Responses in fisheries catch data to a warming ocean along a latitudinal gradient in the western Pacific Ocean

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Abstract Ocean warming has been affecting marine ecosystems over the past few decades. The signature of ocean warming in global fisheries catch data has been identified through a variety of methods, one of which is the mean temperature of the catch (MTC) index. The MTC is derived from the average temperature preference of fished species weighted by their contribution to annual catches. Here, we used MTC to explore the fisheries catch responses to warming, from 1950 to 2016, along a latitudinal gradient in the western Pacific Ocean, from 37° N, via 2.5° S in the central western Pacific, to 36° S. The tropicalization of catches in a given geographic space, i.e., the increased catch of species with affinity to warmer waters, as a result of increasing sea temperature and the associated poleward migration of species, rather than any large-scale oceanographic variability, was apparent through the increasing MTC at higher latitudes. In particular, MTC in temperate Japan increased by 0.33 °C per decade over the time series. The MTC in subtropical/temperate southeast Australia increased by 0.24 °C per decade over the full time period and by 1.24 °C per decade after 2002. The observed MTC increase was caused by the increasing dominance of thermophilous (preferring warmer waters) over psychrophilous (preferring cooler waters) taxa in the catches in these waters. On the other hand, the MTC in tropical Indonesian waters, as well as the ratio of thermophilous to psychrophilous taxa, showed a gentle yet consistent decrease of 0.05 °C per decade over the full time period. This finding supports the tropicalization hypothesis, given the limited scope for further tropicalization of catches in the already tropical ecosystem of Indonesia. Ocean warming has indeed been altering the distribution of marine organisms, particularly in temperate ecosystems as thermophilous taxa become more abundant, while psychrophilous taxa abundance decreases. Tropicalization impacts

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fisheries and catch composition and is, therefore, expected to cause conflicts among fishers and challenge fisheries management.

Introduction

Human activities affect the world's oceans, with fishing and climate change having the most profound impacts on marine populations and ecosystems (Cheung et al. 2009; Pauly 2018; Lotze et al. 2019). Fishing and overfishing have caused notable fish biomass declines (Palomares et al. 2020) and globally declining catch trends (Pauly and Zeller 2016), as well as alterations to fish population structure such as decreases in body length (Pauly et al. 1998) and size at maturity (Olsen et al. 2004). Furthermore, ocean warming due to anthropogenic climate change affects the biological characteristics of fishes (Cheung et al. 2013a; Tsikliras and Stergiou 2014a) and invertebrates (O'Connor et al. 2007), altering community structure as well as the distribution and abundance of marine populations (Perry et al. 2005; Cheung et al. 2009; Simpson et al. 2011), ultimately affecting fisheries (Cheung et al. 2010; Sumaila et al. 2011; Pinsky and Fogarty 2012; Le Bris et al. 2018). Apart from human-driven effects, further impacts on marine ecosystems can be caused by large-scale, natural climatic phenomena (Bakun and Broad 2003; Alheit et al. 2014) and oceanographic variability (Logerwell et al. 2007; Pineda et al. 2018). Thus, it is important to identify and understand the responses of marine populations to a changing ocean, as anthropogenic non-climate human stressors, such as fishing, interact with climate-induced changes, increasing the sensitivity of marine fish and invertebrates to stressors (Cheung & Pauly 2016).

The composition of fish communities is being altered as species shift their distributions poleward in response to ocean warming (Cheung et al. 2009) to maintain themselves in environments that lie within their species' preferred temperature range. The so-called tropicalization of catches, i.e., the increase in the proportion of thermophilous or warm-water species in higher latitude catches in recent decades, has serious implications for the fisheries sector (Cheung

et al. 2012). Changing fishing locations and yields, along with potential declines in fisheries revenues due to climate change, may give rise to conflict in both high- and low- or middle-income countries (Lam et al. 2016; Mendenhall et al. 2020). Coastal fishing communities in tropical regions that rely on fisheries resources for food security and economic livelihoods are expected to be particularly affected by such changes (Golden et al. 2016; Blasiak et al. 2017). Assessing the effects of climate change on marine fish and fisheries is essential to adapt sustainable management practices in a rapidly changing marine environment. Shifting ecosystems call for adaptable and responsive management strategies in order to minimize negative impacts on the economy and food security (Burden and Fujita 2019).

Several approaches to assess change have been used, including tracking species distribution range shifts (Cheung et al. 2009; Pinsky et al. 2013; Shackell et al. 2014), changes in population biomass (Lotze et al. 2019; Bryndum-Buchholz et al. 2019; Palomares et al. 2020), and ocean warming effects on recruitment and fisheries catches (Cheung et al. 2010; Britten et al. 2016; Free et al. 2019). Another approach aims to identify the signature of ocean warming in the most readily and most widely available time series datasets for fisheries, namely, fisheries catch data. The mean temperature of the catch index (MTC) refers to the average inferred temperature preference of exploited fish and invertebrate species weighted by their annual catch for a given area (Cheung et al. 2013b). Globally, the rise in ocean temperature (monitored through the variation of the sea surface temperature (SST)) is reflected in an increase in the MTC of fisheries catches across 52 large marine ecosystems, after also accounting for the effects of fishing and large-scale oceanographic variability (Cheung et al. 2013b). SST has been chosen to indicate ocean warming as "the only thermal parameter routinely measured worldwide that can be used to characterize thermal conditions in each LME [large marine ecosystem]" (Belkin 2009). In principle, an increasing MTC indicates underlying changes in the catch composition, in favor of warmer water (thermophilous) species (Cheung et al. 2013b) (Fig. 1), which may be the result of catching higher volumes of thermophilous species, lower volumes of cooler water (psychrophilous) species, or both (Tsikliras and Stergiou 2014b; Auber et al. 2017).
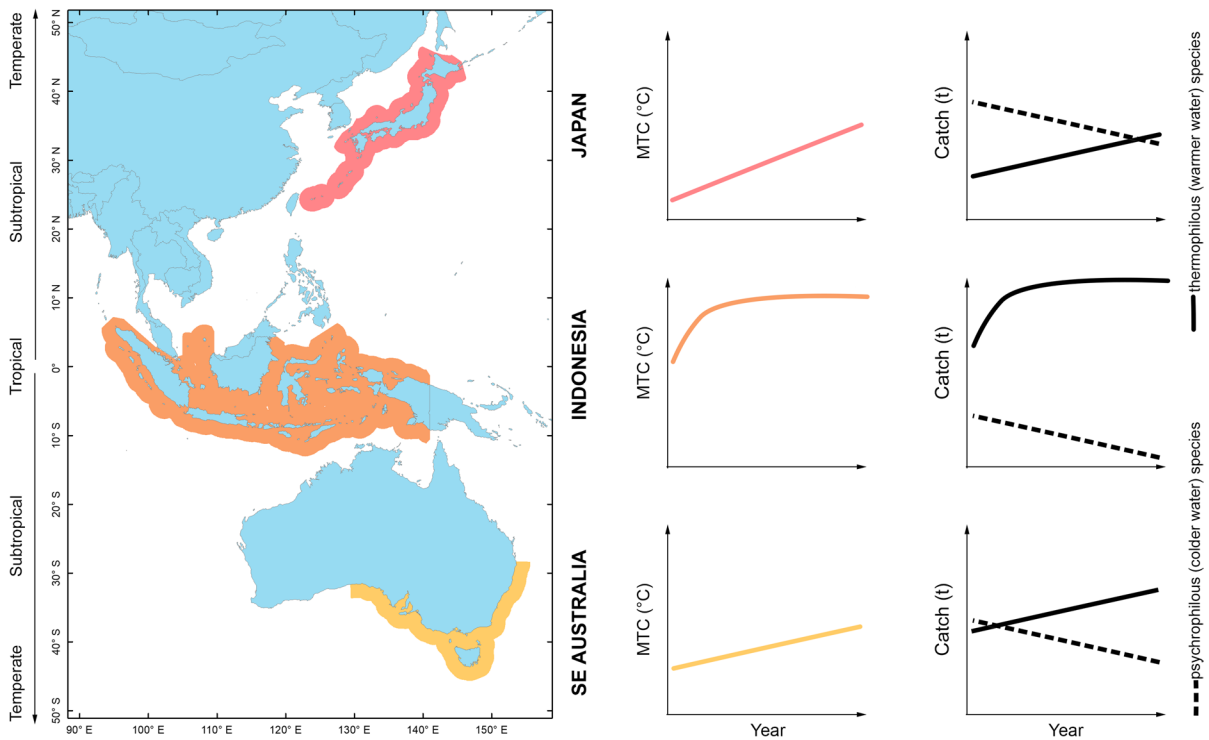
Fig. 1 Map of the three geographic regions (Japan, Indonesia, southeast Australia) included in this study, along with conceptual graphs of the hypothesized patterns of the mean temperature of the catch (MTC) (°C) and the catch of thermo-

philous (warmer water) and psychrophilous (colder water) taxa for each region. The underlying principles for the conceptual graphs are derived from Cheung et al. (2013a, b) and Cheung and Pauly (2016) (Dimarchopoulou et al.)

Since its first global use, the MTC index has been successfully applied at finer regional scales in the Mediterranean Sea (Keskin and Pauly 2014; Tsikliras and Stergiou 2014b; Fortibuoni et al. 2015; Tsikliras et al. 2015; Peristeraki et al. 2019), in parts of the Pacific along China's coast (Liang et al. 2018; Pauly and Liang 2020), and in the Atlantic Ocean (Auber et al. 2017; Leitão et al. 2018; Gianelli et al. 2019). A preliminary application of the MTC index on archeological data (paleothermometer) of ancient indigenous fisheries catches in two villages of British Columbia islands also showed MTC increase over five millennia (Hillis et al. submitted). The MTC trend is expected to differ between tropical and temperate climates (Cheung and Pauly 2016). In temperate ecosystems, local extirpation of cooler water (psychrophilous) species through their disappearance from previously occupied regions due to fishing or poleward range shifts to newly suitable habitats may be compensated for by local invasions of warmer

water (thermophilous) species (Cheung et al. 2013a, b; Cheung and Pauly 2016) (Fig. 1). On the other hand, in tropical waters, further community tropicalization may not be possible due to a lack of sources for more warm-water species, and thus, species richness is expected to decline. Indeed, species that inhabit warm tropical waters tend to have a narrower thermal window in comparison to temperate fishes that have adapted to live in an environment with considerable seasonal temperature changes (Booth et al. 2018 and references therein; Pauly 2019) and thus may have limited capacity to adapt or survive in climate change-induced "hyper-tropical" waters. Understanding the response of marine organisms to ocean warming along a latitudinal axis is crucial to explain and potentially predict geographic patterns of climate change. Such knowledge can assist in and inform management plans that affect the fisheries sectors of single or even multiple countries, i.e., in transboundary regions where stocks are shared.

Cheung et al. (2013b) illustrated the broad-scale signature of ocean warming in global fisheries catch data. However, the MTC signal may be even stronger when catches are analyzed at finer geographic scales and with higher taxonomic resolution (Tsikliras et al. 2015). Thus, the objective of this study was to investigate the MTC patterns in the western Pacific Ocean, presenting a more detailed and longer time series of data at a finer spatial resolution. Our work covered three areas along a latitudinal temperate–tropical–temperate gradient in the western Pacific Ocean, namely, Japan, Indonesia, and southeast (SE) Australia. To achieve our goal, we derived the MTC over time (1950–2016) in the exclusive economic zone (EEZ) waters, or parts thereof, in each of the studied regions (Fig. 1), and examined (1) the MTC changes in temperate Japan, tropical Indonesia, and subtropical/temperate SE Australia over time; (2) the relation of the MTC trends with SST and large-scale oceanographic variability, such as the Pacific Decadal Oscillation, Southern Oscillation, or El Niño; and (3) the changes in the ratio of thermophilous to psychrophilous taxa catches in each region over time.

Materials and methods

The EEZ waters, or parts thereof, for three countries located in different latitudes of the western Pacific Ocean were included in the present study (Fig. 1), namely, Japan (37° N, from 26° to 48° N), Indonesia (2.5° S, from 7.2° N to 12.2° S), and southeast (SE) Australia (36° S, from 26° to 46° S). For Japan, we considered the total marine biomass removed by fisheries from the Japanese mainland exclusive economic zone, including catches by foreign (Russian, Chinese, and South Korean) vessels (Swartz and Ishimura 2014; Tsui et al. 2020) (Supplementary Fig. S1A). For Indonesia, the available catch exists for three separate EEZ-subdivisions, western (Indian Ocean), central, and eastern (Pauly and Budimartono 2015; Polido et al. 2020). However, in this study, we considered the entire Indonesian EEZ as one entity, by combining the data from all three subdivisions (Supplementary Fig. S1B). Subdivision-specific findings are presented in the Supplementary Materials (Supplementary Figs. S2 and S3). Finally, for SE Australia, we analyzed the catches in the Australian EEZ corresponding to four maritime states in the southeast

of the country, i.e., New South Wales (NSW), South Australia (SA), Victoria (VIC), and Tasmania (TAS) (Kleisner et al. 2015; White et al. 2020) (Supplementary Fig. S1C). Catches in Western Australia and Queensland were excluded from the analyses as the latitudinal ranges extend from temperate or subtropical to tropical ecosystems, and the data were currently not available at a finer spatial scale.

Fisheries catch data for the 67 years from 1950 to 2016 for the three study areas were obtained from the *Sea Around Us* database (Zeller et al. 2016; www.seaaroundus.org) (Supplementary Fig. S1). The *Sea Around Us* database presents freely available reconstructed catch data for every country in the world, as well as the high seas (Zeller et al. 2016; Pauly and Zeller 2016; Coulter et al. 2020). Reconstructed catch data complement officially reported landings data with comprehensive estimates of unreported landings from industrial, artisanal, subsistence, and recreational fisheries, as well as estimates of major discards. Official reported data are mainly based on the data reported by the Food and Agriculture Organization of the United Nations (FAO) on behalf of countries, as made available via FishStat.

For the calculation of the MTC, we took into account both species-level and genus-level catch data (total reconstructed catches from artisanal, industrial, recreational, and subsistence fisheries) but did not use data aggregated to higher, uninformative taxonomic groupings. Including genus-level catch data increased the percentage of the total catch from each area used to estimate the MTC. Also, the MTC calculated using both species- and genus-level catch data was highly correlated with the MTC calculated using only species-level catch data (Supplementary Table S1). The preferred temperature for each species (min, max, and mean value in °C) was acquired from AquaMaps (Kaschner et al. 2019; www.aquamaps.org) through FishBase (Froese and Pauly 2021; www.fishbase.org) for fishes and SeaLifeBase (Palomares and Pauly 2021; www.sealifebase.ca) for other marine organisms (Supplementary Table S2), while for each genus-level catch entry, a mean temperature value (plus standard error SE) (Supplementary Table S3) was derived from all the species in a given genus that occur in the area, as provided by these two databases. The mean thermal preferences of the various species constituting a genus had higher differences (SE > 2) in only 9% of the cases, all of which

contributed less than 1% to each region's catch (Supplementary Table S3). Thus, taking the mean temperature to represent genus-level data was considered to be an acceptable approach that did not affect our results. The thermal preferences of the species are derived from occurrence data available in online databases, such as GBIF (gbif.org) and OBIS (obis.org), as well as from independent knowledge reported in the literature included in FishBase and SeaLifeBase regarding the distribution and habitat usage of each species (Kesner-Reyes et al. 2020).

In the case of Japan, the species- and genus-level catch records included in this study for the calculation of the MTC represented 73% of the total catches over the full time period, while in Indonesia, they accounted for 56% of the catches, and in SE Australia, they represented 65% of the catches. However, two species caught in SE Australia, i.e., the orange roughy (*Hoplostethus atlanticus*) and the greenback horse mackerel (*Trachurus declivis*) were excluded from the SE Australia dataset, and thus, only 59% of the southeast Australian catches were included in the analyses. The two species were excluded, as their patterns of catches over time, and particularly in recent years, are strongly influenced by management-induced changes in fishing effort (e.g., orange roughy rebuilding strategy) and changes in gear types used (i.e., purse-seiners vs. trawlers fishing greenback horse mackerel), as well as changing market demands (Smith et al. 2015; Georgeson and Helidoniotis 2018; Ward and Grammer 2018).

The MTC index was computed for each year in each spatial study region based on the mean temperature preference of each exploited fish and invertebrate taxon species and genus, weighted by their annual catch in each study area according to the following formula:

$$MTC_{yr} = \frac{\Sigma_i^n T_i C_{i,yr}}{\Sigma_i^n C_{i,yr}}$$

where $C_{i,yr}$ are the catches of taxon i in year yr in each study area (Japan, Indonesia, or SE Australia), T_i is the mean temperature preference of taxon i, and n is the total number of taxa in the annual catch data subset of each region (Cheung et al. 2013b).

For each study region, an average assemblage temperature value was calculated by averaging the preferred temperatures of all the taxa included in each catch data subset over the entire time period. The average temperature preference values were 19.5 °C for Japan, 25.8 °C for Indonesia, and 16.5 °C for SE Australia. These average assemblage temperatures were used as an assumed approximate cut-off value (see Tsikliras et al. 2015; Leitão et al. 2018) to characterize taxa as either thermophilous, i.e., taxon-specific preferred temperature ≥ average assemblage temperature, or psychrophilous, i.e., taxon-specific preferred temperature < average assemblage temperature in each region). Thus, thermophilous implies taxa that prefer warmer waters, while psychrophilous implies taxa that prefer colder waters within each region. The ratio and percentage of the thermophilous taxa catches were estimated as a relative percentage of the total catches of each area and compared to that of psychrophilous taxa. Note that, in Indonesia, the taxa are mainly tropical and subtropical, but we still use the term psychrophilous for consistency.

To be able to attribute any changes in the MTC index to ocean warming, the MTC was cross-correlated with each area's mean annual sea surface temperature (SST) anomaly that was extracted from ICOADS v2.5 SST (Freeman et al. 2017) through the Climate Explorer (https://climexp.knmi.nl/select.cgi?id=someone@somewhere&field=coads_sst) of the World Meteorological Organization. With regard to SST, we follow Tsikliras and Stergiou (2014b) and Tsikliras et al. (2015) and use anomaly data, because temperature anomalies are more important in climate change studies than absolute temperature, as they minimize the effect of confounding factors on the data (https://www.ncdc.noaa.gov/monitoring-references/dyk/anomalies-vs-temperature). Linear regression was applied to examine the MTC and SST temporal trends. In particular, segmented (or piecewise or break-point) linear regression was used to test if the MTC time series could be described by one or several trend lines (package "segmented" in R), while simple linear regression was used for the SST time series (Ciaburro 2018). To account for the potential effects of large-scale oceanographic variability, the MTC was also cross-correlated (ccf function in R), at time lags of 0–4 years, with the Pacific Decadal Oscillation (PDO) (Mantua and Hare 2002; https://psl.noaa.gov/gcos_wgsp/Timeseries/PDO/), Southern Oscillation (SOI) (https://psl.noaa. gov/gcos_wgsp/Timeseries/SOI/), and El Niño (EN) (Stenseth et al. 2003; https://psl.noaa.gov/gcos_wgsp/Timeseries/Nino34/)
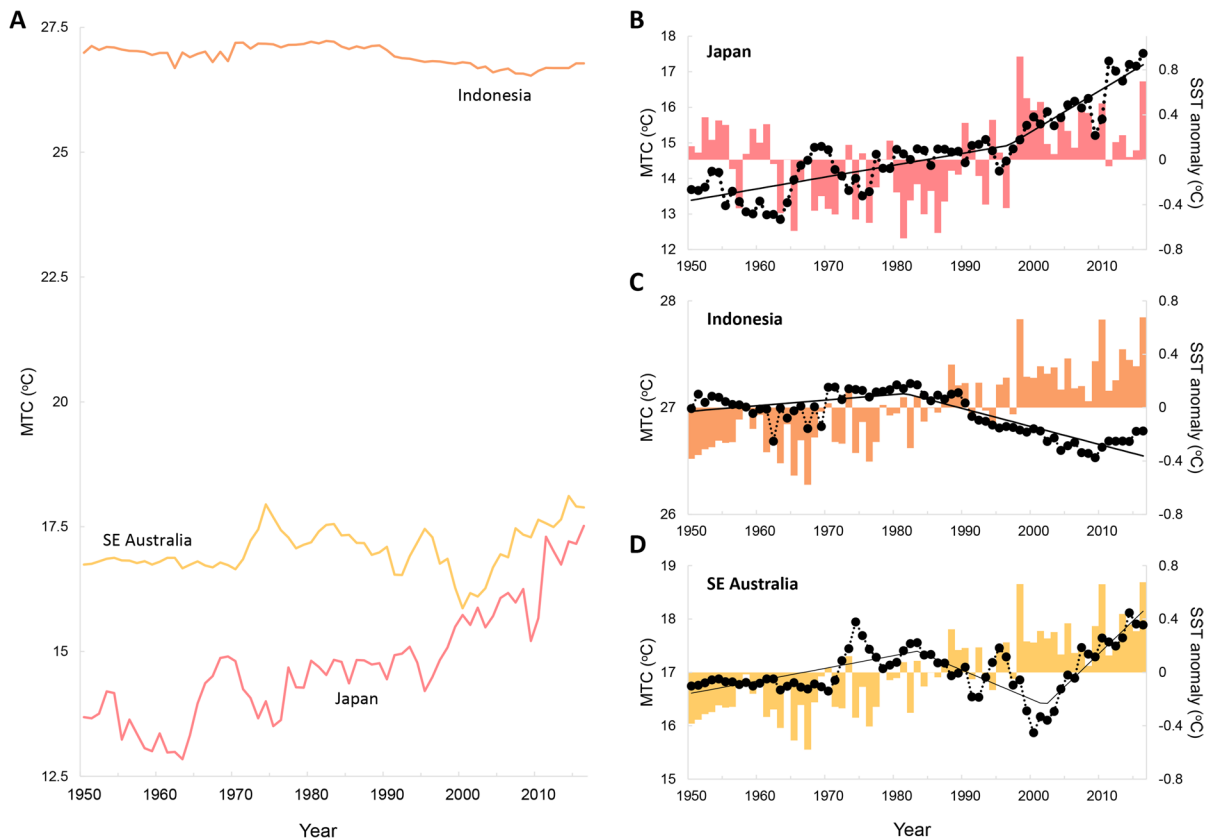
Fig. 2 **A** The mean temperature of the catch (MTC) presented comparatively for the three studied regions for 1950 to 2016, based on reconstructed fisheries catches and preferred temperature for each exploited species and genus, and the sea surface temperature (SST) anomaly time series for **B** Japan, **C** Indonesia, and **D** southeast Australia overlaid by each region's MTC analyzed with segmented linear regression (see Table 1 for the results of the segmented regression) (Dimarchopoulou et al.)

indices, all of which have been implicated in variations in Pacific marine ecosystems. To explain the variation in the MTC index, we performed multiple linear regression analyses (Ciaburro 2018) considering SST, PDO, SOI, and EN. All analyses were performed using the R statistical software (R Core Team 2021).

Results

The MTC index in the three regions exhibited different trends (Fig. 2A). The MTC index for Japan increased consistently and strongly over time by 0.33 °C per decade ($p < 0.001$) (Table 1, Fig. 2A–B), with this increase being stronger after the mid-1990s (1.2 °C per decade) (Fig. 2A-B, Table 2). Interestingly, the MTC index of Indonesia declined gradually

and slightly over the 67 years examined here, by a rate of 0.05 °C per decade, with this decline being stronger after the 1980s ($p = 0.012$) (Table 1, Fig. 2A, C). The overall MTC index in Indonesia mostly reflected the MTC of catches from the eastern EEZ subdivision of the country (Supplementary Fig. S3), since it is this area that contributes most (34–70%) to the total catch each year (Supplementary Fig. S2). The MTC index of SE Australia was variable until the late 1990s but rose strongly after 2000 (Fig. 2A). Over the full time period, this suggested a MTC change of 0.24 °C per decade ($p < 0.001$) (Table 1), whereas for the more recent period after 2002, the rate of MTC index change was 1.24 °C per decade (Fig. 2A, Table 2). The MTC index changes documented in this study are presented alongside previously reported MTC indices from around the world for comparison (Table 2).

Table 1 Linear regression outputs of the temporal trends of the mean temperature of the catch (MTC) (segmented regression, break-point(s)=year(s)±standard error) and sea surface temperature (SST) (simple regression) anomaly time series

Variables (~ year)	Residuals (median)	Intercept	Slope	R^2	p value	Break-point(s)±SE
MTC Japan	0.0753	−51.3853	0.0332	0.8415	7.42e^{-09} ***	1996±3
MTC Indonesia	−0.0033	16.6414	−0.0053	0.7199	0.012*	1981±2
MTC SE Australia	0.0046	−29.8414	0.0238	0.6598	5.88e^{-06} ***	1983±2
						2002±1
SST Japan	0.0309	−11.1305	0.0056	0.0950	0.0112 *	-
SST Indonesia	0.0141	−22.8810	0.0115	0.6411	4.218e^{-16} ***	-
SST SE Australia	0.0109	−23.7678	0.0120	0.6117	5.553e^{-15} ***	-

Table 2 Comparison of the decadal change in the mean temperature of the catch (MTC) index estimated in this study with previously reported values from around the world. *LME*, large marine ecosystem; *NE*, northeast; *NW*, northwest; *SW*, southwest; *S*, south; and *SE*, southeast

Region	Years	Climate zone	MTC change (°C/decade)	Reference
Global	1970–2006	-	0.19	Cheung et al. (2013b)
Non-tropical LMEs		-	0.23	
NE Pacific Ocean		Temperate	0.48	
NE Atlantic Ocean			0.49	
Tropical LMEs	1970–1980	Tropical	0.60	
	1981–2006		-	
West Mediterranean Sea	1970–2010	Temperate	0.56	Tsikliras and Stergiou (2014b)
Central Mediterranean Sea			1.05	
East Mediterranean Sea			0.29	
Yellow Sea	1950–2010	Temperate	0.41	Liang et al. (2018)
East China Sea		Subtropical/temperate	0.22	
South China Sea		Tropical	-	
NW Portugal	1989–2009	Subtropical/temperate	0.54	Leitão et al. (2018)
SW Portugal			0.49	
S Portugal			0.70	
English Channel	1987–2012	Temperate	0.20	Auber et al. (2017)
Lake Peipsi	1931–1986	Temperate	-	Kangur et al. (2021)
	1987–2019		0.85	
Japan	1950–2016	Temperate	0.33	Present study
	1996–2016		1.20	
Indonesia	1950–2016	Tropical	− 0.05	
SE Australia	1950–2016	Subtropical/temperate	0.24	
	2002–2016		1.24	

The MTC index time series in all three regions cross-correlated with the respective sea surface temperature (SST) anomalies. The SST anomaly in Japan exhibited a unique pattern with mostly positive values from 1950 to 1961, mostly negative values from 1962 to 1996, and again almost entirely
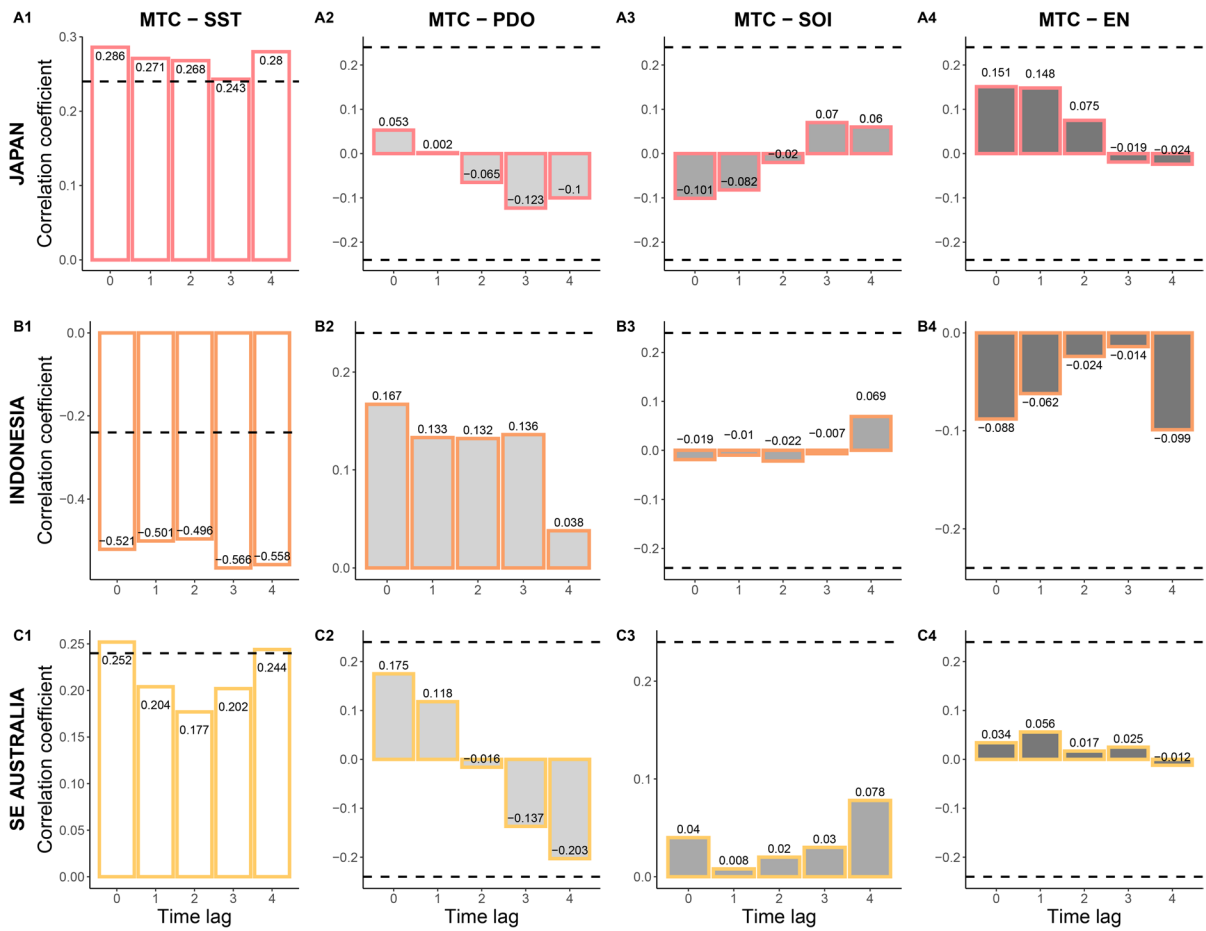
Fig. 3 Bar plots of the cross-correlations of each studied region's mean temperature of the catch (MTC) time series (1950–2016) with the sea surface temperature anomaly (SST) (white bars, A1, B1, C1), Pacific Decadal Oscillation (PDO) (light gray bars, A2, B2, C2), Southern Oscillation index (SOI) (dark gray bars, A3, B3, C3), and El Niño (EN) (darker gray bars, A4, B4, C4) at time lags of 0–4 years; dashed lines represent the 0.05 significance level (Dimarchopoulou et al.)

positive values until 2016 (Fig. 2B). The overall SST anomaly in Japan increased by 0.006 °C per year ($p = 0.011$) (Table 1), and it was positively cross-correlated with MTC (albeit weakly, correlation coefficient = 0.286, $p < 0.05$) (Fig. 3A1) without any time lag. Although the explanatory multiple linear regression model of Japan's MTC index performed quite poorly ($R^2 = 0.08$) (Table 3), it also showed that only the SST anomaly had a significant positive effect on MTC (Table 3). The SST anomaly in Indonesia exhibited an overall increasing trend of 0.01 °C per year ($p < 0.001$) (Table 1), presenting mostly positive values after 1986 in comparison to the mean SST value between 1950 and 2016 (Fig. 2C). The Indonesian MTC index

was negatively cross-correlated with the SST anomaly (correlation coefficient = -0.566, $p < 0.05$) (Fig. 3B1) at a time lag of 3 years which could be expected given that MTC declined while SST anomaly increased. The regression model of Indonesia's MTC index performed better ($R^2 = 0.39$) (Table 3), demonstrating that the SST anomaly was the only variable significantly negatively affecting the MTC (Table 3). The SST anomaly in SE Australia was mostly negative until 1996 and consistently positive thereafter (Fig. 2D). Over the full time period, however, the SE Australian SST anomaly had an overall increasing trend of 0.01 °C per year ($p < 0.001$) (Table 1). The SE Australia MTC index and SST anomaly were positively cross-correlated (albeit

Table 3 Multiple linear regression models of the mean temperature of the catch (MTC) index with sea surface temperature (SST) anomaly, the Pacific Decadal Oscillation index (PDO), the Southern Oscillation index (SOI), and the El Niño (EN) index. Statistically significant results are indicated using asterisks: $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *

Region	Coefficients	Estimate	SE	t value	Pr ($>|t|$)	Adjusted R^2	p value
Japan	(Intercept)	14.80	0.15	99.37	$<2e^{-16}$ ***	0.08	0.04 *
	SST (0 lag)	1.11	0.42	2.68	0.009 **		
	PDO	0.15	0.21	0.73	0.467		
	EN	0.23	0.27	0.85	0.397		
Indonesia	(Intercept)	26.93	0.02	1151	$<2e^{-16}$ ***	0.39	$4.1e^{-07}$ ***
	SST (3 lag)	-0.45	0.08	-5.98	$1.33e^{-07}$ ***		
	PDO	0.05	0.03	1.74	0.087		
	SOI	0.02	0.04	0.52	0.608		
SE Australia	(Intercept)	17.10	0.06	269	$<2e^{-16}$ ***	0.08	0.04 *
	SST (0 lag)	0.38	0.18	2.10	0.040 *		
	PDO	0.16	0.08	2.11	0.039 *		
	SOI	0.12	0.09	0.09	0.178		

Since SOI and El Niño are highly negatively correlated (Spearman's rho $= -0.93$, $p < 2.2e^{-16}$), one of the two was dropped from the analysis in each regression

weakly, correlation coefficient $= 0.252$, $p < 0.05$) (Fig. 3C1) without any time lag. The multiple regression analysis of SE Australia's MTC index performed quite poorly too ($R^2 = 0.08$) (Table 3) and showed that both the SST and PDO affected the MTC significantly positively. Nevertheless, none of the three MTC index time series cross-correlated at any time lag with any of the climatic variability indices examined, namely, the Pacific Decadal Oscillation, the Southern Oscillation, or the El Niño index (Fig. 3A2–4, B2–4, C2–4).

Generally, the share of thermophilous taxa in the catch compared to psychrophilous taxa increased overall in Japan and SE Australia between 1950 and 2016, while that ratio declined slightly in Indonesia (Fig. 4). The Japanese catch volumes were consistently dominated by psychrophilous taxa, which were on average 3.7 (1.4–9.8) times higher than the catch of thermophilous taxa (Fig. 4A). However, the catch volume of thermophilous taxa increased by 4.6 times over the full time period; from about 344,000 tonnes in 1950 to about 1.6 million tonnes in 2016 (Fig. 4A). In contrast, the catch volume of psychrophilous taxa has declined consistently over the last three decades, following the peak catch period in the 1980s driven by record catches of South American pilchard (*Sardinops sagax*) (Fig. 4A). The result is the observed increase in the ratio between thermophilous and psychrophilous taxa in the overall catches (Fig. 4A). The Indonesian catch volumes were consistently dominated by thermophilous taxa, whose catch was on average 7.7 times higher than catches of psychrophilous taxa (Fig. 4B). However, the catch volumes of psychrophilous taxa increased steadily over time, while the catches of thermophilous taxa in Indonesia had been plateauing since the late 1990s (Fig. 4B). This subtle shift has resulted in a gradual decline in the ratio between thermophilous and psychrophilous taxa (Fig. 4B). In SE Australia, there was a near equal contribution of thermophilous and psychrophilous taxa in the catches until the late 1990s, after which thermophilous taxa began dominating the catches (Fig. 4C). This pattern resulted in the ratio of thermophilous to psychrophilous taxa in the catches being more or less stable until 2000 but being increasingly dominated by thermophilous taxa thereafter (Fig. 4C).

Discussion

The previous global application of the mean temperature of the catch index (MTC) demonstrated that fisheries catches originating from latitudinally different

Fig. 4 Reconstructed catch time series for 1950–2016 (Zeller et al. 2016; www. seaaroundus.org) of psychrophilous (cooler water preference, dashed black line) and thermophilous (warmer water preference, solid black line) marine fish and invertebrate species and genera in **A** Japan, **B** Indonesia, and **C** southeast Australia. The temperature threshold was set at the average inferred temperature preference value for all taxa in each region, i.e., 19.5 °C in Japan, 25.8 °C in Indonesia, and 16.5 °C in southeast Australia. The ratio of thermophilous to psychrophilous taxon catch is given in the underlying percentage area plot (blue, cooler water preference; red, warmer water preference) as a percentage of each category to the total catch (secondary *Y*-axis) (Dimarchopoulou et al.)
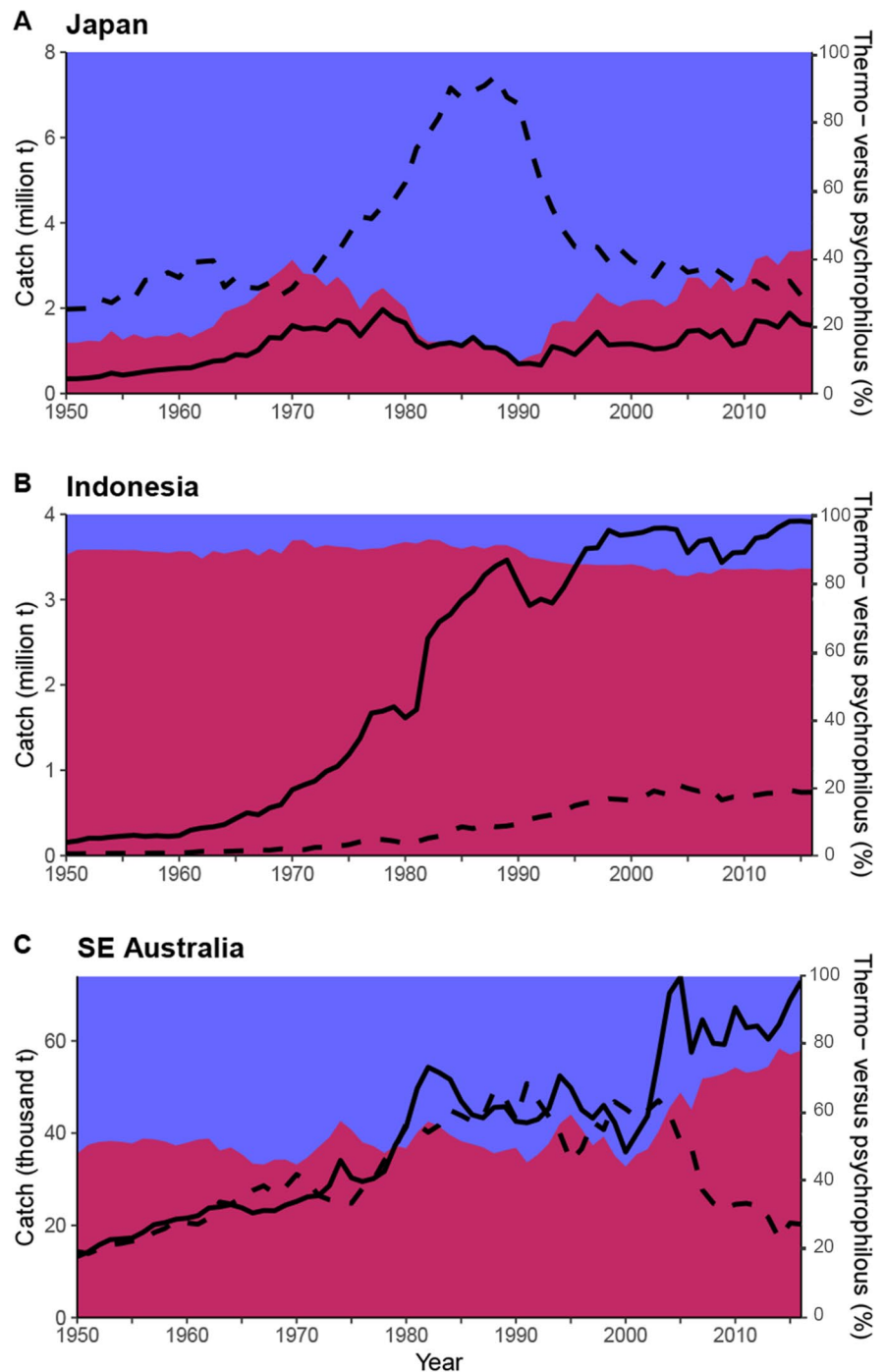
geographical areas respond differently to ocean warming, with subtropical and temperate areas generally exhibiting an overall MTC increase with rising sea surface temperatures (SST) and tropical areas showing an asymptotic MTC change pattern (Cheung et al. 2013b) (Fig. 1, Table 2). This has been partly confirmed by Liang et al. (2018) who reported that the tropical South China Sea did not demonstrate any significant MTC increase over the 60 years examined (1950–2010) compared to the subtropical/temperate

and temperate East China and Yellow Seas (Table 2). This was also broadly supported by the findings of the present study, with distinct increase in the MTC in the two temperate regions, but with the tropical Indonesian MTC index exhibiting a different pattern.

Our results indicated that Japan and southeast (SE) Australia have been and continue to experience climate change-driven alterations in fisheries catches that require adaptations of management and policies in light of the resulting increasing occurrence of warm-water taxa. Nevertheless, unlike the asymptotic pattern of the tropical MTC found by Cheung et al. (2013b) and the flat trajectory found by Liang et al. (2018), the mean temperature of the Indonesian catches showed an overall slightly decreasing trend of 0.05 °C per decade starting in the 1980s. This slight decrease in the Indonesian MTC index may be an indication of fishing down the deep due to fisheries expansion further offshore into deeper waters over the last 6 decades (Morato et al. 2006), following overfishing of shallow-water, nearshore, thermophilous reef fish, and invertebrates (Habibi et al. 2007). Indeed, in various Pacific Islands, small-scale commercial deep-water fisheries started in the 1970s primarily to reduce pressure on populations of shallow inshore reef fish (Williams et al. 2012). The significant correlation of the Indonesian MTC index with SST anomaly could potentially be mediated by fishing down the deep. Overfishing of warmer shallow waters, combined with constant SST increase that causes species to move poleward, may have consistently driven fishers to operate further offshore and deeper catching proportionally more psychrophilous species. Therefore, the negative correlation of MTC and SST may be manifested through these opposite but parallel in time trajectories, i.e., the increasing SST due to ocean warming and the decreasing MTC due to fishing deeper.

The clearest increasing trend in MTC over a long time period in the present study was observed in the temperate waters of Japan, with an increase of 0.33 °C per decade, a value that is comparable to other temperate ecosystems in the NE Pacific and Atlantic Oceans (Cheung et al. 2013b), the Mediterranean Sea (Tsikliras and Stergiou 2014b), Yellow Sea (Liang et al. 2018), and Portugal (Leitão et al. 2018) (Table 2). The MTC index for SE Australia catches exhibited a slightly smaller overall increase of 0.24 °C per decade if taken over the full 67-year time

period, which is about the same as the MTC change in the East China Sea, another subtropical/temperate region (Liang et al. 2018) (Table 2). Nevertheless, the SE Australia MTC has been strongly increasing since 2002, by 1.24 °C per decade, a rate even higher than the central Mediterranean Sea (Tsikliras and Stergiou 2014b) (Table 2). This is likely related directly to the very high rate of warming experienced in this region of the world (Fogarty et al. 2019).

All three geographic regions examined here displayed a correlated pattern between the observed MTC and the rate of regional SST changes, suggesting strongly that the change in the MTC was directly connected to ocean warming. This is in line with Cheung et al. (2013b) and others. The earth's temperature has warmed by approximately 1 °C since pre-industrial levels, with the SST of the Indian, Atlantic, and Pacific Oceans having increased by 0.11 °C, 0.07 °C, and 0.05 °C per decade, respectively, between 1950 and 2016, but with the greatest changes occurring at the higher latitudes (IPCC 2018). This may not be very apparent here when looking at the entire time series, since Japan's SST showed a gradual decrease from 1950 to 1985. However, in the late 1980s, a positive SST anomaly caused by a weak wind in the central–eastern Pacific reached Japanese waters increasing the temperature, reducing the mixed layer depth, and affecting Pacific stocks of anchovy and sardine (Makino 2018). When looking at the SST trend after 1985, the regional SST in Japan increased by 1.4 °C overall, at a rate of 0.17 °C per decade, which is higher than observed for Indonesia and SE Australia. These patterns reflect the global trend, wherein the warming of many marine ecosystems accelerated around the early 1980s (Belkin 2009). It has been shown previously that the Indian Ocean and most ecosystems around Australia and between Australia and Southeast Asia have experienced slower but steady warming without any major regime shift resembling those observed in the North Atlantic and North Pacific Oceans (Belkin 2009). This is supported by our findings of MTC trends over time only strongly accelerating in SE Australia after 2002. Australia, and the southeast region in particular, has been undergoing significant shifts to higher temperatures, with record hot years after 2000 combined with severe rainfall deficiencies from 1996 to 2006 (Murphy and Timbal 2008).

In contrast to the distinct connection between MTC and SST anomaly, the MTC changes observed here could not be linked to large-scale oceanographic variability, such as the Pacific Decadal Oscillation, the Southern Oscillation, or El Niño, which are known to affect the Pacific Ocean ecosystems (Mantua and Hare 2002; Stenseth et al. 2003). Similar to Auber et al. (2017), fishing effort per se was not considered here as a confounding factor, since it has been shown that there is little evidence that fishing systematically changes the MTC (Cheung et al. 2013b). However, we did exclude the data for two species from the dataset analyzed for SE Australia (orange roughy, *Hoplostethus atlanticus,* and the greenback horse mackerel, *Trachurus declivis*), as substantial and intense management actions and local market demands are known to influence observed catch trends for these taxa over time (Smith et al. 2015; Georgeson and Helidoniotis 2018; Ward and Grammer 2018). Given that these two species had considerable catch volumes, we excluded these two taxa to avoid undue influence on natural signals in the catch data.

As shown in Fig. 1, it is confirmed here that, despite some fluctuations, the contribution of thermophilous taxa to the total catch had been consistently increasing for the last 25 years in Japan and for the last 18 years in SE Australia. The tropicalization of catches due to ocean warming has also been observed in other temperate and subtropical ecosystems of the western Pacific (Yellow Sea and East China Sea) (Liang et al. 2018), the northeast Atlantic (Portugal) (Leitão et al. 2018), and the Mediterranean Sea (Greece) (Tsikliras et al. 2015). On the other hand, in tropical Indonesia, the pattern differed slightly, with a gradually declining MTC over time due to a gradually increasing contribution of psychrophilous species to the catches. That was despite the increase of the regional SST by 0.1 °C per decade, thus resulting in a negative correlation to the SST anomaly. And although thermophilous taxa catches have not decreased as would be expected in Indonesia (Cheung and Pauly 2016), the rate of their increase did indeed decline considerably after 1989, and the thermophilous taxa catch volumes have been plateauing since the late 1990s. The general catch potential of fisheries in the tropics may reflect the impacts of ocean warming where a drop of up to 40% in maximum catch potential has been projected between 2005 and 2055

(Cheung et al. 2010), and a decline in species richness with potential ocean warming-driven local extinctions is expected (Cheung and Pauly 2016). Nevertheless, no decrease in the catches (Supplementary Fig. S1B) or richness (Supplementary Fig. S4) of the catches in Indonesia was observed from 1950 to 2016. On the contrary, Indonesia has experienced substantial development of its fisheries for decades, with subsidies by both the national government and external agencies that boosted the growth of industrial trawl and purse-seine fisheries, especially after the late 1960s, creating conflicts with the numerous artisanal fishers (Pauly and Budimartono 2015 and references therein). Fisheries data collection in Indonesia was very sporadic in the earlier decades, hence the very low catches at the beginning of the time series in Supplementary Fig. S1B. Also, because Indonesian fisheries are taxonomically highly diverse, reported catch data include taxonomic over-aggregation, with each higher taxon representing dozens of species, which makes species-by-species studies like this one difficult (Pauly and Budimartono 2015). Nonetheless, in the case of the MTC estimates presented here, it was shown that including genus-level catch data, with available temperature preference information, averaged for all species within a given genus that had biological distributions within a given region was advantageous. It did increase the amount of data that could be analyzed by 15–25%, with the largest contribution for the Indonesian catches. The MTC that was estimated using both species- and genus-level catch data correlated with the MTC that was calculated using only species-level catches (Supplementary Table S1).

For a more holistic view of climate-induced impacts on fish abundance and fisheries catches, the MTC index should be used alongside other approaches, such as identifying species distribution shifts through climate velocity (Burrows et al. 2014) and species' life history traits (MacLean and Beissinger 2017). The MTC index relies on detailed, comprehensive, and reliable fisheries statistics. However, in many cases, especially in lower- to middle-income countries like Indonesia, many of which lie in tropical regions, consistent and comprehensive reporting of catches at the species level is not always possible, due to limited resources (Buchary et al. 2006). It can be equally problematic for indices like MTC when taxonomic disaggregation or general improvements

in fisheries catch reporting systems happen suddenly, without the corresponding past catches being corrected retroactively, thus leading to distorted, biased results impacted by the "presentist bias" (Zeller and& Pauly 2018), which has been clearly demonstrated in several countries (Jacquet et al. 2010; Tsikliras et al. 2020). Combining different approaches will help overcome the caveats and limitations of any single measure.

In conclusion, it was shown here that the MTC index can be used to investigate changes in western Pacific Ocean fisheries catches induced by ocean warming. As species respond to rapid anthropogenic ocean warming by moving their distributions poleward, regions in higher latitudes, like Japan and SE Australia, will increasingly lose cooler water (psychrophilous) species from their catches but gain species from subtropical and tropical areas. On the other hand, tropical regions like Indonesia have limited scope for further tropicalization of the catches, thus making the tropics a hotspot of ocean warming-driven local extinctions (Cheung and Pauly 2016). As this is expected to put the economy and food security of fisheries-dependent tropical countries at an even higher risk and can create domestic and transboundary fisheries conflicts especially in transboundary regions, current and future management plans need to be climate-adaptive and take into consideration the challenges of accelerated environmental and ecosystem change. To that end, an ecosystem approach to fisheries management that includes monitoring fisheries for climate impacts and building climate resilience has been previously proposed as a priority for the Asia–Pacific region (Heenan et al. 2015; Muawanah et al. 2018).

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