

# Linking observed changes in pelagic catches to temperature and oxygen in the Eastern Tropical Pacific

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## Abstract

Warming increases the metabolic rates of fishes and drives their oxygen demands above environmental oxygen supply, leading to declines in fish growth and smaller population sizes. Given the wide variability in species' sensitivity to changing temperature and oxygen levels, warming and oxygen limitation may be altering the composition of fish communities and hence, that of fisheries catches. Here, we test the hypothesis that changing temperatures shape the composition of pelagic fisheries catches in the Eastern Tropical Pacific. We expect that under warmer conditions, pelagic fisheries catches will be dominated by tropical species with higher oxygen demands and less surplus oxygen for growth. To test this hypothesis, we combined an index of the physiological vulnerability of exploited large pelagic fishes (e.g. tuna and billfish) to changing ocean temperatures and oxygen levels with fisheries catch data from 1970 to 2016. We found that warming is the main driver of changes in the physiological performance and catch composition of this fishery, and that oxygen limitation may be causing a significant breakpoint in the relationship between sea surface oxygen and the index of vulnerability of pelagic catches in the Ecuador and Galapagos Exclusive Economic Zones. Warm temperature anomalies due to El Niño were projected to cause reductions in the physiological performance of large pelagic fishes, although this only led to changes in catch composition during the extremely warm events. Our results suggest that catches are vulnerable to future warming, as the increasing frequency, duration and magnitude of marine heatwaves associated with climate change impact catch composition.

## KEYWORDS

aerobic scope, deoxygenation, El Niño, index of physiological vulnerability, large pelagic fishes, warming

## 1 | INTRODUCTION

Ocean warming affects the physiological performance of marine fishes and invertebrates, with cascading effects on growth, body size, reproduction, survival and abundance (Cheung, Sarmiento,

et al., 2013; Deutsch et al., 2015; Pauly, 2021). Metabolism scales positively with temperature (Clarke & Johnston, 1999) and, therefore, more oxygen is needed to support aerobic metabolism in warming waters. Increases in oxygen demand under ocean warming may surpass the ability of some fishes to maintain sufficient oxygen supply,

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even in well-oxygenated pelagic environments (Deutsch et al., 2015). This may lead to a contraction of the aerobic scope (difference between the maximum metabolic rate and the standard metabolic rate), forcing trade-offs between vital physiological processes that require oxygen, such as growth and reproduction (Baudron et al., 2014; Pauly, 2021; Pörtner et al., 2017; Sokolova, 2013).

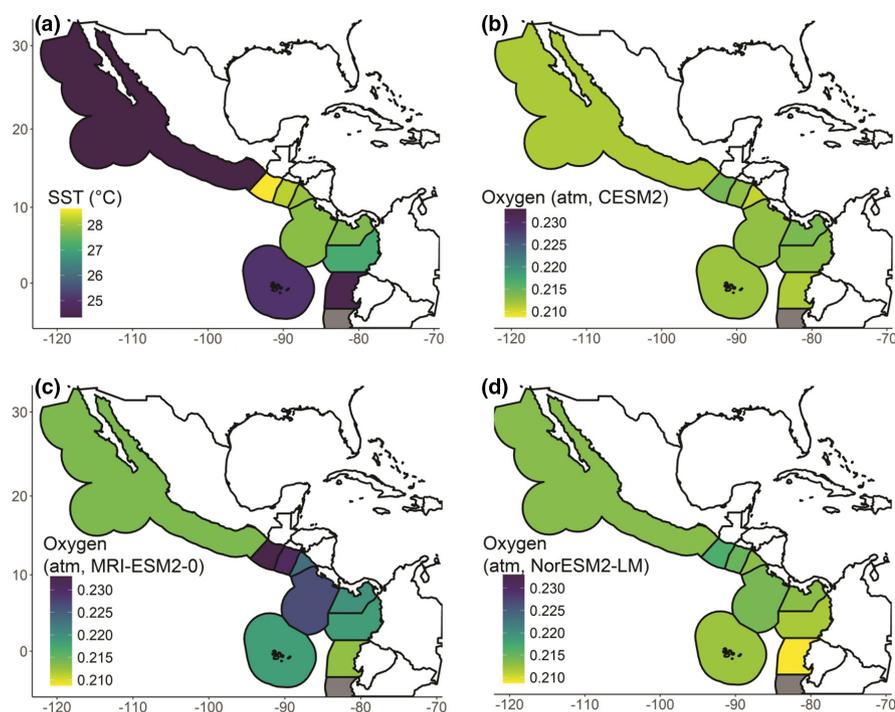
The impacts of warming on individual organisms can have knock-on effects at the population level, causing species distributions to shift towards favourable environmental conditions. Shifting species distributions can then alter community structure (Baudron et al., 2014; Cheung, Sarmiento, et al., 2013; Deutsch et al., 2015) and eventually the species composition of fisheries catches (Cheung, Watson, & Pauly, 2013; Gamito et al., 2015; Martínez-Ortiz et al., 2015). Warming is causing both non-exploited marine biological communities and fisheries' catches to become increasingly populated and even dominated by species with warmer thermal preferences (Bates et al., 2014; Bianchi & Morri, 2003; Cheung, Watson, & Pauly, 2013; Liang et al., 2018; Vergés et al., 2014).

The impacts of warming and oxygen limitation on the physiological performance of marine fishes and invertebrates can be assessed with the Aerobic Growth Index (AGI), which is a ratio of oxygen supply to demand of the average organism in a population or species (Clarke, Wabnitz, et al., 2021). AGI captures how warming increases species' oxygen demand and reduces oxygen supply, causing a decline in the surplus of oxygen for growth (Clarke, Wabnitz, et al., 2021; Deutsch et al., 2015). Therefore, AGI is an indicator of the risk of aerobic scope compression, and species with lower AGI will have lower growth rates and smaller populations, making them more susceptible to long term warming and marine heatwaves.

Combining AGI with fisheries catch data can help elucidate the relationship between ambient temperature and oxygen, the physiological performance of species and catch composition (Figure 1). If

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biomasses of exploited fish populations decline because their aerobic scope is compressed under warming, we would expect their representation in the composition of catches to also decrease. The relationship between aerobic scope, warming and oxygen limitation is represented here by a catch-based indicator (Aerobic Growth Index of the Catch, AGIC) that is calculated from the average AGI of the exploited species weighted by their catch. In addition, we use a second catch-based indicator (Mean Oxygen Demand of the Catch, MODC) that is computed as the metabolic demand for oxygen at the species' preferred temperature weighted by their annual catch. We apply the MODC to elucidate the impacts of varying ambient



**FIGURE 1** Average observed sea surface temperature (SST, °C; panel a) and simulated oxygen partial pressure (atm; panels b–d) from three different Earth system models (CESM2, MRI-ESM2-0, NorESM2-LM) across the nine studied EEZs in the Eastern Tropical Pacific, between 1970 and 2016

temperature and oxygen on changes in catch composition over time. We expect short term changes in catch composition to reflect shifting species distributions, and long-term changes in catch composition to reflect impacts on growth, reproduction and survival.

In the Eastern Tropical Pacific, the latitudinal temperature gradient (annual mean SST ranges from 24.3°C off Mexico to 29.3°C off Guatemala) and the important temperature (Philander, 1983) and oxygen inter-annual fluctuations (Eddebbbar et al., 2017; Yang et al., 2017) driven by the El Niño Southern Oscillation, provide a 'natural experiment' to examine the relationship between temperature, oxygen and the changes in physiological performance that shape community structure. Commercial pelagic fisheries in the Eastern Tropical Pacific may act as bellwethers of the impacts of warming on pelagic ecosystems (Woodworth-Jefcoats et al., 2019), as they target many species with high oxygen demands, such as tuna and billfish (Bertrand et al., 2011; Mislán et al., 2017; Prince & Goodyear, 2006). Furthermore, in the tropics, temperature and oxygen levels are closer to species' physiological tolerance limits, so even a small degree of warming could drive species to shift towards cooler, more oxygenated waters (Breitburg et al., 2018).

In this study, we test the hypothesis that changing ocean temperatures are shaping the composition of fisheries catches in the Eastern Tropical Pacific. Specifically, by analysing fisheries catch data from nine Exclusive Economic Zones (EEZs) between 1970 and 2016, we hypothesize that temperature and/or oxygen thresholds may separate different species assemblages, and that under warmer conditions, pelagic fisheries catch is dominated by tropical species with higher oxygen demands and higher aerobic scope compression (lower AGI).

## 2 | MATERIALS AND METHODS

### 2.1 | Catch data

This study encompassed the EEZs of countries in the Eastern Tropical Pacific from Mexico in the north, to Ecuador and Galapagos in the south. Our analysis focused on fisheries for large oceanic pelagic fishes, which mainly target skipjack (*Katsuwonus pelamis*, Scombridae), yellowfin (*Thunnus albacares*, Scombridae) and bigeye (*Thunnus obesus*, Scombridae) tuna (Schaefer et al., 2009) in all EEZs. These fisheries also commonly caught mackerels (*Acanthocybium* spp., *Scomber* spp., *Scomberomorus* spp., *Euthynnus* spp.), other tuna species (*Thunnus* spp.), mahi mahi (*Coryphaena hippurus*, Coryphaenidae), billfishes (*Istiophorus* sp., *Makaira* sp., *Xiphias* sp.) and sharks (*Alopias* spp., *Carcharhinus* spp., *Sphyrna* spp., *Prionace glauca*) (Lluch-Cota et al., 2019). We used the reconstructed historical catch time-series data from the Sea Around Us database, spanning from 1950 to 2016 to calculate the catch-based indicators because it has a high degree of taxonomic resolution and includes estimates of potential discards (Cisneros-Montemayor et al., 2015; Donadi et al., 2015; Haas et al., 2015; Harper et al., 2014; Lindop, 2015; Lindop et al., 2015; Pauly et al., 2020; Pauly & Zeller, 2016; Trujillo et al., 2015). We filtered the Sea Around Us catch databases according to functional categories to include large and medium pelagic fishes. The databases for large pelagic fishes were produced by

integrating catch data from regional fisheries management organizations, the FAO Atlas of Tuna and Billfish Catches, country level records of artisanal landings, and discard estimates based on literature reviews (Le Manach et al., 2015; Pauly & Zeller, 2016). We only included catch time-series from species that were caught for more than 30 years in each EEZ, to avoid the confounding effects of changes in taxonomic resolution of reported fisheries catches (Table S1).

### 2.2 | Environmental data

We obtained sea surface temperature data from the Centennial in-situ Observation Based Estimates (COBE) provided by NOAA/OAR/ESRL (<https://psl.noaa.gov/data/gridded/data.cobe.html>; Ishii et al., 2005). This temperature time-series was selected for our analyses because it has data available for the analysed time period (1970–2016), at a relatively high spatial resolution of 1° latitude by 1° longitude capable of distinguishing patterns across the narrow EEZs in Central America.

In the absence of time-series data for dissolved oxygen, we used sea surface oxygen concentration, temperature and salinity from ocean model hindcast simulations to calculate oxygen partial pressure (units in atm) following the approach outlined by Bittig et al. (2018). Hindcast outputs are obtained from the ocean/sea-ice components of three Earth system models included in the Coupled Models Intercomparison Project Phase 6 (CMIP6): the second generation Earth system model developed by the Community Earth system model Version 2, CESM2 (Danabasoglu et al., 2020), Meteorological Research Institute Earth System Model Version 2.0, MRI-ESM2-0 (Seiji et al., 2019) and the second version of the coupled Norwegian Earth System Model, NorESM2-LM (Seland et al., 2020). The forcing of the global ocean/sea-ice-only simulations of all three models is based on the Coordinated Ocean-ice Reference Experiments interannually varying observation-based atmospheric datasets (Griffies et al., 2016). The hindcast simulations are 60-years long (720 months) covering the period from 1958 to 2018 (Griffies et al., 2016; Orr et al., 2017). All model data were re-gridded on the same 1° latitude by 1° longitude map of the ocean as the observation based COBE temperature data.

We produced baseline global 1971–2000 climatologies of sea surface temperature and sea surface oxygen partial pressure, assuming the species distribution data is in equilibrium with the average historical conditions throughout this period (Tai et al., 2021). For each EEZ, we calculated the annual average sea surface temperature and oxygen partial pressure time-series.

### 2.3 | Mean Oxygen Demand of the Catch and the Aerobic Growth Index of the Catch (AGIC)

To calculate AGIC and MODC, we first computed the theoretical oxygen level ( $pO_{2,demand}$  in atm) required by an individual to support its maintenance metabolic rate (Clarke, Reygondeau, et al., 2021; Clarke, Wabnitz, et al., 2021):

$$pO_{2,demand} = \left( \frac{W^{1-d} \left( e^{-\frac{j_2}{T}} pO_{2,thresh} e^{-\frac{j_1}{T_{pref}}} \right)}{W_{\infty}^{1-d} \left( e^{-j_1/T} e^{-j_2/T_{pref}} \right)} \right) \quad (1)$$

where  $W$  is average body weight (in g) and  $W_{\infty}$  is the asymptotic weight (in g), estimated from the asymptotic length  $L_{\infty}$  (in cm) and the species' length-weight relationship (Froese & Pauly, 2019).  $d$  is an anabolic scaling coefficient with a value of 0.7 (Pauly & Cheung, 2018). An abbreviated form of the Arrhenius equation (Clarke & Johnston, 1999)  $e^{-j_1/T}$  and  $e^{-j_2/T}$  is included in (1) to account for the temperature-dependence of anabolism and catabolism. Parameters  $j_1$  and  $j_2$  are the activation energies (0.388 and 0.689 eV; Cheung et al., 2011) divided by the Boltzmann constant, resulting in a  $j_1$  and  $j_2$  of 4500 and 8000K, respectively (Cheung et al., 2011).  $T$  is the ambient sea surface temperature in Kelvin. The species-specific oxygen threshold ( $pO_{2,thresh}$ , expressed in atm) is the 10th percentile of the sea surface oxygen partial pressures across its distribution.  $T_{pref}$  is the species temperature preference (in Kelvin), expressed as the median sea surface temperature across the species' distribution (Cheung et al., 2008; Cheung, Sarmiento, et al., 2013).

The AGI (Clarke, Wabnitz, et al., 2021) is the ratio of oxygen supply to demand:

$$AGI = \frac{pO_{2,supply}}{pO_{2,demand}} \quad (2)$$

where  $pO_{2,supply}$  is the average annual dissolved oxygen concentration in each EEZ (in atm) and  $pO_{2,demand}$  is the species' oxygen demand (in atm) computed in Equation 1.

We then calculated the yearly (yr) AGIC based on the averaged AGI (from Equation 2) weighted by the catch over the year:

$$AGIC_{yr} = \frac{\sum_i^n AGI_{i,T} \cdot Catch_{i,yr}}{\sum_i^n Catch_{i,yr}} \quad (3)$$

where  $Catch_{i,yr}$  is the weight of the catch of species  $i$  in each EEZ,  $AGI_{i,T}$  is the oxygen demand of species  $i$  at sea surface temperature  $T$  (in Kelvin) and  $n$  is the total number of species.

We also calculated a MODC that represents the average oxygen demand ( $pO_{2,demand}$ ) from Equation (1) weighted by the annual catch of species  $i$ :

$$MODC_{yr} = \frac{\sum_i^n pO_{2,demand_{i,T_{pref}}} \cdot Catch_{i,yr}}{\sum_i^n Catch_{i,yr}} \quad (4)$$

where  $Catch_{i,yr}$  is the catch of a species  $i$  in each EEZ,  $pO_{2,demand_{i,T_{pref}}}$  is the oxygen demand of species  $i$  at each species' temperature preference,  $T_{pref}$ . We computed the annual AGIC and MODC for each EEZ from 1970 to 2016, assuming that most changes in catch composition before the 1970s will be due to fishing (Pauly & Palomares, 2005; Rodgers et al., 2015).

## 2.4 | Analytical methods

### 2.4.1 | Spatial trends in MODC and AGIC

We applied linear regressions to explore the relationship between standardized temperature and oxygen, and MODC and AGIC. A visual inspection of the data suggested a non-linear relationship between oxygen and MODC as well as AGIC for the EEZs of Ecuador and Galapagos. Therefore, we applied segmented regressions to examine the relationship between oxygen and AGIC and MODC, respectively, using the R package 'segmented' (Muggeo, 2003, 2017). The oxygen levels that demarcated significant changes in their relationship with AGIC and MODC may suggest environmental thresholds that separate different biological communities (e.g. tropical, temperate, subtropical and upwelling). We recognize the uncertainties inherent in the limited amount of data analysed in this study, therefore, the results of the spatial trends are intended to provide insights into the potential role of temperature and oxygen in shaping fisheries catches. We encourage further examination of our hypotheses and findings in future studies using fisheries dependent and independent data from different locations.

### 2.4.2 | Temporal trends in MODC and AGIC

We applied a wavelet coherency analysis to detect any transient linear correlations between AGIC and MODC with the El Niño Southern Oscillation (ENSO; Gouhier et al., 2019), represented by the sea surface temperature anomalies in the Niño 3.4 region (5°N–5°S, 120°W–170°W). We chose the anomalies in this region because it is key for coupled ocean-atmospheric interactions for ENSO and is commonly used to define El Niño and La Niña events (Trenberth, 1997). We conducted separate wavelet analysis for each geographic area categorized according to its average MODC, AGIC and sea surface temperature: Group 1: Mexico; Group 2: Guatemala, El Salvador, Nicaragua, Costa Rica, Panama and Colombia; Group 3: Ecuador and Galapagos. Firstly, we averaged the AGIC and MODC time-series across Earth system models to obtain an ensemble model for each indicator and then standardized each time-series by applying a Continuous Wavelet Transform function. Specifically, we applied the Morlett wavelet function, which is commonly used to analyse ecological data. The Morlett function is a continuous wavelet from which we can extract time-dependent amplitude and frequency. All wavelet analyses were performed with the wavelet library developed by Gouhier et al. (2019).

## 3 | RESULTS

### 3.1 | Spatial trends in MODC and AGIC

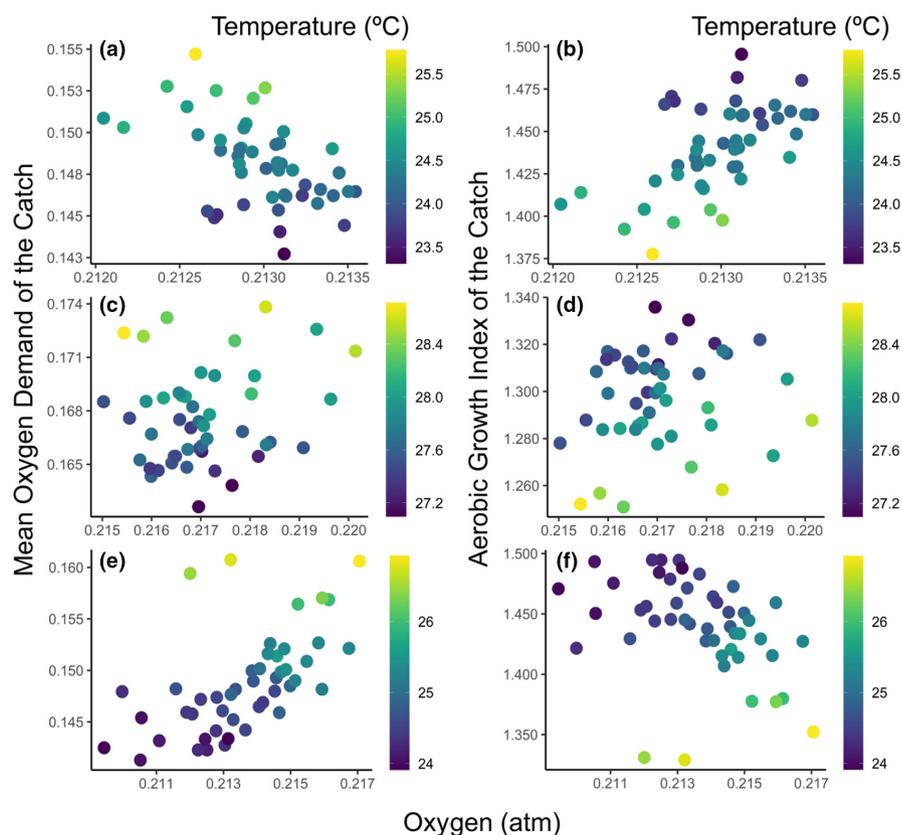
Average temperature and oxygen partial pressure across the 9 studied EEZs over the 1970–2016 period ranged between 24.3–29.4°C and 0.209–0.232 atm, respectively (Figure 1). The northern and

southern most EEZs of the Eastern Tropical Pacific (Mexico, Ecuador) had the lowest temperatures due to an overlap with the California current in the north and equatorial upwelling along the southern border of the study area (Figure 2a, Figures S1 and S2), while Guatemala, El Salvador and Nicaragua had the highest temperatures. EEZs overlapping equatorial upwelling and the California Current (Ecuador and Mexico) had lower oxygen concentrations in all three Earth system model simulations than their neighbouring EEZs (Guatemala, El Salvador and Nicaragua; Figure 1). Catches from all EEZs were dominated by skipjack tuna and yellowfin tuna, with a larger proportion of skipjack tuna in Colombia, Galapagos and Ecuador and a larger proportion of yellowfin tuna in the EEZs of Mexico through Panama (Table S1).

Temperature was the most important variable driving changes in the relative biomass of species in the catch, or catch composition (MODC) and physiological performance of species in the catch (AGIC; Table 1). The relationship between temperature and MODC was always positive, while the relationship between temperature and AGIC was always negative (Table 1). There was a breakpoint in the relationship between oxygen, AGIC and MODC in Ecuador and Galapagos at 0.213 atm ( $p < .001$ ). At oxygen levels lower than the breakpoint, MODC and AGIC remained constant as oxygen increased, at oxygen levels higher than the threshold MODC increased and AGIC decreased as oxygen increased (Figure 3). Breakpoints in the relationship between oxygen, MODC and AGIC were not observed for Central America, where temperatures and oxygen levels were higher (Figures S1 and S2).

### 3.2 | Temporal trends in MODC and AGIC

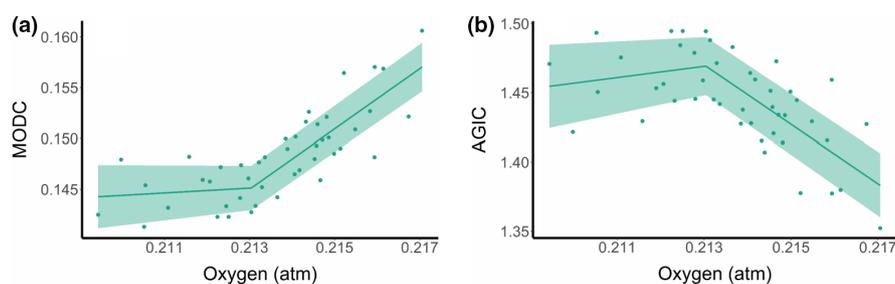
Long-term trends in temperature, oxygen, MODC and AGIC were small relative to the magnitude of their interannual variabilities (Figures S1–S4). The interannual variability in MODC and AGIC time series followed a pattern similar to that of ENSO (dashed grey lines in time-series plots of Figure 4 represent standardized maximum Niño 3.4 anomalies). Specifically, the wavelet coherence analysis used to detect transient linear correlations between ENSO and AGIC, revealed that coherence between these two time-series was strong and consistent ( $R^2 > .8$  for up to 6-year periods) from the 1980s to late 2000s in all EEZs except Mexico (Figure 5). This can be observed in the thick red band spanning the wavelet coherence plot in Figure 5d,f. Changes in AGIC represent changes in the physiological performance of the average species within the catch and have a high correlation with changes in temperature, which are built into the estimation of the AGI by driving increases in the oxygen demand of species. The warming and cooling during the different ENSO phases, were closely related to changes in AGIC, correlations between both time-series had between a zero and 8-year lag. Coherence between ENSO and MODC time-series on the other hand was episodic (Figure 5), representing changes in the catch composition or the relative biomasses of species in the catch. The wavelet coherence analysis, used to detect transient linear correlations between MODC and temperature anomalies, revealed that the correlations between these two time-series in the Mexican EEZ (Figure 5a) became evident after the 1982–1985 episode, when the coherence had a lag of around 4 years. In the same



**FIGURE 2** Mean Oxygen Demand of the Catch and Aerobic Growth Index of the Catch across oxygen (atm) and sea surface temperature (°C) gradients occurring throughout 1970–2016 in the Exclusive Economic Zones of Mexico (a, b), Guatemala, El Salvador, Nicaragua, Costa Rica Panama and Colombia (c, d) and Ecuador and Galápagos (e, f)

**TABLE 1** Linear regression analysis between oxygen (atm), sea surface temperature (°C) and the catch-based indices of Mean Oxygen Demand of the Catch (MODC) and the Aerobic Growth Index of the Catch (AGIC) of pelagic fisheries in the Eastern Tropical Pacific (from Mexico to Ecuador) from 1970 to 2016

Dependent variable	Region	Independent variable	R <sup>2</sup>	Estimate	Std. Error	t	p-Value
MODC	1	Intercept	.85	0.1482	0.0001	1033.1220	<.01
		Temperature		0.0022	0.0002	13.8240	<.01
		Oxygen		-0.0005	0.0002	-3.1050	<.01
	2	Intercept	.76	0.1676	0.0002	878.9310	<.01
		Temperature		0.0023	0.0002	11.9970	<.01
		Oxygen		0.0001	0.0002	0.3980	.69
	3	Intercept	.91	0.1773	0.0345	5.1370	<.01
		Temperature		0.0048	0.0003	16.9520	<.01
		Oxygen		-0.0286	0.0345	-0.8280	.41
AGIC	1	Intercept	.86	1.4401	0.0014	1007.6750	<.01
		Temperature		-0.0207	0.0016	-13.2770	<.01
		Oxygen		0.0069	0.0016	4.4360	<.01
	2	Intercept	.75	1.2976	0.0015	867.0680	<.01
		Temperature		-0.0178	0.0015	-11.5870	<.01
		Oxygen		0.0059	0.0015	3.8540	<.01
	3	Intercept	.87	-0.1257	0.3438	-0.3660	.72
		Temperature		-0.0444	0.0028	-15.7460	<.01
		Oxygen		1.5652	0.3438	4.5520	<.01



**FIGURE 3** Segmented regressions between (a) sea surface oxygen (atm) and the Mean Oxygen Demand of the Catch (MODC); (b) sea surface oxygen (atm) and the mean Aerobic Growth Index of the Catch (AGIC). For the Exclusive Economic Zones of Ecuador and Galapagos 1970–2016

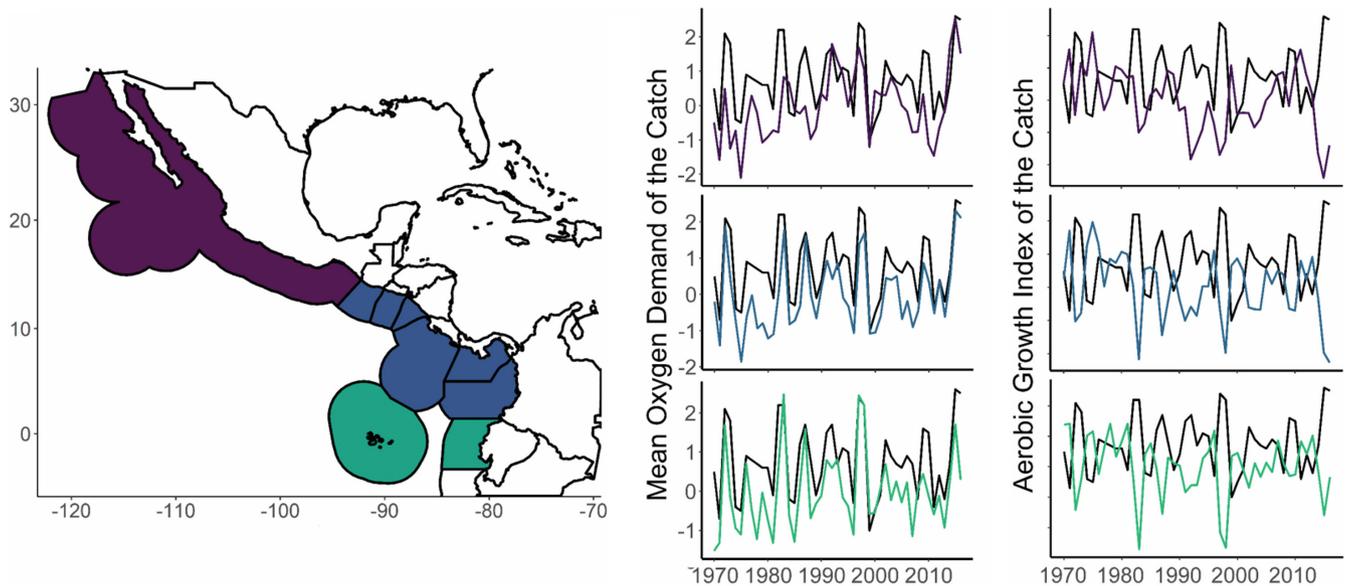
region, the wavelet coherency analysis between AGIC and ENSO revealed a strong correlation after the 1997/1998 episode.

## 4 | DISCUSSION

Our study shows that the constraints of temperature and oxygen limitation on species' physiological performance shape catch composition of large pelagic fisheries across the Eastern Tropical Pacific. We demonstrate this by applying the AGIC to detect trends in the physiological performance of species in the catch and the MODC to detect shifts in the relative biomass of species in the catch. Our results are supported by studies showing that the distribution, abundance and size of tuna, billfish and mahi-mahi within the ETP vary with interannual changes in temperature, and in some cases, oxygen (Ayala-Duval & Maldonado-Monroy, 2019; Erauskin-Extramiana

et al., 2019; Lehodey et al., 2013; Marín-Enríquez et al., 2018; Zhou et al., 2021). For example, the size distributions of the most dominant species in the catch (skipjack tuna and yellowfin tuna) vary with temperature (Ayala-Duval & Maldonado-Monroy, 2019; Dell'Apa et al., 2018; Lehodey et al., 2013), and the species distribution of the less abundant, but highly valuable bigeye tuna (*T. obesus*, Scombridae) is defined by its tolerance to low oxygen environments (Zhou et al., 2021).

Warming is the main driver of changes in MODC and AGIC in these pelagic fisheries, driving increases in oxygen demand that can lead to oxygen limitation in low oxygen environments. This oxygen limitation is represented by the breakpoints in the relationship between oxygen and MODC and AGIC (~0.213 atm) in the Ecuador and Galapagos EEZs. Upwelling in the Ecuador and Galapagos EEZs leads to these low oxygen levels (i.e. lower oxygen partial pressures), and biological communities that are dominated by species with lower



**FIGURE 4** Map showing the three main geographic areas in the Eastern Tropical Pacific with distinct Mean Oxygen Demand of the Catch (MODC), Aerobic Growth Index of the Catch (AGIC) and positive sea surface temperature anomalies in the Niño 3.4 region. Mean Oxygen Demand of the Catch and Aerobic Growth Index of the Catch of pelagic fish catches normalized to the long term mean in mapped geographic areas (1970–2016). Purple represents group 1 and includes Mexico, blue represents group 2 that includes Guatemala, El Salvador, Nicaragua, Costa Rica, Panama and Colombia, green represents group 3 and includes Ecuador and Galapagos. Standardized maximum Niño 3.4 Index is plotted in grey dashed lines

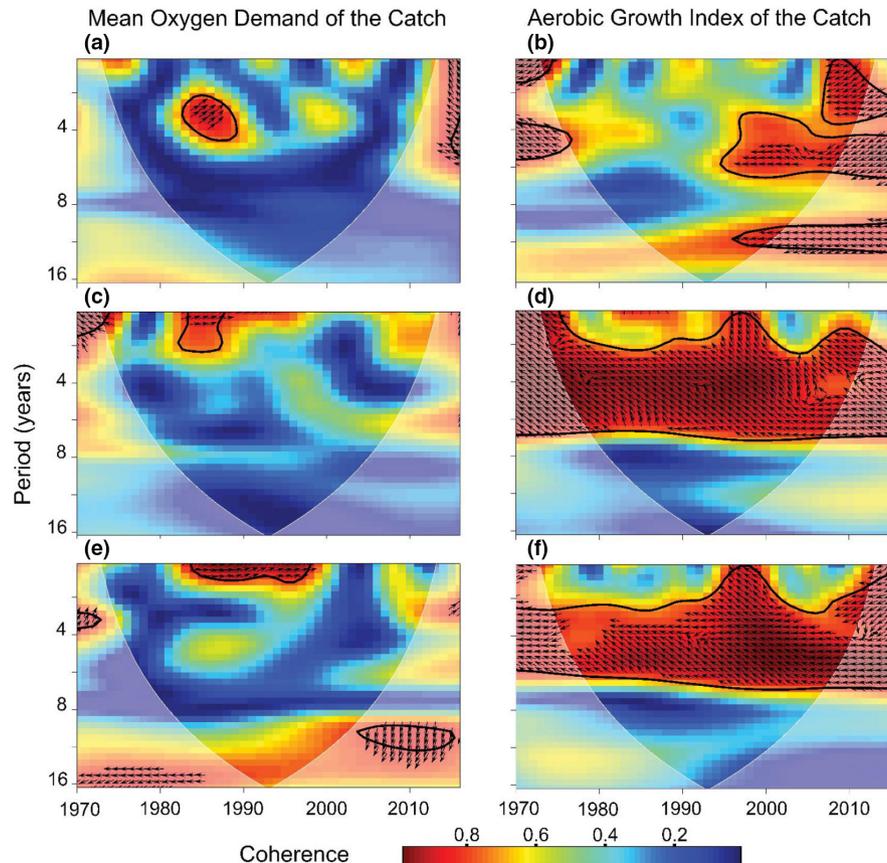
oxygen demands (lower MODC). Oxygen levels above the threshold provide favourable conditions to species with higher oxygen demands, increasing their relative representation within the catches (higher MODC). An oxygen threshold was not detected in the indices from Mexico despite its similarly low average oxygen levels, as most of the tuna and billfish were caught the warmer waters with higher oxygen levels, similar to those along Central America ([searounds.org](http://searounds.org)). In the Central American EEZs, temperature was the main variable driving increases in MODC and AGIC, as higher metabolic oxygen demands in warmer waters increased the risk of aerobic scope compression of the exploited species (i.e. lower AGIC). Yet, oxygen limitation did not reach the threshold that would cause the community composition to change, possibly due to the dominance of tropical species within the catches and the higher oxygen levels in these waters. Yet, further ocean warming and an increase in the frequency and intensity of marine heatwaves (Frölicher et al., 2018) may reduce the biomass of even the tropical exploited species with high metabolic oxygen demand (Clarke, Reygondeau, et al., 2021). These results provide a mechanistic underpinning to previous projections of future reductions in abundance of commercial species and species diversity in the tropics (Bates et al., 2014; Bianchi & Morri, 2003; Cheung, Watson, & Pauly, 2013; Clarke, Reygondeau, et al., 2021; Clarke, Wabnitz, et al., 2021; Vergés et al., 2014).

The oxygen thresholds detected in this study may represent a critical tipping point—where a small change in oxygen or temperature could push the system into an alternate and potential irreversible state (Griffiths et al., 2013; Heinze et al., 2021). These tipping points may lead to profound shifts in fisheries catch composition with important consequences for the communities that depend on

them (Dakos et al., 2019; Guerin et al., 2013). Such tipping points are typically hard to identify, yet if known can help shape monitoring and management programs for sustainable fisheries (Halpern, 2017; Rilov et al., 2019; Selkoe et al., 2015).

Large pelagic fishes caught in the Eastern Tropical Pacific warm pool (Guatemala, El Salvador, Nicaragua, Costa Rica) had a small scope between oxygen demand and supply, indicating warming may be affecting the physiological performance of species via a higher oxygen demand. Species in these warmer EEZs may be particularly vulnerable to additional factors that cause physiological stress and limit organisms' aerobic scope, such as ocean acidification, overfishing and declining habitat quality (Horwitz et al., 2020; Laubenstein et al., 2018). Consequently, this region may be less resilient to El Niño events that can drive temperatures above the physiological tolerance limits of many species (Smale et al., 2019).

Within the Eastern Tropical Pacific, the interannual variability of the catch produced by ENSO dominates over the long-term trends, given a constant fishing effort (Watters et al., 2003). The sharp, positive temperature anomalies associated with El Niño increase species oxygen demand, thereby reducing the surplus of oxygen available for growth, which then drives changes in catch composition during extremely strong El Niño events. We found ENSO's impact on the physiological performance of species in the catch (AGIC) to last longer and be more immediate after El Niño events within Central America, Colombia and Ecuador, which could reflect the different ways in which El Niño affects a population. The short-term changes may be caused by these highly mobile pelagic species moving away from unfavourable conditions (Carlisle et al., 2017; Farchadi et al., 2019; Marín-Enríquez et al., 2018), quickly crossing borders of



**FIGURE 5** Coherence between Mean Oxygen Demand of the Catch and the Niño 3.4 Index for pelagic fisheries in the Eastern Tropical Pacific in geographic areas 1 [Mexico] (a), 2 [Guatemala, El Salvador, Nicaragua, Costa Rica, Panama and Colombia] (c), 3 [Ecuador and Galapagos] (e). Coherence between Aerobic Growth Index of the Catch and the Oceanic Niño Index for pelagic fisheries in the Eastern Tropical Pacific in geographic areas 1 (b), 2 (d), 3 (f). The horizontal axis represents time, while the vertical axis represents frequency. Red colours represent areas where the two time series co-vary, while blue colours represent areas where there is a low dependence between both time series. The absence of arrows means both time series co-vary with no lag or lead. Arrows to the right indicate the time series are in phase (they move in the same direction), arrows to the left mean the time series are in anti-phase (they move in opposite directions). Right-down or left-up arrows: first variable leads, right-up, left-down: second variable leads. The translucent areas represent the cone of influence, where the edge effects may distort patterns in the coherence between both time series

the narrow EEZs within the region and altering each country's catch. The longer-term effects may be due to impaired population growth, recruitment and reproductive success caused by warming (Watters et al., 2003).

Strong El Niño conditions are known to affect fisheries catches and species distributions throughout the Eastern Tropical Pacific region (Fiedler, 2002; Haulsee et al., 2022; Lehodey et al., 1997; Leung et al., 2019; Mora & Robertson, 2005; Zapata Padilla, 2002). This is because these highly mobile pelagic species can shift with the environmental conditions they are adapted to. For example, during El Niño events, the catches of bigeye tuna increase in the Eastern Tropical Pacific, when the oxygen minimum zone deepens and the optimal temperature is above the minimum oxygen threshold for this species (Espinoza-Morriberón et al., 2019; Zhou et al., 2021). Although the distribution and abundance of skipjack tuna tended to increase in the Eastern Tropical Pacific during El Niño events (Receveur et al., 2016), extremely strong El Niño events (e.g. the 1982/1983 El Niño; see contributions in Pauly and Tsukayama (1987)) led to poor tuna fishing conditions in the ETP for both skipjack and yellowfin tuna (Mediodia et al., 2020).

However, these studies do not consider the effects of oxygen or the distribution of Oxygen Minimum Zones.

Deoxygenation is likely one of the key factors driving changes in the catch composition of pelagic fisheries in the Eastern Tropical Pacific, yet our study was only able to capture the effect of oxygen limitation. Oxygen may become limiting in pelagic environments as hypoxic waters are upwelled to the surface and oxygen minimum zones expand (Duteil et al., 2018; Mislán et al., 2017; Stramma et al., 2012). While our two-dimensional analysis is able to capture some of the effect from upwelling, it was not able to capture the vertical compression of pelagic habitats. Future research should explore the three-dimensional impacts of warming and deoxygenation on metabolically viable pelagic habitats, and how this may affect fisheries.

Fishing impacts may also confound trends in AGIC and MODC, by influencing the relative composition of the catch. Both fishing and oxygen limitation select for smaller body sizes and faster growth rates. Fisheries eliminate individuals with high performance aerobic scopes that invest more of their aerobic capacity in growth instead of the skittish behaviours that keep them small and thus allow them

to avoid interactions with fishing gear (Duncan et al., 2019; Pauly & Froese, 2020). A population consisting of smaller sized individuals will in turn have a lower biomass and reproductive output, which can reduce population growth and lead to unsustainable fisheries. Future studies should account for fishing effort and fishing behaviour in models detecting factors causing trends in both indices (Haulsee et al., 2022).

The key role that temperature and oxygen limitation plays in structuring catch composition of pelagic fisheries, suggests that catches may be vulnerable to future warming. Here, we showed how the application of AGIC and MODC can help improve our understanding warming and deoxygenation's impact on marine fisheries. Together, these indicators reveal how reductions in physiological fitness caused by warming can change the catch composition of pelagic fisheries during strong warming events. Importantly, we identified thresholds that can help inform monitoring methods that support sustainable management measures for marine resources in the Eastern Tropical Pacific.

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## DATA AVAILABILITY STATEMENT

The catch data that support the findings of this study are available in the Sea Around Us website ([www.seaaroundus.org](http://www.seaaroundus.org)), the Earth system model hindcast outputs are available in: <https://esgf-node.lnl.gov/search/cmip6/>, the sea surface temperature is available here: <https://psl.noaa.gov/data/gridded/data.cobe.html>

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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