	ΔAIC_c	Ak.wt
1	in-phase (8–12 yr)	-0.829 ± 0.337	84.0 ± 13.9	0.355	3	0.00	0.383
2	anti-phase (12–16 yr)	0.643 ± 0.308	42.0 ± 5.97	0.284	3	1.36	0.194
3	intercept-only		51.1 ± 4.60	0.000	2	2.23	0.126
4	anti-phase (4–8 yr)	0.584 ± 0.427	41.8 ± 8.15	0.145	3	3.66	0.061
5	anti-phase (2–4 yr)	0.569 ± 0.449	42.9 ± 7.87	0.127	3	3.93	0.054
6	in-phase (12–16 yr)	-0.251 ± 0.219	63.9 ± 12.0	0.107	3	4.22	0.046
7	in-phase (4–8 yr)	-0.229 ± 0.207	61.9 ± 10.7	0.100	3	4.33	0.044
8	in-phase (2–4 yr)	-0.283 ± 0.264	66.0 ± 14.6	0.094	3	4.41	0.042
9	number of taxa	0.094 ± 0.197	43.8 ± 16.1	0.020	3	5.43	0.025
10	anti-phase (8–12 yr)	0.095 ± 0.270	49.6 ± 6.43	0.011	3	5.55	0.024

Notes: Rankings were based on the difference in second-order Akaike information criterion (ΔAIC_c). Predictors included percentage of in-phase relationships (in-phase), percentage of anti-phase relationships (anti-phase), and the number of taxa in each region (number of taxa). In-phase and anti-phase predictors were calculated separately by timescale bands of 2–4, 4–8, 8–12, and 12–16 years (yr). Coefficients (mean $\pm$ SE) are shown for each predictor. Akaike weights (Ak.wt), variance explained (R^2), and degrees of freedom (df) are also shown for each model.

fishery catches were in-phase rather than anti-phase or phase-lagged, particularly at the smallest spatial scale of FAO regions. The handful of global studies of synchrony have focused on in-phase relationships between species of overwintering birds in North America (Koenig and Liebhold 2016), phytoplankton (Defriez and Reuman 2017), or predator–prey interactions (Kharouba et al. 2018). Few global studies have examined anti-phase relationships, with two examples being the alternations of sardine and anchovy (Izquierdo-Peña et al. 2019, Siple et al. 2020), and only one global study, to our knowledge, examined a variety of phases (Johnson et al. 2005). Our analysis examined community synchrony across all types of phase relationships and found a prevalence of in-phase relationships among fishery catches, both within regions and between different species. Our findings that coherences were regionally clustered and that in-phase relationships were common suggest that external factors drive the observed coherence.

Fisheries are coupled social-ecological systems, so external factors that can drive coherence in fishery catches include climate variation (a bottom-up effect acting through population biomass) or shared fisheries harvest (a top-down effect through fisheries effort). Our observation that most coherent phase relationships occurred at short timescales of less than 8 yr fits with the variability of El Niño-Southern Oscillation (ENSO) patterns (McPhaden et al. 2006) and supports environmental variability as a driver of synchronous fishery catches. Our examination of biomass and fishing mortality time series in three regions also provided evidence that bottom-up effects acting through population biomass were more common. Alternatively, shared fisheries management or economic conditions can drive similar changes in harvest rates across fisheries within regions (Rouyer et al. 2008, Frank et al. 2016), and these top-down effects should not be discounted. Skipjack tuna and blue shark catches in the eastern Indian Ocean displayed in-phase relationships, for example, as might be expected from shared targeting by the longline fleet (Kroodsma et al. 2018). Commercial fishing effort patterns are driven largely by economics (Sethi et al. 2010), and both fuel costs (Parker and Tyedmers 2015) and revenue (the price of fish and fish products like surimi) fluctuate together in a global market (Fernandez-Polanco 2016). Global geopolitical events such as the two World Wars and the widespread extension of Exclusive Economic Zones in the 1970s, regional holidays, and fishing closures can also result in synchronous changes in harvest rates at nearly global spatial scales (Smith 1994, Kroodsma et al. 2018). Hence, the effects of management and economics can extend across multi-species fisheries and across large spatial scales in these social-ecological systems.

The northeast Atlantic, western central Pacific, and eastern Indian Ocean geographic regions stood out as hotspots of coherence among fishery catches. Of these, the northeast Atlantic and western central Pacific have both been intensively fished (Swartz et al. 2010, Kroodsma et al. 2018) and have high cumulative human impacts (Halpern et al. 2008). Previous studies have found that populations of exploited species tend to fluctuate more than unexploited species, in part due to age-truncation of populations and weakening of density-dependent processes (Hsieh et al. 2006, Anderson et al. 2008, Shelton and Mangel 2011). Intense fishing activity in these two regions may have increased population responsiveness to climate variability, resulting in substantial coherence of both catch and biomass in these two regions. Such responses to climate variability would be similar to those observed in heavily fished demersal populations in the Mediterranean (Quetglas et al. 2013). Our result that sardine and anchovy, both intensely fished forage species, were not coherent contrasts with previously held notions of strong asynchrony (Lluch-Belda et al. 1992, Schwartzlose et al. 1999), but supports a recent analysis showing a lack of asynchrony between these two species (Siple et al. 2020). Within the Indian Ocean, tuna catch rates have also been strongly associated with climate signals (Ménard et al. 2007). However, an alternative mechanism for high coherence in fishery catches is a change in fishing effort within a multi-species fishery (Hilborn et al. 2012, Frank et al. 2016), such as tunas and billfishes both targeted by the eastern Indian Ocean longline fleet (Kroodsma et al. 2018). Similarly, Atlantic Ocean tuna and billfish caught with the same gear type are more likely to fluctuate together than species caught with different gears (Rouyer et al. 2008). It is likely that both fishing effort and climate, or interactions between the two (Corbineau et al. 2008, Quetglas et al. 2013), have contributed to fishery catch coherence in these regional hotspots.

The variability of marine fishery yields are a key concern given the importance of marine resources to food security and livelihoods for many countries (FAO 2014). Harvesting a greater diversity of fisheries helps buffer economies from natural fisheries variability (Cline et al. 2017) and species diversity tends to decrease temporal variability of ecosystem functioning (Hooper et al. 2005). However, our results show instead that a more important factor can be the type of phase relationship among fishery catches. The two regions with the weakest portfolio effects for fishery catches (western central Pacific and eastern Indian Ocean) were dominated by in-phase relationships. Both regions include parts of Southeast Asia, which accounted for 20% of the global production of marine capture fisheries in 2014 and is an important influence on global markets (SEAFDEC 2017). In contrast, the northeast Atlantic had the strongest portfolio effect, driven by strong contributions of anti-phase and phase-lagged relationships. The importance of asynchrony observed in this study agrees with existing theory that portfolio effects depend on both a synchrony effect and a weighted average population variability effect (Thibaut and Connolly 2013). It is likely that a substantial degree of synchrony among marine

fishery catches reduces the effective number of taxa and thus the importance of species diversity. Our calculation of portfolio effects was based on catch data, which, as discussed in the previous paragraph, could reflect either changes in biomass or changes in fishing effort (Pauly et al. 2013). Our analyses of biomass and fishing mortality data in three regions helped to highlight that both can be coherent, though coherence was more common among biomass than among fishing mortality time series. This study provides deeper insight into the synchrony effect by accounting for all types of phase relationships, allowing us to show the relative importance of these effects in nature as opposed to a single measure of synchrony or asynchrony.

In conclusion, we have shown that a large fraction of marine fishery catches are coherent across global, oceanic basin, and regional scales, and that the northeast Atlantic, western central Pacific and eastern Indian Ocean are hotspots of coherence. The majority of the coherent relationships among catches were in-phase, which weaken portfolio effects among fishery catches and leads to instability of marine fisheries yields. Understanding variability in marine food resources is critical because of its importance to society, and the vulnerability of this wild food source to environmental and anthropogenic forces such as climate and overfishing.

Literature Cited

Alheit, J., and A. Bakun. 2010. Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical–biological linkage mechanisms. Journal of Marine Systems 79:267–285.

Anderson, C. N. K., C.-H. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. Nature 452:835.

Barton, K. 2015. Multi-model inference. R package version 1.13.4. http://CRAN.R-project.org/package=MuMIn

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) 57:289–300.

Branch, T. A., O. P. Jensen, D. Ricard, Y. Ye, and R. Hilborn. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. Conservation Biology 25:777–786.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Buttay, L., B. Cazelles, A. Miranda, G. Casas, E. Nogueira, and R. González-Quirós. 2017. Environmental multi-scale effects on zooplankton inter-specific synchrony. Limnology and Oceanography 62:1355–1365.

Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. Canadian Journal of Fisheries and Aquatic Sciences 68:1579–1589.

Cazelles, B., M. Chavez, D. Berteaux, F. Ménard, J. O. Vik, S. Jenouvrier, and N. C. Stenseth. 2008. Wavelet analysis of ecological time series. Oecologia 156:287–304.

Cheal, A. J., S. Delean, H. Sweatman, and A. A. Thompson. 2007. Spatial synchrony in coral reef populations and the influence of climate. Ecology 88:158–169.

Cline, T. J., D. E. Schindler, and R. Hilborn. 2017. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. Nature Communications 8:14042.

Corbineau, A., T. Rouyer, B. Cazelles, J.-M. Fromentin, A. Fonteneau, and F. Ménard. 2008. Time series analysis of tuna and swordfish catches and climate variability in the Indian Ocean (1968–2003). Aquatic Living Resources 21:277–285.

Corbineau, A., T. Rouyer, J. M. Fromentin, B. Cazelles, A. Fonteneau, and F. Ménard. 2010. Patterns of variations in large pelagic fish: a comparative approach between the Indian and the Atlantic Oceans. Progress in Oceanography 86:276–282.

Defriez, E. J., and D. C. Reuman. 2017. A global geography of synchrony for marine phytoplankton. Global Ecology and Biogeography 26:867–877.

FAO. 2014. The State of World Fisheries and Aquaculture—2014 (SOFIA). Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO. 2018. The State of World Fisheries and Aquaculture 2018—Meeting the sustainable development goals. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fernandez-Polanco, J. M. 2016. An overview of the global tuna market. Pages 63–65 in A. Child, editor. GLOBEFISH s. Food and Agriculture Organization, Rome, Italy.

Figge, F. 2004. Bio-folio: applying portfolio theory to biodiversity. Biodiversity & Conservation 13:827–849.

Frank, K. T., B. Petrie, W. C. Leggett, and D. G. Boyce. 2016. Large scale, synchronous variability of marine fish populations driven by commercial exploitation. Proceedings of the National Academy of Sciences USA 113:8248–8253.

Grenfell, B. T., K. Wilson, B. F. Finkenstädt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. Nature 394:674.

Halpern, B. S., et al. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Haynes, K. J., O. N. Bjørnstad, A. J. Allstadt, and A. M. Liebhold. 2013. Geographical variation in the spatial synchrony of a forest-defoliating insect: isolation of environmental and spatial drivers. Proceedings of the Royal Society B 280:20122373.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences USA 100:6564–6568.

Hilborn, R., I. J. Stewart, T. A. Branch, and O. P. Jensen. 2012. Defining trade-offs among conservation, profitability, and food security in the California current bottom-trawl fishery. Conservation Biology 26:257–268.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Hsieh, C.-H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature 443:859–862.

Huitu, O., K. Norrdahl, and E. Korpimäki. 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. Ecography 27:197–206.

Izquierdo-Peña, V., S. E. Lluch-Cota, M. E. Hernandez-Rivas, and R. O. Martínez-Rincón. 2019. Revisiting the Regime Problem hypothesis: 25 years later. Deep Sea Research Part II: Topical Studies in Oceanography 159:4–10.

Johnson, D. M., A. Liebhold, O. N. Bjørnstad, and M. L. McManus. 2005. Circumpolar variation in periodicity and synchrony among gypsy moth populations. Journal of Animal Ecology 74:882–892.

Kasperski, S., and D. S. Holland. 2013. Income diversification and risk for fishermen. Proceedings of the National Academy of Sciences USA 110:2076–2081.

Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences USA 115:5211–5216.

Koenig, W. D., and A. M. Liebhold. 2016. Temporally increasing spatial synchrony of North American temperature and bird populations. Nature Climate Change 6:614.

Kroodsma, D. A., et al. 2018. Tracking the global footprint of fisheries. Science 359:904–908.

Laevastu, T., and R. Marasco. 1982. Fluctuations of fish stocks and the consequences of the fluctuations to fishery and its management. National Oceanic and Atmospheric Administration, Seattle, Washington, USA.

Lluch-Belda, D., R. A. Schwartzlose, R. Serra, R. Parrish, T. Kawasaki, D. Hedgecock, and R. J. M. Crawford. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. Fisheries Oceanography 1:339–347.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. American Naturalist 172: E48–E66.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2006. ENSO as an integrating concept in earth science. Science 314:1740–1745.

Ménard, F., F. Marsac, E. Bellier, and B. Cazelles. 2007. Climatic oscillations and tuna catch rates in the Indian Ocean: a wavelet approach to time series analysis. Fisheries Oceanography 16:95–104.

Moore, J. W., M. McClure, L. A. Rogers, and D. E. Schindler. 2010. Synchronization and portfolio performance of threatened salmon. Conservation Letters 3:340–348.

Moran, P. 1953. The statistical analysis of the Canadian Lynx cycle. Australian Journal of Zoology 1:291–298.

North, B. V., D. Curtis, and P. C. Sham. 2002. A note on the calculation of empirical P values from Monte Carlo procedures. American Journal of Human Genetics 71:439–441.

Ong, J. J. L. 2020. Data and code for 'Global hotspots of coherent marine fishery catches' (Version v1.0.0). Zenodo. https://doi.org/10.5281/zenodo.3981539

Parker, R. W. R., and P. H. Tyedmers. 2015. Fuel consumption of global fishing fleets: current understanding and knowledge gaps. Fish and Fisheries 16:684–696.

Pauly, D., R. Hilborn, and T. A. Branch. 2013. Fisheries: Does catch reflect abundance? Nature 494:303–306.

Quetglas, A., F. Ordines, M. Hidalgo, S. Monserrat, S. Ruiz, Á. Amores, J. Moranta, and E. Massutí. 2013. Synchronous combined effects of fishing and climate within a demersal community. ICES Journal of Marine Science 70:319–328.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raimondo, S., M. Turcáni, J. Patoèka, and A. M. Liebhold. 2004. Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. Oikos 107:462–470.

Reuman, D. C., T. L. Anderson, J. A. Walter, L. Zhao, and L. W. Sheppard. 2018. Wavelet approaches to studies of synchrony in ecology and other fields. R package version 1.0.1. https://cran.r-project.org/web/packages/wsyn/index.html

Ricard, D., C. Minto, O. P. Jensen, and J. K. Baum. 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish and Fisheries 13:380–398.

Robinson, J. P. W., M. Dornelas, and A. F. Ojanguren. 2013. Interspecific synchrony of seabird population growth rate and breeding success. Ecology and evolution 3: 2013–2019.

Rouyer, T., J.-M. Fromentin, F. Ménard, B. Cazelles, K. Briand, R. Pianet, B. Planque, and N. C. Stenseth. 2008. Complex interplays among population dynamics, environmental forcing, and exploitation in fisheries. Proceedings of the National Academy of Sciences USA 105:5420–5425.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13:257–263.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Schwartzlose, R. A., et al. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21:289–347.

SEAFDEC. 2017. Southeast Asian State of Fisheries and Aquaculture 2017. Southeast Asian Fisheries Development Center, Bangkok, Thailand.

Sethi, S. A., T. A. Branch, and R. Watson. 2010. Global fishery development patterns are driven by profit but not trophic level. Proceedings of the National Academy of Sciences USA 107:12163–12167.

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proceedings of the National Academy of Sciences USA 108:7075–7080.

Sheppard, L. W., J. R. Bell, R. Harrington, and D. C. Reuman. 2016. Changes in large-scale climate alter spatial synchrony of aphid pests. Nature Climate Change 6:610–613.

Sheppard, L. W., P. C. Reid, and D. C. Reuman. 2017. Rapid surrogate testing of wavelet coherences. EPJ Nonlinear Biomedical Physics 5:1.

Siple, M. C., T. E. Essington, L. A. K. Barnett, and M. D. Scheuerell. 2020. Limited evidence for sardine and anchovy asynchrony: re-examining an old story. Proceedings of the Royal Society B 287:20192781.

Smith, T. D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855–1955. Cambridge University Press, Cambridge, UK.

Sugihara, G., R. May, H. Ye, C.-H. Hsieh, E. Deyle, M. Fogarty, and S. Munch. 2012. Detecting causality in complex ecosystems. Science 338:496–500.

Swartz, W., E. Sala, S. Tracey, R. Watson, and D. Pauly. 2010. The spatial expansion and ecological footprint of fisheries (1950 to present). PLoS ONE 5:e15143.

Thibaut, L. M., and S. R. Connolly. 2013. Understanding diversity–stability relationships: towards a unified model of portfolio effects. Ecology Letters 16:140–150.

Torrence, C., and G. P. Compo. 1998. A Practical guide to wavelet analysis. Bulletin of the American Meteorological Society 79:61–78.

Tsikliras, A. C., P. Licandro, A. Pardalou, I. H. McQuinn, J. P. Gröger, and J. Alheit. 2018. Synchronization of Mediterranean pelagic fish populations with the North Atlantic climate variability. Deep Sea Research Part II: Topical Studies in Oceanography 159:143–151.

Zhao, L., T. L. Anderson, J. A. Walter, L. W. Sheppard, and D. C. Reuman. 2018. R package for Reuman lab. R package version 0.1.0. https://github.com/reumandc/reumannplatz

Zimmermann, F., M. Claireaux, and K. Enberg. 2019. Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management. Fish and Fisheries 20:518–536.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2321/full

Data Availability

Compiled data and R scripts (Ong 2020) are available on Zenodo: https://doi.org/10.5281/zenodo.3981539.