

# Recent trends in abundance and fishing pressure of agency-assessed small pelagic fish stocks

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## Abstract

Small pelagic fishes are used for human consumption, fishmeal and fish oil. They constitute 25% of global fish catch and have been of considerable conservation concern because of their intermediate position in aquatic food webs, often being a dominant dietary component of marine predators. This paper provides an overview of trends in abundance and fishing pressure on small pelagic fish stocks from single-species scientific assessments that constitute 60% of global small pelagic catch. While most individual stocks have exhibited wide variability in abundance (typical of small pelagics compared with other fish taxa), across stocks there has been remarkable stability in average fishing pressure and biomass since 1970. On average, since 1970, the biomass of assessed small pelagic stocks is estimated to have been slightly above the biomass that would produce maximum sustainable yield, but estimation of this quantity for highly fluctuating stocks is quite uncertain. There were significant differences among assessed regions, with the Mediterranean and Black Sea of greatest concern for high and growing fishing pressure. The 40% of global small pelagic fish catch not covered by single-species quantitative stock assessments since 1970 comes largely from Asia,

Correction added on July 07, 2022, after first online publication: Table S1 has been updated

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where catches have continued to increase. At regional levels, the average abundance of assessed small pelagic fish is largely unrelated to average fishing pressure, which we argue results both from the portfolio effect, where numerous stocks fluctuate with little correlation in abundance, and from the short life span of small pelagics coupled with recruitment largely independent of spawning abundance.

#### KEYWORDS

fisheries management, overfishing, small pelagic fish, small pelagic fishes, sustainable fishing

## 1 | INTRODUCTION

The small pelagic fishes of the world are often called 'forage fish' because they are among the most abundant fishes in the ocean and serve as a dominant item in the diet of higher trophic levels. They are also a major item in the human food system, both for direct human consumption, and used in aquaculture either directly, or as fishmeal and fish oil. There has been concern about the status of small pelagic fish and the impact of fishing for small pelagic fish on marine predators (Cury et al., 2011; Pikitch et al., 2014; Smith et al., 2011), although Christensen et al. (2014) estimated that small pelagic fish are now more than twice as abundant as before industrial fishing began due to depletion of their predators.

Most small pelagic fish are from the taxonomic order Clupeiformes (sardines, herring, menhaden, shad, sprat, sardinella and anchovies), but normally include the order Belanoformes (saury), and families Ammodytidae (sandlance), Atherinidae (smelt), Osmeridae (capelin and eulachon), Argentinidae (argentinines), Caesionidae (fusiliers) and Plecoglossidae (sweetfish). While other taxa such as euphausiids, shrimp and squid are also common forage species, we follow the example of Pikitch et al. (2014) and Cury et al. (2011) in excluding shrimp, and squid are excluded because they are commonly of a higher trophic level than most small pelagic species. We are also unaware of any quantitative stock assessments estimating time series of biomass and fishing pressure relative to biological reference points of euphausiids. Throughout the rest of the paper we use the term small pelagic fish to refer specifically to the fish taxa listed above, and exclude invertebrates.

Small pelagic fishes are characterized by high natural mortality rates and intrinsic rates of population growth, and large fluctuations in abundance that have been documented to occur over many centuries (Barange et al., 2009; Baumgartner et al., 1992; Schwartzlose et al., 1999; Soutar & Isaacs, 1969, 1974). Their abundance seems to be strongly dependent on environmental conditions (Cushing, 1982) and periodic regimes of high and low abundance are common (Vertpre et al., 2013). Szuwalski et al. (2019) found that in only 14 out of 52 small pelagic fish stocks, the relationship between spawning stock and recruitment was best explained by a Ricker spawner recruit curve, while for the other stocks temporal changes in productivity provided a better explanation. Because natural mortality rates for small pelagic fishes are on average high relative to recent fishing mortality rates (Kolding et al., 2016), small pelagic fish may respond less to moderate changes in fishing pressure than do species at higher trophic levels.

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Concerns about the impact of fishing small pelagic fish on their predators have arisen both globally and in specific regions (Cury et al., 2011; Hilborn et al., 2017; Pikitch et al., 2014; Smith et al., 2011; Walters et al., 2016). Many of these papers have recommended that appropriate fishing pressure targets should be below those related to maximum sustainable yield in order to provide higher biomass

for their predators. By contrast, Garcia et al. (2012) suggested that balanced harvesting, which would include more intense fisheries on low trophic levels, could increase global fish production. Cury et al. (2000) and Fauchald et al. (2011) focused on the wasp-waist nature of some ecosystems in which a few dominant small pelagic species provide a high proportion of the energy that reaches upper trophic levels, and on the need to maintain the abundance of these important species.

Regional reviews of the status of small pelagic fish stocks have been presented for many regions, including Alaska (Ormseth, 2018), NW Africa (Lakhnigie et al., 2019), the North Sea (Engelhard et al., 2014), the Salish Sea (Therriault et al., 2009), Japan (Yatsu, 2019) and along the Southern Humboldt Current Ecosystem (Alheit & Niquen, 2004; Canales et al., 2020; Garcés et al., 2019). Alder et al. (2008) looked at trends in catch and use but not in abundance. Barange et al. (2009) considered trends in catch and abundance of 29 small pelagic fish stocks. Canales et al. (2020) explored the drivers of anchovy biomass off central-Southern Chile integrating fishing, climate variability and endogenous effects and concluded that fishing played the most significant role. Birge et al. (2021) reviewed the conservation status of small pelagic fish and found that, compared to other fish taxa, small pelagic fish had the lowest risk of extinction but the highest proportion of unevaluated status against IUCN red list criteria.

The purpose of this paper is to: (1) synthesize the results of single-species stock assessments included in the RAM Legacy Stock Assessment Database (RAMLDB, 2021) that quantify the current and recent historical trend in abundance and fishing pressure of small pelagic fish since 1970; (2) understand why the regional average trends in both abundance and fishing pressure are much more stable in the last 50 years than those of other taxa despite the fact that some individual small pelagic fish stocks fluctuate greatly; and (3) consider the available information on small pelagic fish from the 40% of global production that is not currently in RAMLDB for lack of estimated time series of biomass and fishing pressure.

## 2 | MATERIALS AND METHODS

Analyses outlined below depend almost exclusively on two kinds of data: stock assessments of trends in abundance and fishing pressure (exploitation rate or  $F$ ), and catch tonnage. The abundance trends come from the RAMLDB and catch data from the FAO landings database. Both are described in the following sections.

### 2.1 | RAMLDB

The RAMLDB ([www.ramlegacy.org](http://www.ramlegacy.org)) is a compilation of stock assessments that contain time series of stock abundance, catch, fishing mortality rates or fishing pressure, and recruitment, as well as a range of biological and management parameters (Ricard et al., 2012). These assessments are gathered by local regional coordinators and

are performed by national science agencies or regional fisheries management organizations. Since 2007, we have endeavoured to include all stock assessments that contain time series data resulting from agency stock assessments, are publicly available, and use methods that are considered reliable for estimating time series of stock status relative to biological reference points. We do not include yield-per-recruit analyses, and assessments estimating the stock status or fishing mortality at a single time that might result from length based methods like LBSPR (Hordyk et al., 2015). We do not include assessments that do not contain publicly available time series of catch and abundance, nor assessments from individual journal papers that are not the product of government or international agency research staff.

Version 4.494 (RAMLDB, 2021) contains data for over 1200 stocks, which together constitute almost 50% of fish catch reported to FAO (2019). RAMLDB includes coverage of most of the small pelagic fish landings reported to FAO from North America, Europe, West Africa, Peru, Chile, Argentina, Australia, Japan, Russia and South Africa (Figure 1). In contrast, almost no time series of abundance and fishing pressure of small pelagic fish stocks are covered in RAMLDB from Asia (apart from Japan), Mexico, and the Middle East (Figure 1). The assessments in RAMLDB cover a variety of temporal durations, with some extending back to the 19th century, but in general coverage is quite poor until about 1970; therefore, our summarized trends begin in 1970. The small pelagic fish stocks covered by the RAMLDB account for 60% of global small pelagic fish landings reported to FAO between 1970 and 2017.

Many countries or regions have stock assessments covering most or all of their small pelagic fish catch, including the USA, Iceland, Norway, Japan, Russia, the European Union, Chile, Peru, Morocco, Mauritania, most of West Africa and South Africa (Figure 1). There are no stock assessments available in RAMLDB for the large fisheries in South and Southeast Asia, China, Korea and Pacific Russia, which constitute the majority of the 40% of global small pelagic fish landings that are not covered by RAMLDB and thus are not included in analyses here. There are some published assessments from these countries, but none have yet been vetted into the RAMLDB and few contain estimated time series of stock-specific abundance. They will be discussed later in the paper but our analysis of trends in abundance and fishing mortality will be confined to stocks currently in RAMLDB. Our analysis is therefore based on stocks that primarily come from countries with relatively strong fisheries management systems, although the Mediterranean and West Africa do have many countries typically considered to have somewhat weaker fisheries management systems. Stock assessments for small pelagic fish in RAMLDB originate from different government agencies, and assessments for individual stocks do not cover the same ranges of years. Most assessments tend to begin between 1960 and 1980, so years are unbalanced with respect to the number of stocks covered. Similarly, after 2012, fewer and fewer stocks have assessments covering those years. For some stocks, the most recent available assessments are several years out of

date; for other stocks, there may be a lag between an assessment's publication and it being entered into RAMLDB. Reconstructing the average abundance or fishing pressure in any year must therefore account for these 'ragged ends' of unequal data coverage in both early years and late years. The data coverage is most complete between the late 1990s and 2012. To overcome this problem of unbalanced coverage, we used a state-space model approach to estimate the mean trends in abundance and fishing pressure across stocks, treating time series of individual stocks as observations around the group mean (Hilborn et al., 2020; Hilborn et al., 2021; Melnychuk et al., 2020). A key feature of this state-space model is that it assumes auto-correlation from year to year, so that if the number of stocks with data available in a given year is low, the estimated mean will change slowly from years when many stocks had estimates available, thus will not chase sparse data points. When sample sizes are large, the state-space model estimate reflects the geometric mean of individual stocks. In the analysis of data in RAMLDB, we used the data from 1970 to 2020 or whatever years data were available for each stock within that range.

In addition to unequal temporal coverage across stocks, geographic coverages of small pelagic fish catch and abundance are not uniformly distributed worldwide. Because of the regional variation in small pelagic fish stocks, most of our analyses below are stratified by major FAO statistical area.

Almost all of our subsequent analysis rely on the estimated trends in abundance and fishing mortality from these assessments in RAMLDB; in our analysis, we treat these model outputs as input data, assuming these trends are known without error. While this

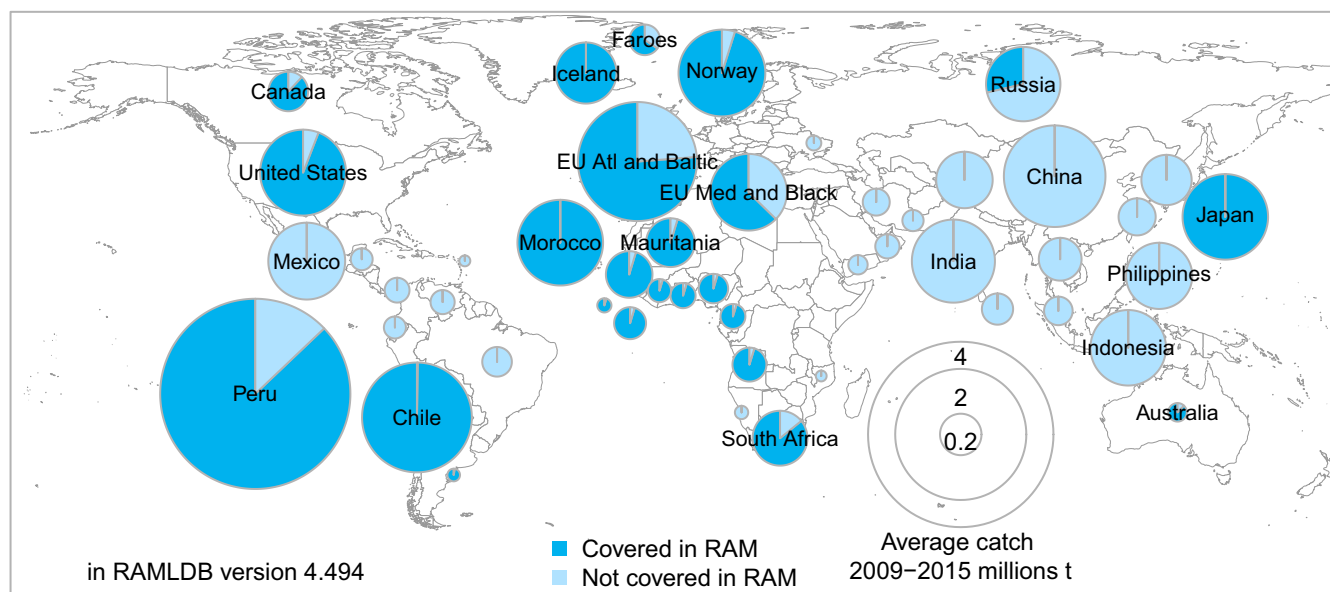
is common practice in cross-stock analyses such as ours, we acknowledge critiques of making these assumptions (e.g. Brooks & Deroba, 2015).

## 2.2 | FAO catch data

Global landings data are reported by individual countries to the Food and Agricultural Organization of the United Nations, which maintains these data with a consistent format across countries (FAO, 2019). The publicly available data contain the country, the FAO statistical area of the catch, scientific name, common name, and catch in metric tonnes. The database we used covers 1950–2017 (FAO, 2019). We included FAO landings data for the same orders and families we used to classify RAMLDB stocks as small pelagic fish. In some cases, landings are reported to FAO at a highly aggregated taxonomic level (e.g. 'Marine fish not elsewhere included'). The catch of small pelagic fish reported in those highly aggregated groups would not be included as small pelagic fish in Figure 1.

## 2.3 | EcoPath data

We use results of a large-scale EcoPath analysis to explore the relationship between fishing mortality and natural mortality for a range of taxa. These data come from 110 EcoPath models listed in the online supplementary material of Kolding et al. (2016), and the models are available in the EcoPath model repository (<http://ecobase.ecopath.org/>).



**FIGURE 1** Coverage by country or aggregated region of assessed small pelagic fish stocks contained in RAMLDB. Circle area is proportional to the country or region's average 2009–2015 annual catch of small pelagic fish as reported to FAO. Dark blue shading of circles represents the fraction of the country's recent average small pelagic fish catch covered by assessed stocks in RAMLDB. Circles are plotted for the following regions instead of individual countries: the Mediterranean (European Union countries), ICES Atlantic and North Sea waters (UK and EU countries). There is some imprecision in the assigned fractions because, with the exception of Northeast Atlantic stocks, assessed catches of transboundary stocks are assigned to the country with the highest catch fraction

## 2.4 | Estimation of stock status relative to target or MSY reference points

The status of stocks is commonly represented as estimated biomass and fishing pressure relative to biological reference points, which represent optimal levels in terms of maximizing yield while ensuring long-term stock conservation. For stocks subject to regime shifts in productivity, the reference points should change over time; in a period of low productivity, MSY will be lower and achieved with lower fishing pressure, but also at a lower biomass. Management targets could shift as a function of stock productivity to accommodate these changes over time and some agencies now do that (Canales & Cubillos, 2021; Siple et al., 2021). However, none of the assessments we used contain time varying biological reference points and thus represent the average across periods of high and low productivity.

A more common way to assess the status of fish stocks is by comparing time series of estimated biomass ( $B$ ) and fishing pressure ( $U$ ) to time-invariant biological reference points. Biomass is measured as spawning stock biomass if available in the assessment, otherwise total biomass. Fishing pressure is measured either as instantaneous fishing mortality rate ( $F$ ), or catch divided by total biomass, whichever units are used in the assessment. This is the approach used by FAO (FAO, 2020) and by most national fisheries agencies and Regional Fisheries Management Organizations (RFMOs) if they have not adopted productivity or regime-based reference points. Worm et al. (2009) and Hilborn et al. (2020) preferentially used MSY-based reference points when available for calculating ratios of  $B/B_{MSY}$  and  $U/U_{MSY}$ ; these ratios represent current or historical stock status. In this analysis, we preferentially use management target reference points when available because agencies may have considered ecosystem impacts of fishing on small pelagic fish predators or fluctuating productivity when setting management targets. If actual targets are not specified in the published assessments, we use MSY-based reference points. If neither management targets nor MSY reference points were available from the published assessment, they were estimated *post hoc* by fitting surplus production models to time series data from assessments as described in Hilborn et al. (2020) and Melnychuk et al. (2020). We recognize that constant values of reference points have limitations, but our interest is primarily in the trends in abundance and fishing pressure rather than in relation to the specific values of static reference points.

Throughout the rest of the paper, we will refer to management targets as  $U_{targ}$  and  $B_{targ}$ . Table S1 lists all stocks included in our analysis and summarizes values of status relative to reference points. Of the 120 small pelagic fish stocks in RAMLDB, 38 have no estimate of the biomass reference point, 29 have published management targets, 28 have published  $B_{MSY}$  values, and 25 have *post hoc* estimated  $B_{MSY}$ . For the  $U$  reference point, 38 have no estimate, 51 have published exploitation rate or  $F$  targets, and 31 have *post hoc* estimated  $U_{MSY}$ . While 31% of the 120 stocks do not have biomass or exploitation rate reference points, these are primarily small stocks and only constitute 9% of the average

catch. When calculating the geometric mean of  $U/U_{targ}$  across stocks, a small offset of 0.001 was added to all values to avoid values of zero.

## 2.5 | The portfolio effect

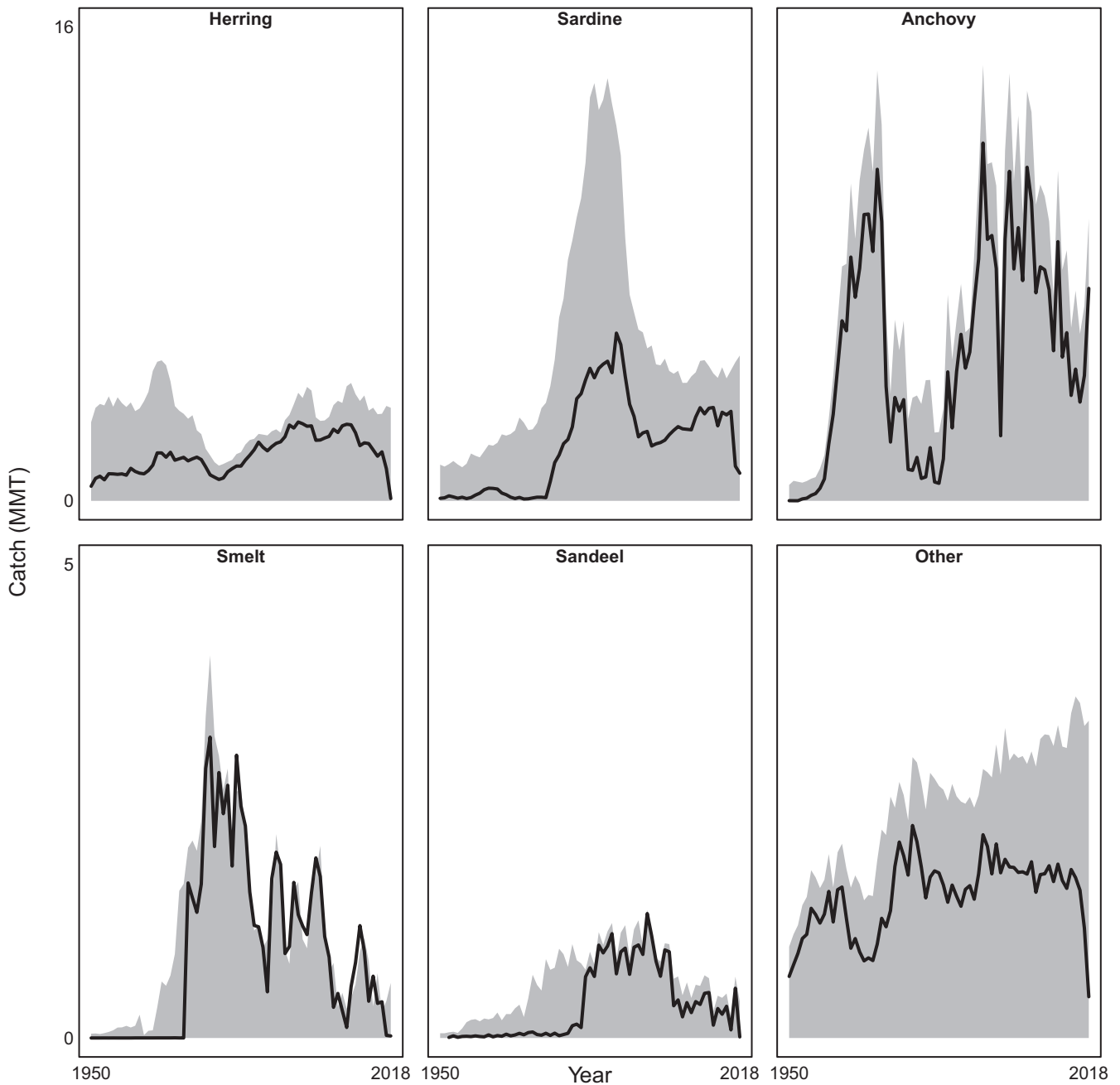
The portfolio effect is the idea that the mean of a mixture of stocks over time is more stable than individual stocks (Schindler et al., 2010). Results of the trends in abundance of small pelagic fish showed remarkable stability (shown later Figures 4 and 6), which led us to pursue a number of additional analyses relating to potential causes of this stability. The asynchrony of abundance of sardines and anchovies in many regions around the world has led to the hypothesis that such asynchrony may have biological causes and lead to stability in the total abundance of small pelagic fish (Lluch-Belda et al., 1989; Schwartzlose et al., 1999). Such asynchrony could provide a 'portfolio effect' for predators much as the portfolio effect can provide stability for fishing fleets (Schindler et al., 2010). Siple et al. (2020) have questioned some of the elements of the sardine/anchovy story, showing that the magnitude of the changes in abundance can be very different, and the asynchrony may be more apparent in catch than abundance. Nevertheless, it is worth exploring if asynchrony exists within regions in the abundance of small pelagic fish. To do this, we simply used the population abundance time series from RAMLDB and summarized the distribution of correlation coefficients between pairs of species within a region. We compared the distributions of correlations between small pelagic fish, groundfish and invertebrates and tested for significance using the Wilcoxon Mann Whitney rank sum test.

## 2.6 | Variability in biomass and fishing pressure

Another possible explanation for the observed stability of average small pelagic fish abundance compared to other taxa is that stocks are simply less variable, or fishing pressure is less variable, so we compared the variability in biomass and fishing pressure in two ways. First, we calculated the coefficient of variation of  $B/B_{targ}$  and  $U/U_{targ}$  for each stock and calculated the average for each region across major taxa. This allowed us to compare small pelagic fish to other taxonomic groups such as gadids and tunas. Then we explored year to year variation in the same quantities by calculating the coefficient of variation of the ratio of biomass at year  $y + 1$  divided by biomass at year  $y$ , and the change in fishing pressure similarly.

## 2.7 | Correlation between biomass change and current fishing pressure

Another way to explore fluctuations in abundance is to relate them to fluctuations in fishing pressure. Population dynamics models assume that stocks are more likely to increase at times of low fishing pressure and low abundance, and more likely to decrease at times of



**FIGURE 2** Trends in the total global catch (as reported to FAO) of six major groups of small pelagic fishes (filled grey area) and catch in RAMLDB (solid black line) from the same groups. Assignments of small pelagic fish stocks into these six groups are listed in Table S1. Coverage of RAMLDB stocks tends to decline in most recent years as few assessments go to 2018

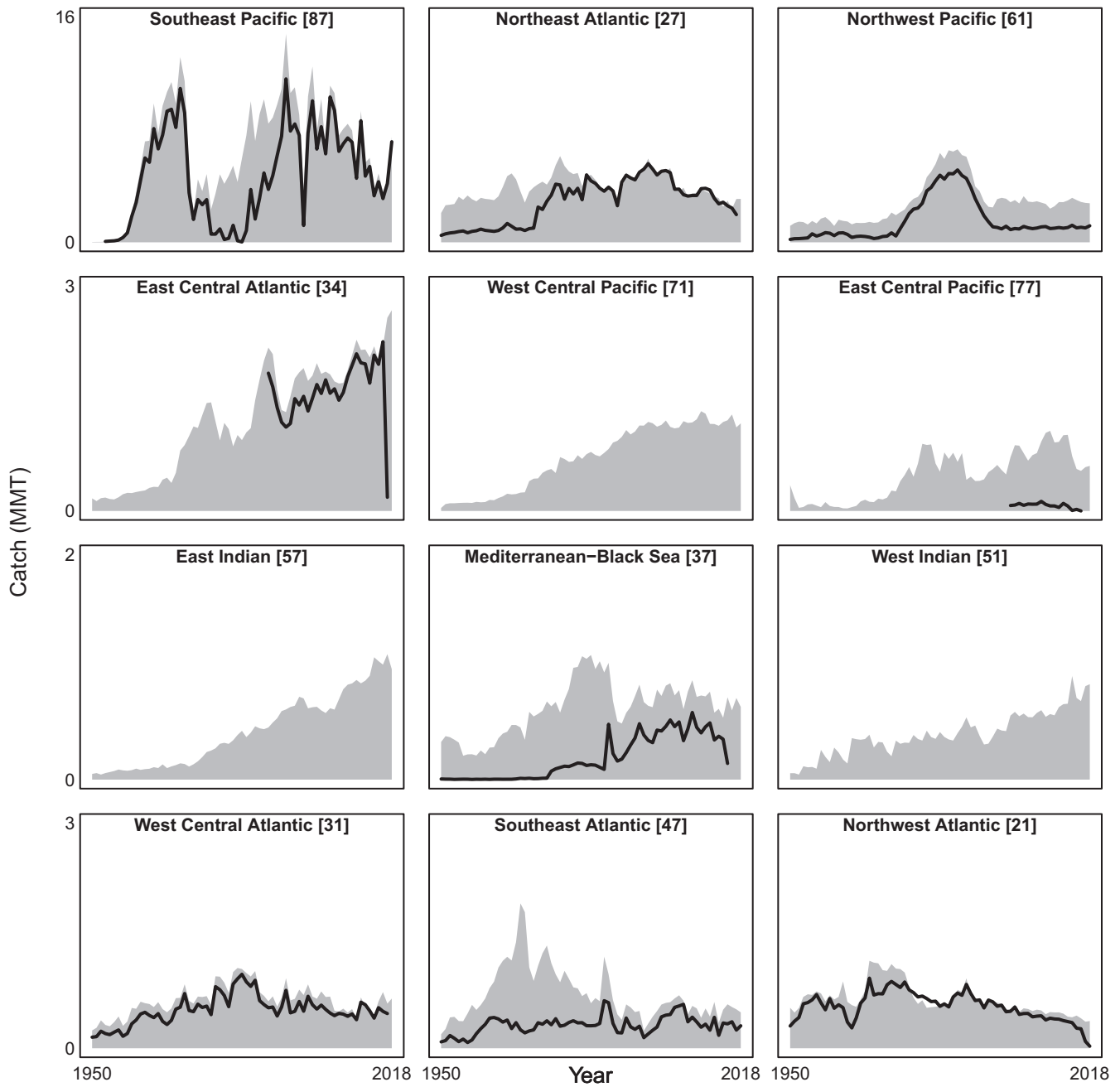
high fishing pressure and/or high stock abundance. This is certainly true when averaged across all stocks in the RAMLDB (Figure 3a in Hilborn et al. (2020)).

To see how much changes in fishing pressure impact changes in abundance, we can manipulate the logistic growth Equation (1) to a regression that explains the changes in  $B/B_{\text{targ}}$  based on current  $B/B_{\text{targ}}$  and  $U/U_{\text{targ}}$ .

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{k}\right) - B_t U_t. \quad (1)$$

Under this model,  $U_{\text{MSY}} = (r/2)$ , and  $B_{\text{MSY}} = (k/2)$ , we can transform Equation 2 into Equation 3 and simplify to Equation 4, which has the form of a linear regression model with no intercept. In this regression, the dependent variable is the rate of change of the population (with zero representing no change),  $r$  is the coefficient and the independent variable depends on both the biomass relative to  $B_{\text{targ}}$  and the fishing pressure relative to  $U_{\text{targ}}$ . When both biomass and fishing pressure are at the target reference point, then the right hand side is zero.

$$\frac{B_{t+1}}{B_t} - 1 = r \left(1 - \frac{B_t}{k}\right) - U_t \quad (2)$$



**FIGURE 3** Trends in catch of small pelagic fish in 12 FAO regions, from the FAO landings database (shaded grey area) and RAMLDB (solid black line). The number in square brackets [N] is the FAO region, and the n is the number of stocks included in each region

$$\frac{B_{t+1}/B_{targ} - 1}{B_t/B_{targ} - 1} = r \left( 1 - \frac{B_t/B_{targ}}{2} \right) - r \frac{U_t/U_{targ}}{2} \quad (3)$$

$$\frac{B_{t+1}/B_{targ} - 1}{B_t/B_{targ} - 1} = r \left[ \left( 1 - \frac{B_t/B_{targ}}{2} \right) - \frac{U_t/U_{targ}}{2} \right] \quad (4)$$

This analysis makes two simplifying assumptions, (1) that the production function is logistic and (2) that even when fishing

pressure is an instantaneous rate the model based on the discrete rate (Equations 1-4) still holds. While these equations are formulated using the logistic growth model, the regression is used simply to ask how much of the change in abundance can be explained by fishing pressure and by stock abundance. We performed three separate regressions to quantify the degree to which changes in biomass can be explained by: a joint regression of biomass and fishing pressure (Equation 4) together as explanatory variables; by biomass alone; and by fishing pressure alone.

### 3 | RESULTS

#### 3.1 | Trends in catch

Aggregate catches of major small pelagic fish groups worldwide are shown in Figure 2. The trends in catch have been highly variable: sardines showed a boom in the 1970s, the same time that anchovy declined; herring showed a decline in the 1970s and rebuilding in the 1980s–1990s, while smelt and sandeel showed a strong decline since the 1970s and 1990s, respectively. Other species of small pelagic fish have shown an increasing trend in aggregate catch since 1950.

If trends in aggregate catches are instead separated by FAO region (Figure 3), the most striking result is the general increasing trend in Asia (FAO Areas 71, 57 and 51) where there is no coverage of stocks in RAMLDB. Regions where we have high coverage with stock assessments in RAMLDB tend to show stable or declining landings with the exception of the East Central Atlantic (FAO area 34).

#### 3.2 | Mean trends in stock status

Mean trends across small pelagic fish stocks from all species groups and all FAO areas in RAMLDB show a remarkable stability in both abundance and fishing pressure (Figure 4). In this plot, the average

trend estimated under the state space model generally aligns with the median of assessed stocks in each year. Since the mid-1970s, the trend in relative fishing pressure has been continuously downward, with the estimated mean  $U/U_{\text{target}}$  greater than 1 in the 1970s and 1980s (i.e. fishing pressure was greater than target levels on average), slightly above 1 around the 1990s, and less than 1 during the 2000s and 2010s (Figure 4b). Currently, fishing pressure on average is about 70% of targets. Throughout this period, average biomass of stocks in RAMLDB has fluctuated slightly but has generally remained near or slightly greater than target levels (Figure 4a).

In all years, there is wide variation in individual stock status, but there does seem to be a reduction in very high fishing mortality rates after 2010 times when reductions in fishing pressure and catch were taking place in RAMLDB stocks, but in the unassessed parts of the world catches were generally increasing.

#### 3.3 | Individual stock status

Stock status is commonly expressed visually in co-plots of relative fishing pressure plotted against relative abundance, as shown in Figure 5 for individual small pelagic fish stocks in RAMLDB. The upper left quadrant is the area of greatest management concern; stocks in this quadrant have abundance below  $B_{\text{target}}$  and exploitation rate above  $U_{\text{target}}$ . We see 17 individual stocks in this quadrant.

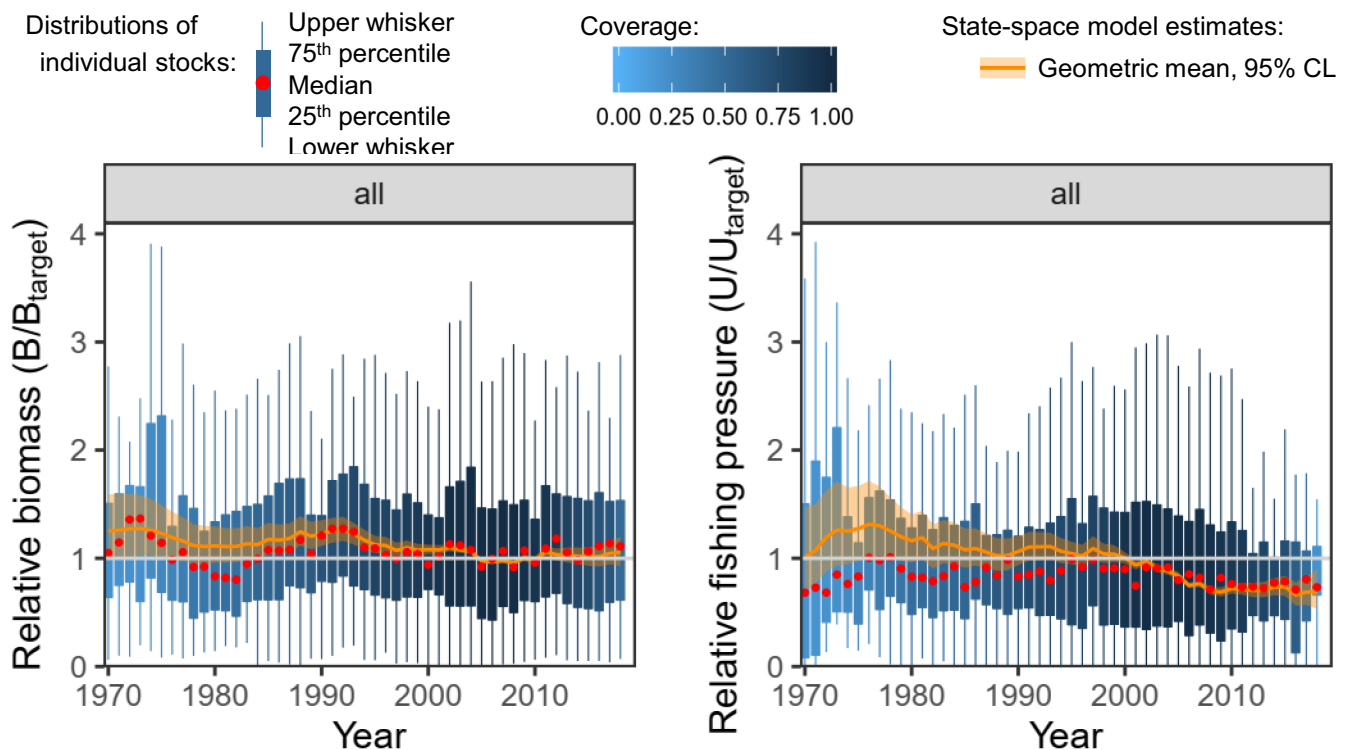
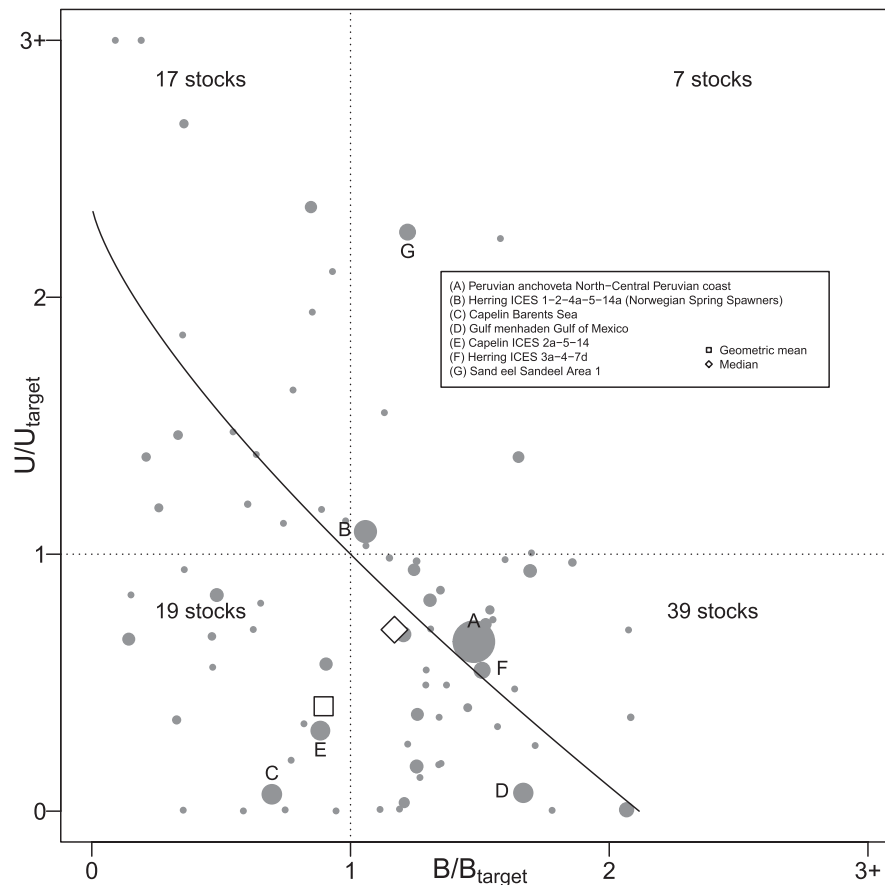


FIGURE 4 Trends in small pelagic fish global estimates from RAMLDB of: (a) relative abundance,  $B/B_{\text{target}}$ ; and (b) fishing pressure,  $U/U_{\text{target}}$ , relative to MSY-based or other target reference points from 1970–2018. Geometric mean trend is re-scaled to the median in years of >90% coverage. Shaded bands around mean denote 95% finite population-corrected confidence bounds (applicable to all years with <100% coverage). Red dots show the median of all stocks assessed in that year. Boxplots show distributions of individual stocks in each year, with shading reflecting the fraction of stocks with assessments covering that year. Stocks are equally weighted





**FIGURE 5** Geometric mean status of individual small pelagic fish stocks in their last 10 years of joint available in RAMLDB estimates of  $U/U_{\text{target}}$  and  $B/B_{\text{target}}$ . Vertical and horizontal dotted lines represent agency management target or MSY-based targets. The solid line going from upper left to lower right is the predicted equilibrium abundance for a given level of fishing pressure using a Pella-Tomlinson production model. Area of circles is proportional to MSY of the stock, or if an estimate of MSY was not available, to the average catch from 2000 to 2012. The seven largest stocks are labelled. Open square represents the geometric mean, and open diamond the median across stocks

The lower left quadrant contains stocks below  $B_{\text{target}}$ , but with fishing pressure also below  $U_{\text{target}}$ , which are thus expected to rebuild to  $B > B_{\text{target}}$  if fishing pressure is the dominant control on abundance. None of the largest stocks in RAMLDB (labelled A–G) are below a  $B/B_{\text{target}}$  of 0.5, which in some regions defines a threshold for a stock to be declared as overfished (in other regions, more conservative thresholds such as 0.8 are defined). Approximately half of all assessed small pelagic fish stocks, including most of the larger stocks, are contained in the lower right quadrant where fishing pressure is below target levels and abundance is greater than targets. There are few stocks in the upper right quadrant, where fishing pressure and biomass are both relatively high. One large stock in this quadrant is North Sea sandeel, with its most recent estimate of  $U \gg U_{\text{target}}$  but  $B$  is still  $> B_{\text{target}}$ . Given the large impact of natural variability on small pelagic fish abundance, it is not surprising that many stocks are well below biomass targets, and because quotas are set before the actual abundance in a year is known, it is not too surprising that fishing pressure is sometimes above and other times below the target. If the management goal is to set  $F = F_{\text{target}}$ , and  $B = B_{\text{target}}$  we would expect half of the stocks to be above and the other half below each target in any given year but ideally close to those targets. Trends

in individual stock abundance and status relative to biomass reference points of stocks in RAMLDB are shown for each region in Figure S1. Trends in fishing pressure are shown for individual stocks in Figure S2. While we have focused on the abundance and fishing pressure since 1970, we do have some data in RAMLDB from as early as 1950 and Figure S3 shows the distribution of fishing pressure relative to exploitation reference points from 1950 to present. Note that fishing pressure was much higher prior to 1970 than it has been since then.

### 3.4 | Regional trends in stock status

There are some regional differences in average abundance trends of small pelagic stocks contained in RAMLDB (Figure 6) although all show considerable stability. The Northwest Pacific stands out as the one region where abundance has been below  $B_{\text{target}}$  since the late 1990s. For other regions, stocks have on average had abundance within about 30% of  $B_{\text{target}}$  for the last 20 years. The relatively constant average abundance trends in each region mask considerable variability of individual stocks as shown in Figure S1.

Mean trends in  $U/U_{\text{targ}}$  (Figure 7) are more diverse among regions. The Northeast Atlantic and Northeast Pacific show relatively strong long-term declines in fishing pressure. The Northeast Pacific estimate is particularly low because several herring stocks have been closed to fishing for some time due to low abundance and this strongly influences the geometric mean. The Southeast Pacific shows more variability including declines in the last two decades. The Mediterranean/Black Sea shows long term gradual increases. The average trend in the Northwest Pacific has been stable around  $U_{\text{targ}}$  since the 1980s. Among these regions with assessed stocks, only the Mediterranean/Black Sea appears to now have fishing pressure on average above target levels.

The joint relationship of trends in mean  $U/U_{\text{targ}}$  and  $B/B_{\text{targ}}$  (using the values from Figures 6 and 7 for each region) shows a remarkable lack of influence of fishing pressure on biomass (Figure 8). The Southeast Pacific and Northeast Atlantic, the two regions with the most small pelagic fish catch, show almost no change in average biomass despite considerable change in average fishing pressure.

Among groundfish stocks (Hilborn et al., 2021), and also for tuna stocks (Pons et al., 2016), there was a general trend of increasing fishing pressure and simultaneous or lagged declining abundance. In many cases for groundfish, this led to a later reduction in fishing pressure, producing a counterclockwise pattern in such bivariate trend plots (commonly referred to as 'Kobe plots'). By contrast, there is little hint of such a temporal pattern for small pelagic fish (Figure 8).

The small pelagic fish stocks of West Africa (not shown in Figures 6 and 7 due to few available assessed stocks) have been of considerable concern because of the development of distant-water fisheries in that region and their growing catch. RAMLDB contains data on 13 West African small pelagic fish stocks, but only one has a sufficiently long time series of biomass and fishing pressure relative to reference points. Seven of these stocks have a single estimate of  $B/B_{\text{MSY}}$  and  $U/U_{\text{MSY}}$  for 2017 and five have no reference point estimates. Long-term acoustic surveys of small pelagic fish in West Africa have shown that total abundance of major groups have not

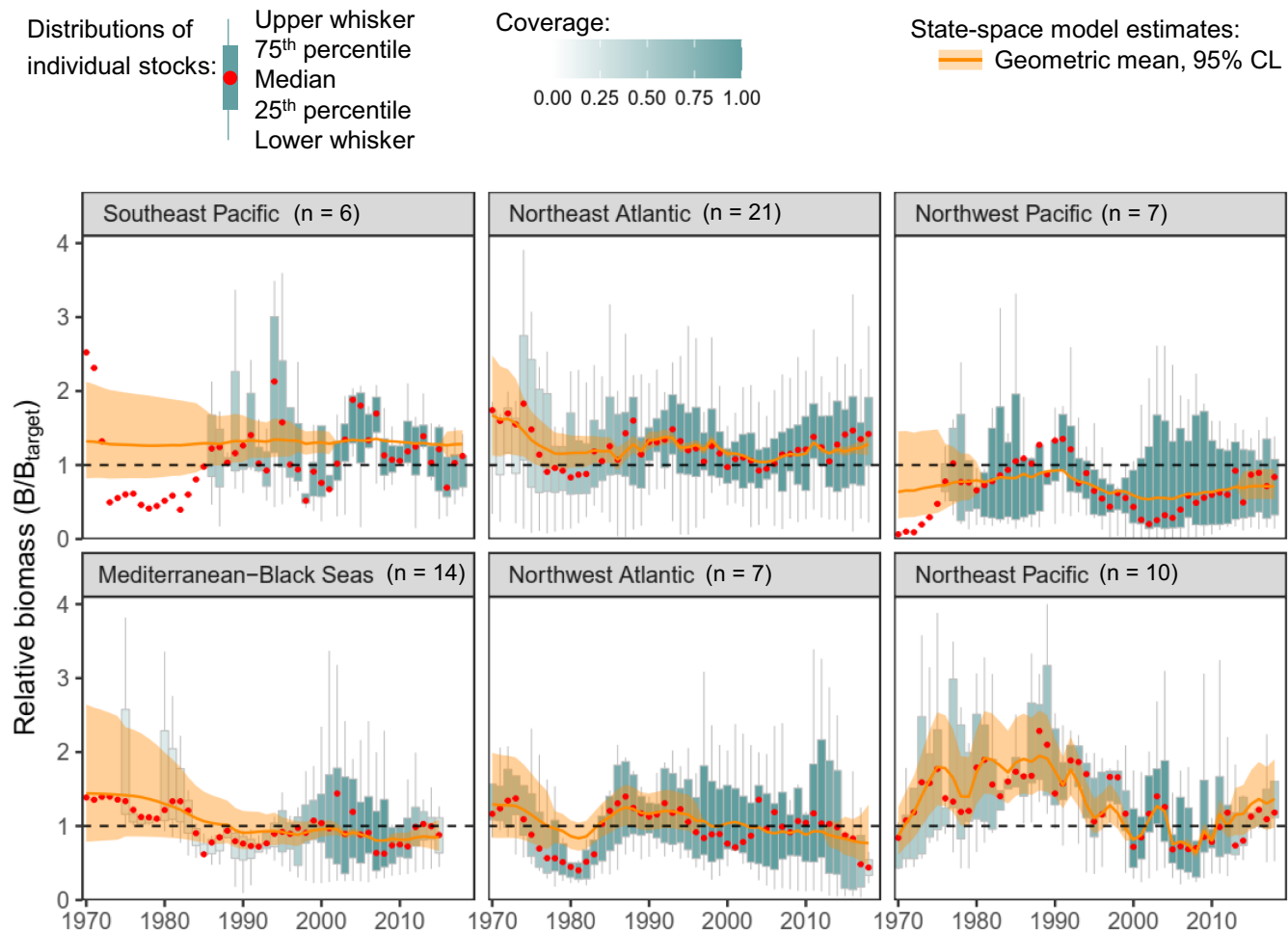


FIGURE 6 Trends in small pelagic fish mean  $B/B_{\text{targ}}$  in RAMLDB by major FAO area. Geometric mean trend estimated under a state-space model is re-scaled to the median in years of >90% coverage. Shaded bands around mean denote 95% finite population-corrected confidence bounds (applicable to all years with <100% coverage). Boxplots show distributions of individual stocks in each year, with shading reflecting the fraction of stocks with assessments covering that year. Stocks are equally weighted. Only regions with  $n > 5$  stocks are included in this figure

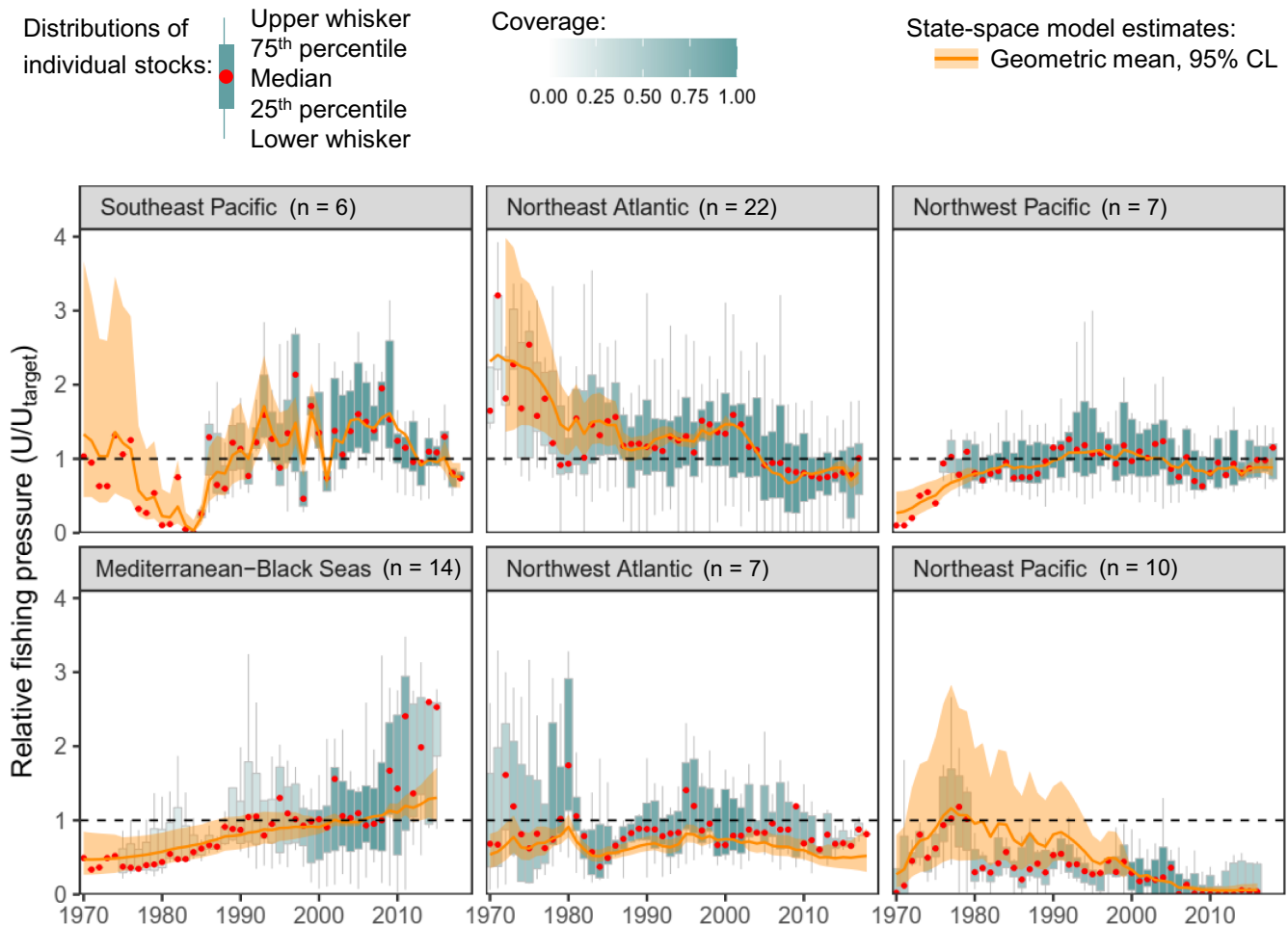


FIGURE 7 Trends in small pelagic fish in RAMLDB mean  $U/U_{\text{target}}$  by major FAO area. Geometric mean trend estimated under a state-space model is re-scaled to the median in years of >90% coverage. Shaded bands around mean denote 95% finite population-corrected confidence bounds (applicable to all years with <100% coverage). Boxplots show distributions of individual stocks in each year, with shading reflecting the fraction of stocks with assessments covering that year. Stocks are equally weighted. Only regions with  $n > 5$  stocks are included in this figure

generally declined from 1999 to 2015 (Lakhniguet al., 2019), but they do estimate that the proportion of stocks which are overexploited has been increasing.

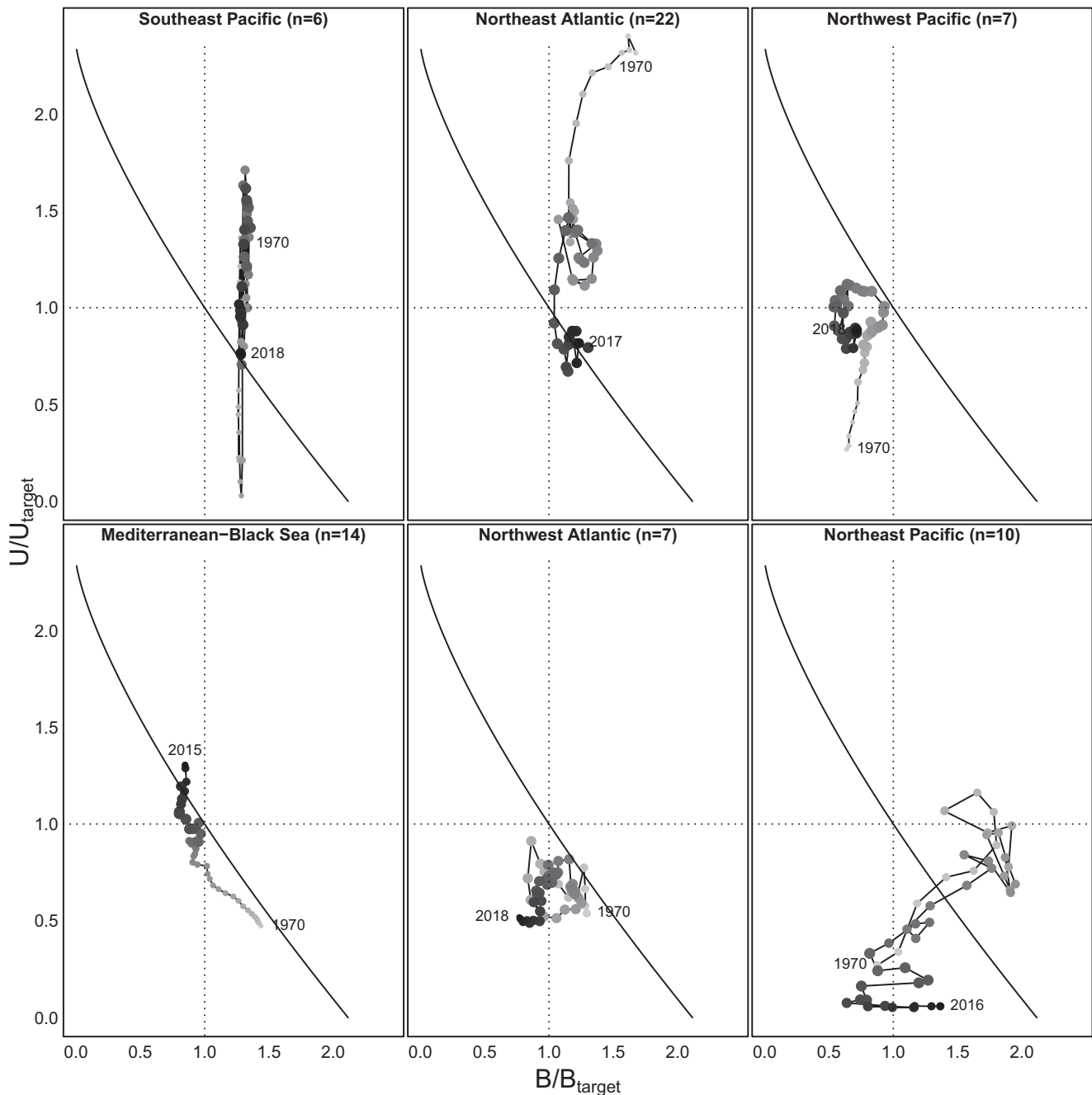
### 3.5 | Factors affecting relative stability of average biomass

Table 1 shows the average correlation between the abundance time series of pairs of stocks in RAMLDB within the same taxonomic group and FAO region. Small pelagic fish show the lowest average correlation, meaning that trends in abundance of small pelagic fish stocks within the same region tended to be significantly less synchronous than those of groundfish, but not significantly different from invertebrates. Figure S4 shows the distribution of correlations between pairs of stocks for each region and taxonomic group.

We compared the variability in biomass and fishing pressure in Table 2, which shows the average coefficient of variation across

individual stocks of each type. There were not large differences in the total coefficient of variation, but this could reflect either high year to year variability, or slow changes but still spanning a large range of abundance. By contrast, the coefficient of variation of interannual changes in biomass and fishing pressure reflects how much change there is from year to year, and there are major differences. Year-to-year variability in biomass is much higher for small pelagic fish, and across the different groups, year-to-year variability may be related to average lifespan.

Correlation coefficients between predicted and observed change in biomass from the regression models described in Equations 1–4 are shown in Table 3. Each stock provides a pair of  $X$  (observed) and  $Y$  (predicted) values for each year, and data for all stocks of each fish type are combined in a single model. The second column of Table 3 shows the correlation between observed and predicted values of changes in biomass ( $B_{t+1}/B_t$ ) as jointly impacted by fishing pressure and biomass by Equation 4. The third and fourth columns show the correlation with only fishing pressure (column 3)



**FIGURE 8** Bivariate mean trends in  $B/B_{\text{target}}$  and  $U/U_{\text{target}}$  from RAMLDB by major FAO area. Values of geometric mean stock status are estimates from the state-space model, the same values as shown in the univariate [Figures 6 and 7](#). Shading transitions from earlier (light) to later (dark) years, with different year ranges among regions. Area of circles is proportional to the maximum number of stocks with data available in that year for that region. The solid line going from upper left to lower right is the predicted equilibrium abundance for each level of fishing pressure. In the region above and to the right of this line, abundance is expected to decrease and is expected to increase in the region below and to the left of the line. Only regions with  $n > 5$  stocks are included in this figure

and by only biomass (column 4). Small pelagic fish have by far the lowest correlation between the annual change in biomass and each given year's relative biomass or relative fishing pressure with fishing pressure only explaining 5% of variance in biomass, biomass only explaining 1% and combined fishing pressure and biomass 12%. By contrast, fishing pressure explains 42% of the change in biomass of sharks rays and skates.

## 4 | DISCUSSION

### 4.1 | Trends in abundance and fishing pressure

At the combined global level since 1970, small pelagic fish stocks in RAMLDB show remarkably little change in average abundance and fishing pressure ([Figures 4 and 5](#)) although at any time the status of

**TABLE 1** Average correlation in annual abundance between pairs of stocks of the same taxonomic group in the same region

FAO Area	FAO Area Number	Small pelagic fish	Groundfish	Invertebrates
NW Atl	21	0.0064	0.227*	-0.0468
NE Atl	27	-0.012	0.0958**	0.0415
Mediterranean	37	0.0108	0.2597**	-0.005
NW Pacific	61	-0.1046	-0.0036	0.1883
SE Pacific	87	0.0663	0.6351*	0.364

Note: Data are from biomass estimates in RAMLDB. Calculated averages ensure a minimum of 4 stocks in each combination of taxonomic group and region. \* indicates significantly different from Small pelagic fish at the 0.05 level. \*\* indicates at the 0.01 level.

**TABLE 2** The coefficient of variation of  $B/B_{\text{targ}}$  and  $U/U_{\text{targ}}$  and interannual changes in these quantities

Fish Type	CV $B/B_{\text{targ}}$	CV $U/U_{\text{targ}}$	CV $B_{t+1}/B_t$	CV $U_{t+1}/U_t$
Small pelagic fish	0.53	0.65	0.43	0.77
Groundfish	0.45	0.61	0.18	0.52
Invertebrate	0.48	0.49	0.28	0.55
Other marine	0.40	0.61	0.14	0.39
Sharks, rays and skates	0.35	0.72	0.09	1.13
Tuna and marlin	0.34	0.61	0.07	0.68

Note: Data from RAMLDB.

**TABLE 3** Amount of variability in change in biomass explained by different combinations of biomass and fishing pressure

Taxonomic Group	$B/B_{\text{targ}}$ and $U/U_{\text{targ}}$	$U/U_{\text{targ}}$	$B/B_{\text{targ}}$
Small pelagic fish	0.12	0.05	0.01
Groundfish	0.22	0.14	0.07
Invertebrate	0.17	0.10	0.05
Other marine	0.26	0.24	0.11
Sharks, rays and skates	0.49	0.42	0.19
Tuna and marlin	0.31	0.18	0.10

Note: Three regression models involved different explanatory variables:  $B/B_{\text{targ}}$  only,  $U/U_{\text{targ}}$  only and both. Data from RAMLDB.

individual stocks is highly variable. Unlike two other major groups of fishes which have been evaluated, tuna (Juan-Jorda et al., 2011; Pons et al., 2016) and groundfish (Hilborn et al., 2020), small pelagic fish abundance of the stocks in RAMLDB—at least in aggregate—is more consistent over time. For both of those other groups, abundance was relatively high in the 1970s while fishing pressure was relatively low. Fishing pressure increased through the 1990s, and then declined for groundfish and stabilized for tunas thereafter. Unlike for tunas and groundfish, a decline in average fishing pressure has not resulted in an increase in average abundance of small pelagic fish.

Certainly, individual small pelagic fish stocks fluctuate greatly (see Figure S1), but the average trend of stocks in RAMLDB since 1970 is surprisingly stable. Even at the regional level, average relative abundance is generally stable when stocks are equally weighted, although we do see regional differences in fishing pressure. This is

not to say that total regional biomass is stable because in many regions a single stock may dominate the total biomass in a given year. The Northeast Atlantic and Northeast Pacific have both seen consistent declines in fishing pressure, while the Southeast Pacific and Mediterranean/Black Sea all saw fishing pressure rising up to the 1990s, and for stocks with available data before 1970 (Figure S3) fishing pressure was much higher.

There was a period of rapid expansion of fishing pressure on pelagic stocks during the 1950s to the early 1970s. As a result, many stocks collapsed, particularly herring stocks in both the NW Atlantic and the NE Atlantic, and remained at low levels for substantial periods (Hilborn, 1997; Hutchings, 2000). The largest of these was Norwegian spring spawning herring stock, which eventually recovered. Most others also recovered but Icelandic spring spawning herring did not. The RAMLDB includes few data for these stocks during the period of collapse and it is not clear whether this would alter our overall conclusions. During this early period, controls on fishing were virtually non-existent and it is possible that a relationship between fishing pressure and stock size could be apparent if stock assessments covering this period were available. Nevertheless, our results are valid for five decades into the past and are likely to remain valid for the immediate future in these assessed stocks.

## 4.2 | Status relative to reference points

Stock status over the last 10 years of assessment for each stock in RAMLDB (Figure 5) is quite optimistic with only two large stocks well below the biomass target, and only one large stock well above  $U_{\text{targ}}$ . In addition, the median and geometric mean fishing pressure across assessed stocks is well below  $U_{\text{targ}}$ . However, there are 17 stocks in the quadrant of most concern, the upper left with  $U > U_{\text{targ}}$  and  $B < B_{\text{targ}}$  and the majority of these stocks come from the Mediterranean and West Africa. Because of their often highly variable and temporally autocorrelated changes in recruitment (Szuwalski et al., 2019), small pelagic fish pose a number of challenges to formulating traditional MSY related reference points. While the mean stock status appears to generally be near  $B_{\text{targ}}$  and mean fishing pressure below  $U_{\text{targ}}$ , we recognize that these quantities are often rather poorly estimated and we place much more faith in the directional trends in abundance estimates than in the status relative to static

reference points. Considering this high variability, we agree with the suggestion by MacCall et al. (1985), adopted in some regions, to use dynamic reference points. There are several approaches to dynamic reference points (Berger, 2019) including having the reference point adjusted based on environmental conditions, or reporting stock depletion not relative to some average unexploited stock size, but instead as a fraction of the biomass that would have been observed in the absence of fishing if historical recruitment trends had remained as estimated or to estimate what biomass would have been given recent recruitment estimates in the absence of harvesting.

An analysis using ecosystem models (Christensen et al., 2014) suggested that small pelagic fish are now likely more abundant than they were before large-scale industrial fishing began, which reduced the abundance of predators of small pelagic fish. The idea of 'changing baselines' has normally been interpreted that human memory has lost track of the real declines in abundance (Pauly, 1995), but for small pelagic fish the current state may actually be of greater abundance than in the past. The values of  $B_{\text{targ}}$  and  $U_{\text{targ}}$  would depend on the amount of predation pressure, so if predation pressure has changed during the period we have data for a stock, the value of biological reference points would also have changed. Thus we need to recognize inherent uncertainty in biological reference points, especially for small pelagic fish.

Many believe that a well-managed fishery should be in the lower right quadrant of the Kobe plot. If the objective is the management target (1.0) on the horizontal axis of Figure 5, then we would expect biomass to be above the target half of the time and below the target half of the time. The amount of spread around the target would depend on the precision of management for fishing pressure, and variation in recruitment and survival for biomass. Similarly, we would expect the fishing pressure to be above 1 half of the time and below 1 half of the time. The observation that fishing pressure is on average well below 1 may be due to at least two reasons. First, the MSY-based reference point assumed may not be the true management target. This is certainly the case in the United States, where  $U_{\text{MSY}}$  is considered a limit not to be exceeded, rather than a target, but in the United States  $B_{\text{MSY}}$  is generally accepted as the target. Secondly, the mean fishing pressure may be below the target because of constraints on by-catch, mixed stock fisheries or habitat protection. Given concern about the potential impacts of small pelagic fish abundance on their predators, management agencies may wish to maintain stocks at higher abundance than  $B_{\text{MSY}}$  and generally see stocks in the lower right hand quadrant.

A final issue regarding stock status is trends in abundance. We expect that well managed stocks will be trending up and down with equal frequency, but a downward trend is of more concern if a stock is currently at low abundance, and when stocks are well below  $B_{\text{MSY}}$  managers would want to see stocks increasing in abundance.

#### 4.3 | Why the lack of fishing impact on abundance?

A second surprising result of this analysis is the relative insensitivity of regional small pelagic fish abundance of stocks in RAMLDB to

changes in fishing pressure, especially as seen in Figure 8, where two- or threefold changes in average fishing pressure appear to have had little impact on average abundance in the same region. The Mediterranean/Black Sea is the only region where the expected decline in abundance with increasing fishing pressure, or increase in abundance with declining fishing pressure, is seen. There are at least three hypotheses why this may be the case; it seems likely they all play some role, and almost certainly interact. These are: (1) fishing pressure is low relative to other sources of mortality; (2) recruitment is highly variable and largely unrelated to spawning stock abundance; and (3) the stocks are subject to strong bottom up and/or top down forcing.

Kolding et al. (2016) analysed 110 individual EcoPath models, representing marine ecosystems throughout the world and covering the period 1970–2007. The relationship between assumed trophic level and the estimated ratio of fishing mortality to predation mortality ( $M_2$ ) extracted from these models is shown in Figure 9a. There is a striking increase in the ratio with increasing trophic level, such that below trophic level 3.5, fishing mortality is typically less than one tenth of natural mortality, and above 3.5 fishing mortality is typically higher, occasionally greater than natural mortality. Figure 9b shows the distribution of trophic levels for small pelagic fish, groundfish and tunas in the RAMLDB. With fishing mortality so small relative to natural predation mortality, it is perhaps not surprising that small pelagic fish in general would show relatively little influence of fishing pressure on stock abundance compared with groundfish and tunas.

Small pelagic fish stocks in RAMLDB are generally highly targeted stocks that are of major economic value; less valuable stocks tend to be less frequently assessed (Neubauer et al., 2018). These assessed stocks might therefore be predicted to have a higher ratio of fishing mortality to natural mortality (mean  $U/M = 0.55$ ) than small pelagic fish in the EcoPath data. However, the mean in the EcoPath data is 0.57, almost exactly the same as that for stocks in RAMLDB. In contrast, average  $U/M$  for groundfish stocks in RAMLDB is 1.15. This confirms that fishing mortality of small pelagic fish is lower in relation to predation than it is for higher trophic level species.

#### 4.4 | The portfolio effect, variability and impact of fishing

The correlation matrix shown in Table 1 indicates that there is less average correlation between small pelagic fish stocks in a region than for other taxa. Figure S4 shows the distribution of correlation coefficients by FAO statistical area (for all pairs of stocks from the same taxonomic group and area). Note that you cannot expect to see an average correlation that is well below 0. Imagine two groups of stocks that showed totally contrasting trends, group 1 was booming, while group 2 was crashing. There would be strong negative correlations between stocks in groups 1 and 2, but strong positive correlation between stocks within group 1 and within group 2. This would result in a net average near 0. An intrinsic property of the portfolio effect is that as you add more elements to the portfolio the variance decreases, even if there is no negative correlation between them.

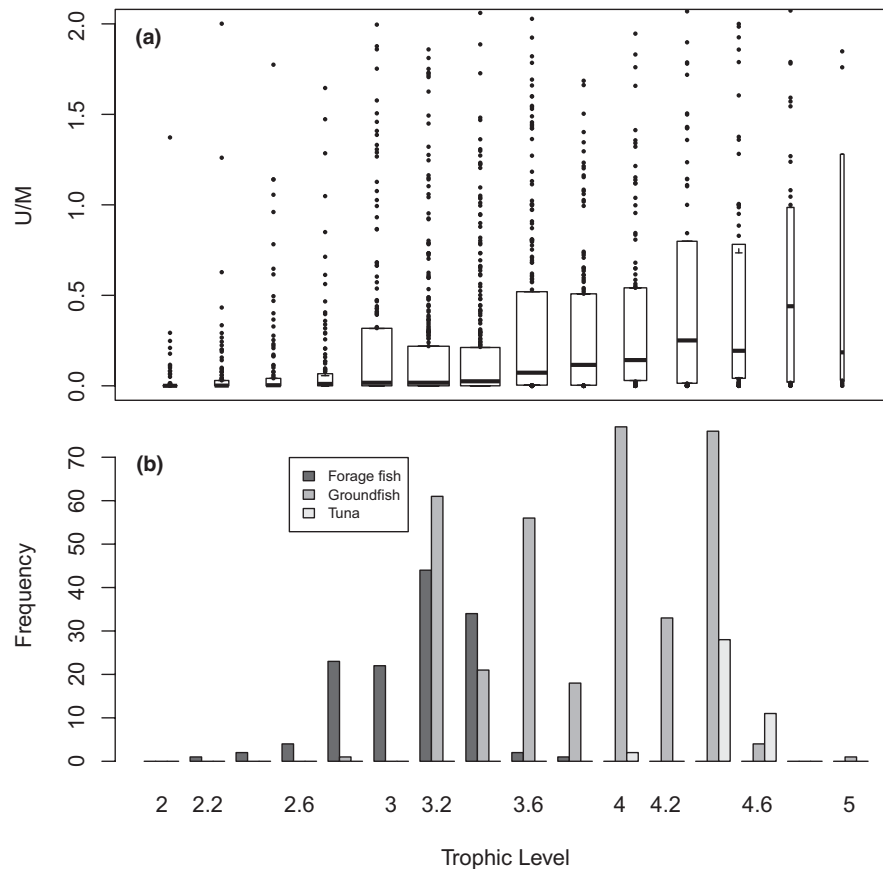


FIGURE 9 (a) Ratio of fishing mortality to other mortality as a function of trophic level from all taxa in Kolding et al. (2016). (b) Distribution of trophic levels among small pelagic fish, groundfish and tuna stocks in the RAM Legacy Stock Assessment Database

There are at least two explanations for the lower correlation. The first is that there is competition for resources so if one stock declines for some reason, additional resources are available for other stocks. The second is that for other taxonomic groups the stocks are more likely to be synchronized by the common fishing pressure, whereas small pelagic fish, for which direct targeting of a single species is common, are less likely to show a common pattern.

Table 2 demonstrates that the year to year variability in small pelagic fish in RAMLDB is on average higher than that of other functional groups, reflecting the short life span and general lack of correlation between spawning biomass and recruitment in small pelagic fishes. Table 3 demonstrates the general lack of relationship between fishing pressure and biomass on change in biomass of small pelagic fish. This illustrates the relatively weak control that fishing pressure has on small pelagic fish at a stock level. It is a partial explanation for why, at a regional level, there is little relationship between changes in fishing pressure and changes in small pelagic fish abundance.

#### 4.5 | The role of management

The data available on trends in abundance and fishing pressure come primarily from countries with relatively strong fisheries management systems and from the last 50 years when fisheries management had become more effective in these countries. Prior to 1970 fishing

pressure on small pelagic fish was generally more intense, and the information from countries not covered in RAMLDB suggests small pelagic fish stocks there are still heavily fished.

Even in countries with intense fisheries management, the high natural variability of many small pelagic fish stocks means that management cannot necessarily prevent stock declines by reducing catches, and it is not clear how much reduced fishing pressure facilitates recovery of small pelagic fish. However, there is little question that variation in fishing pressure does impact individual small pelagic fish stocks (Table 3), that many small pelagic fish stocks have been overfished in the past and some continue to be overfished, and that when stocks decline from natural causes, reduced fishing pressure can help maintain spawning stock biomass (Essington et al., 2015; Siple et al., 2019).

#### 4.6 | The unassessed places

Trends in abundance and fishing pressure from RAMLDB for West Africa and South Africa are not shown in Figures 6 and 7 because the assessments for West and South Africa do not include MSY-based or target reference points. Although target reference points were estimated post hoc for the latter (Table S1, Figure S1), the number of stocks in the region was too small to fit the state-space model. There are no assessments in RAMLDB for Asia outside of Japan because thus far we have found none that meet the desired criteria

for inclusion. For the three large small pelagic fish stocks of West Africa, there are surveys available (Lakhnigie et al., 2019) and those suggest declines for *Sardinella aurita* and *Sardinella maderensis* and fluctuations without trend for *Sardina pilchardus* (Figure S1). Roughly half of the West African stocks are estimated to be overfished (Lakhnigie et al., 2019).

There are no quantitative, single-species stock assessments of small pelagic fish in RAMLDB for Asia except for Japan. The majority of Russian small pelagic fish catches come from fisheries in the NE Atlantic. As we saw in Figure 3, catches in the Western Central Pacific (China) and both the Eastern and Western Indian Ocean rose greatly beginning around 1970. They have continued to increase for the fisheries in the Indian Ocean but have plateaued for China. These trends support the hypothesis that stocks in these two regions have not collapsed in aggregate as it is difficult to maintain historically high catch levels if stocks are collapsed. Expert opinion surveys on the qualitative status of small pelagic fish stocks (Melnichuk et al., 2017) do not suggest that stocks from these regions have poorer status than small pelagic fish stocks in other regions.

Some countries in Southeast Asia have now published assessments of the status of their fisheries, but they typically do not include time series estimates of abundance and fishing pressure, but instead present summaries of current status (e.g. Rohit et al., 2018; Sathianandan et al., 2021). Rohit et al. (2018) estimated that the majority of Indian Oil Sardine stocks are below  $B_{MSY}$ , with fishing pressure slightly above  $U_{MSY}$ . Sathianandan et al. (2021) estimated the status of a large number of small pelagic fishes and estimated that nine are sustainable, 13 are overfished or subject to overfishing and three are recovering. They estimate that 63% of stocks (of all taxa) are below  $B_{MSY}$  and 40% are fished harder than  $U_{MSY}$ .

Indonesia also reports the status of their stocks, but without time series of abundance or fishing pressure, and only in large aggregates of taxa and regions (Suman et al., 2018). They estimate for Indonesian small pelagics that three are overexploited, four are fully exploited, and three are underexploited.

#### 4.7 | The role of small pelagic fish in the ecosystem

Much of the interest in small pelagic fishes concerns their role as key elements in the aquatic food chain and as food for higher trophic levels. The purpose of this paper was simply to summarize trends in abundance and fishing pressure of stocks, not to review the many issues around precautionary management of small pelagic fish to safeguard food supply of their predators, as have been evaluated previously (Cury et al., 2011; Free et al., 2021; Hilborn et al., 2017; Pikitch et al., 2014). Nevertheless, the results showing relatively little relationship between fishing pressure and small pelagic fish abundance, and the historical perspective provided in Christensen et al. (2014) certainly have relevance to these discussions. The models used in Pikitch et al. (2014) assumed no natural variability in the abundance of small pelagic fish and had tight coupling between predators and prey. More detailed modelling

that included natural variability in the abundances of small pelagic fishes, and changes in their spatial distributions between times of high and low abundance, suggested much less impact of fishing on the predators of these small pelagic fish (Punt et al., 2016). Our analysis showing—in aggregate—relatively little change in abundance despite often large changes in fishing pressure will add to this debate.

## 5 | CONCLUSIONS

The abundance of data rich small pelagic fish stocks that are scientifically assessed and included in RAMLDB has been, on average, remarkably stable over the last 50 years. There is relatively little relationship between average fishing pressure and changes in average abundance of small pelagic fish at a regional level (Figure 8). The relationship between fishing pressure and change in abundance was also weak for individual small pelagic fish stocks compared to other taxa (Table 3), but individual stocks have certainly seen high fishing pressure.

It is well known that many small pelagic fish stocks have significant changes in productivity regime (Szuwalski et al., 2014; Vert-pre et al., 2013), and may fluctuate over a wide range of abundance (Schwartzlose et al., 1999), with fluctuations both preceding industrial fishing and largely outside the control of management (Baumgartner et al., 1992; Soutar & Isaacs, 1974). These natural fluctuations, combined with the portfolio effect and fishing being a relatively small portion of total mortality for small pelagic fish, together appear to explain the lack of relationship between fishing pressure and abundance, and the average regional stability of small pelagic fish average abundance. None of this argues that fishing pressure does not need to be regulated, but the impacts of regulation will be less evident in small pelagic fish than other functional groups. Even in the absence of an impact of fishing on recruitment, fishing pressure should be guided by yield-per-recruit considerations. Further, even if fishing has no impact on recruitment it will impact abundance, and presumably both catch rates and food availability for predators. In addition, there remains considerable uncertainty about how fishing impacts the highs and lows of small pelagic fish fluctuations (Essington et al., 2015; Siple et al., 2019), but there is no question that high fishing mortality rates will reduce the abundance of a fish stock regardless of environmentally-driven variations in recruitment.

Attempts to classify small pelagic fish stocks relative to management targets, MSY, or other biological reference points has limited value for stocks that show strong environmentally driven productivity regimes. Dynamic reference points that fluctuate with productivity regimes may be a more promising approach for assessing stock status of small pelagic fishes, provided these dynamic reference points simply reflect fluctuating environmental conditions and do not exacerbate the longer term impacts of prolonged decreases in productivity. At present, relatively few small pelagic fish stocks have dynamic reference points estimated in assessments and employed in



management practices. The pros and cons of this approach should be a top priority for management agencies to evaluate.

## ACKNOWLEDGEMENTS

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## CONFLICT OF INTEREST

RH receives research funding from many groups that have interests in fisheries outcomes including environmental NGOs, foundations, governments and fishing industry groups.

## DATA AVAILABILITY STATEMENT

The availability of sources of data used in this paper are as follows: (1) FAO landings data are available from the FAO web site (<http://www.fao.org/fishery/statistics/global-capture-production/en>) (2) the RAM Legacy Stock Assessment Database version 4.494 ([www.ramlegacy.org](http://www.ramlegacy.org)). The 110 EcoPath models are listed in the online supplementary material of Kolding et al. (2016) and the models and associated data are available in the EcoPath model repository. <http://ecobase.ecopath.org/>

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#### SUPPORTING INFORMATION

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