



Effects of climate warming on energetics and habitat of the world's largest marine ectotherm

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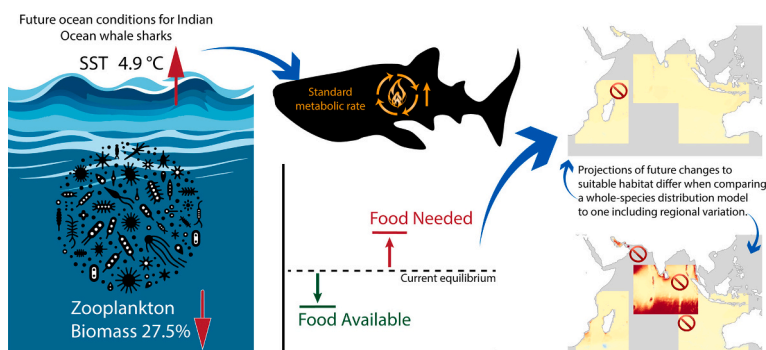
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HIGHLIGHTS

- Ocean temperatures at Indian Ocean whale shark aggregations may rise 4.9 °C by 2100.
- Phylogenetic models show this will increase sharks' metabolic rate and energy needs.
- Concurrent zooplankton decreases may challenge whale sharks' energetic balance.
- Projections of suitable habitat show losses in some areas but gains in others.
- Whole-species and regionally-variable distribution models differ in projections.

GRAPHICAL ABSTRACT



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ABSTRACT

Responses of organisms to climate warming are variable and complex. Effects on species distributions are already evident and mean global surface ocean temperatures are likely to warm by up to 4.1 °C by 2100, substantially impacting the physiology and distributions of ectotherms. The largest marine ectotherm, the whale shark *Rhincodon typus*, broadly prefers sea surface temperatures (SST) ranging from 23 to 30 °C. Whole-species distribution models have projected a poleward range shift under future scenarios of climate change, but these models do not consider intraspecific variation or phenotypic plasticity in thermal limits when modelling species responses, and the impact of climate warming on the energetic requirements of whale sharks is unknown. Using a dataset of 111 whale shark movement tracks from aggregation sites in five countries across the Indian Ocean and the latest Earth-system modelling produced from Coupled Model Intercomparison Project Phase 6 for the Intergovernmental Panel on Climate Change, we examined how SST and total zooplankton biomass, their main food source, may change in the future, and what this means for the energetic balance and extent of suitable habitat for whale sharks. Earth System Models, under three Shared Socioeconomic Pathways (SSPs; SSP1–2.6, SSP3–7.0 and SSP5–8.5), project that by 2100 mean SST in four regions where whale shark aggregations are found will increase by up to 4.9 °C relative to the present, while zooplankton biomass will decrease. This reduction in zooplankton is projected to be accompanied by an increase in the energetic requirements of whale sharks because warmer water temperatures will increase their metabolic rate. We found marked differences in projected changes in the extent of suitable habitat when comparing a whole-species distribution model to one including regional variation. This suggests that the conventional approach of combining data from different regions within a species' distribution could underestimate the amount of local adaptation in populations, although parameterising local models could also suffer from having insufficient data and lead to model misspecification or highly uncertain estimates. Our study highlights the need for further research into whale shark thermal tolerances and energetics, the complexities involved in projecting species responses to climate change, and the potential importance of considering intraspecific variation when building species distribution models.

1. Introduction

The warming of the world's oceans due to human-induced climate change (Fox-Kemper et al., 2021) is having substantial impacts on marine life (Cooley et al., 2022). Effects on species' distributions have been the focus of many studies, with changes to suitable habitat and range shifts predicted and already evident (Parmesan and Yohe, 2003; Perry et al., 2005; Sunday et al., 2012; Poloczanska et al., 2013; Poloczanska et al., 2016; Diaz-Carballido et al., 2022). Responses of organisms to changing conditions are complex, and vary both among and within species (Osgood et al., 2021). Temperature is an important predictor of species' distributions, but thermal effects on the physiology of organisms can vary among individuals and/or populations of a species due to acclimatisation or local adaptation. Although intraspecific variation is often unaccounted for when modelling species responses to warming, including below-species information can improve projections of the effects of climate change on species (Ikeda et al., 2017; Smith et al., 2019; Li et al., 2022), while ignoring it can potentially lead to inaccurate estimates of potential range shifts (Seebacher et al., 2015; Hällfors et al., 2016; Bennett et al., 2019). As the degree to which animals are locally adapted or acclimatised is often unknown, comparisons of population- or region-based distribution models (that consider intraspecific variation in responses of animals from different areas) with whole-species models (which assume consistent responses for the species as a whole) can be valuable (Hällfors et al., 2016). However, projecting future species distributions may not provide the full picture of the effects of climate warming, as it will fundamentally impact organism physiology, with implications for fitness and survival.

Ocean warming will challenge the energetic balance of marine ectotherms. Because metabolic rate in ectotherms accelerates at warmer temperatures (Gillooly et al., 2001), ocean warming will lead to a corresponding increase in energy demand. With mean global surface ocean temperatures potentially rising by up to 4.1 °C by 2100 (Fox-Kemper et al., 2021), the additional energetic costs for ectotherms could be substantial. As the metabolic rate of organisms scales allometrically with body mass (Gillooly et al., 2001), ocean warming could cause greater increases in the absolute energetic requirements of larger individuals and species (Messmer et al., 2017), and those living at warmer

temperatures (Dillon et al., 2010). While physiological measurements can be made directly on smaller-bodied species, it is currently difficult to measure the energetic requirements of marine megafauna directly (Lawson et al., 2019; Watanabe and Goldbogen, 2021); the largest marine ectotherm for which metabolic rate has been directly measured to date is a 126 kg Greenland shark *Sommiosus microcephalus* (Ste-Marie et al., 2020). Where direct measurement is not possible due to logistic constraints, metabolic rate can be estimated using the allometric scaling relationship between body mass and metabolic rate, often from smaller, proxy species (Payne et al., 2015). However, because the scaling exponent, scaling coefficient and sensitivity of metabolic rate to temperature (quantified by the Temperature coefficient, Q_{10}) vary within and among species (White et al., 2007) and are unknown for many species, estimates of metabolic rate can vary widely depending on the values used (Lawson et al., 2019). Consequently, we know neither the current energetic requirements for many large-bodied animals, nor how climate warming may affect these requirements in the future.

Elasmobranchs, a group that comprises sharks, rays and skates, include the world's largest marine ectotherms, and more than a third of species are threatened with extinction (IUCN, 2023). In addition to threats from fishing (Dulvy et al., 2021; Worm et al., 2024), many elasmobranchs are vulnerable to climate warming, with responses dependent on species, body size, and mobility (Osgood et al., 2021). The largest elasmobranch is the whale shark *Rhincodon typus* (Smith, 1828), which can grow to a reported 20 m in total length (TL) (Chen et al., 1997) and weigh up to 42 tons (Hsu et al., 2014). Whale sharks have a pan-tropical distribution, and are an acknowledged exception to 'Bergmann's rule' (Bergmann, 1847), which describes the general decrease in body size at lower latitudes. They aggregate in coastal areas (Norman et al., 2017) to feed on dense, energy-rich and abundant zooplankton and ichthyoplankton that allows them to meet the metabolic costs of being a large organism living in warm waters (Cade et al., 2020). Unlike smaller-bodied and less-mobile ectotherms, their large size and high mobility may provide some protection from climate warming. The large body size of whale sharks provides thermal inertia, where body temperature fluctuates more slowly than environmental water temperature (Nakamura et al., 2020), enhancing their ability to move across habitats with differing thermal regimes, both horizontally and vertically

(Tyminski et al., 2015; Reynolds et al., 2022). Nevertheless, sea surface temperature (SST) influences the presence of whale sharks, with those in the Indian Ocean showing a preference for waters with temperatures ranging 23–30 °C (Sequeira et al., 2012; Reynolds et al., 2017). The Indian Ocean has important aggregation sites for whale sharks (Norman et al., 2017), including the Arabian Gulf, which has extreme thermal variability and can experience SSTs in excess of 35 °C (Robinson et al., 2017). The Indian Ocean is among the fastest-warming ocean basins (Fox-Kemper et al., 2021; Dalpadado et al., 2024), and future warming is projected to cause a slight range contraction of whale sharks away from current aggregations and towards the poles (Sequeira et al., 2014). However, little is known of the thermal tolerance of whale sharks, nor the extent to which they may be locally adapted to thermal regimes. If whale sharks are already operating at, or approaching, their upper thermal limits, ocean warming will have substantial consequences for their ecology and physiology. This is particularly concerning given that the species is listed as both Endangered (Pierce and Norman, 2016) and Largely Depleted (Pierce et al., 2021) by the International Union for Conservation of Nature (IUCN).

Here, we investigated the thermal environment (SST), and food availability (zooplankton biomass, ZB) whale sharks are currently experiencing in four regions of the Indian Ocean (including the Arabian Gulf) and how these may change by 2100 under future climate change scenarios. We used the latest Earth-system modelling from Coupled Model Intercomparison Project Phase 6 (CMIP6), developed for Working Group I of the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6). Under different scenarios of greenhouse gas emissions, also driven by socioeconomic assumptions, called Shared Socioeconomic Pathways (SSPs) (Masson-Delmotte et al., 2021), mean global surface ocean temperatures are projected to rise by 0.9–4.1 °C by 2100 (Fox-Kemper et al., 2021). We examined what these changing conditions may mean for the energetic costs and extent of suitable habitat for whale sharks now and in the future. To provide insights into the complex nature of species' responses to a rapidly changing world, and explore variation produced from models built at different spatial scales, we compared habitat suitability projections from a whole-species model to a region-based model, which allowed variation in responses of sharks from different regions of the Indian Ocean.

2. Materials and methods

2.1. Whale shark movement data

Data on whale shark movements were obtained from 111 deployments of satellite-linked tags between 2010 and 2019 on whale sharks at five aggregations in the Indian Ocean: Australia, Madagascar, Maldives, Mozambique and Qatar (previously reported in Norman et al., 2016, Robinson et al., 2016, Reynolds et al., 2017, Diamant et al., 2018, Rohner et al., 2018, Reynolds et al., 2022). Briefly, sharks were tagged with SPOT or SPLASH tags (Wildlife Computers Inc., WA, USA) and tracked using the Argos-CLS satellite network (www.argos-system.org). Individuals were identified by their unique spot-pattern (Arzoumanian et al., 2005) in *Sharkbook: Wildbook for Sharks* (www.sharkbook.ai). The sex of tagged sharks was recorded, and total body length (TL) was estimated visually by experienced researchers with reference to objects of known size (Sequeira et al., 2016), except for sharks tagged in Mozambique, where laser photogrammetry was used (Rohner et al., 2018). Sharks that were tracked for ≤ 4 days ($n = 6$) were removed from all analyses. Data from sharks tagged in Mozambique and Madagascar were pooled to create four broad regions of the Indian Ocean: South-east Indian Ocean (SEIO — i.e., waters off Australia and Indonesia); South-west Indian Ocean (SWIO — i.e., waters off Mozambique and around Madagascar); Central Indian Ocean (CIO — i.e., waters around the Maldives); and the Arabian Gulf. All analyses were performed in R (R Core Team, 2021).

We used the *foieGras* R package (Jonsen and Patterson, 2019) to

interpolate movement tracks of the tagged sharks from the raw location data (Fig. 1). This interpolation standardises the irregular transmission intervals typical of satellite-tracking data from water-breathing animals such as sharks, accounts for Argos location errors and removes biologically-impossible locations based on species' swimming speeds (here set at 2.7 m/s) to provide the most likely movement path of the animal (Auger-Méthé et al., 2017; Jonsen et al., 2019). For each of these interpolated (hereafter “actual”) tracks, five simulated (hereafter “random”) tracks were generated using the ‘state.CRW’ function in the *SiMRiv* R package (Quaglietta and Porto, 2019) (Fig. 1) for use in our habitat suitability modelling. Random tracks were constrained to the tagging location, tracking duration and travel speed of the actual track on which they were based, but moved as a correlated random walk (CRW) through the available marine environment. Without true absence data, these random tracks represent ‘pseudo-absences’ — i.e., habitat that was available to sharks but that they did not utilise during the tracking period. Rather than simply using random background sampling to generate pseudo-absences, the CRW method provided biologically-plausible tracks that the sharks could have taken but did not, while ensuring sufficient environmental separation from the actual tracks for use in models of habitat suitability (Hazen et al., 2021). The number of random tracks was chosen as a balance between taking a representative sample of the available habitat but not overwhelming the presence data in the models.

2.2. Current thermal and prey-availability conditions

To represent available prey for whale sharks, we have used an estimate of total zooplankton biomass. Unfortunately, zooplankton biomass cannot be measured from satellite and thus there are no global datasets over time, so it is not possible to match the whole shark tracks in time and space. We have thus used the estimate of total zooplankton biomass from Strömberg et al. (2009) (hereafter “current ZB”) (Supplementary Material: Fig. S1), which is an overall mean field for zooplankton biomass. This product is commonly used by biogeochemical modellers (Petrik et al., 2022) and is based on a model that relates the flow of energy from primary production from satellite to zooplankton biomass from a subset of a global dataset of zooplankton biomass. The zooplankton biomass data used was standardised to a 330 μm mesh net, and so it likely represents mesozooplankton well, macrozooplankton moderately well, and microzooplankton poorly (Everett et al., 2017). As zooplankton outputs from Earth System Models (ESMs) are free-running (Schoeman et al., 2023), we used observational products rather than historical ESM outputs for current ZB. We used observational, long-term-mean SST data for the 20-year period to 2021 from NASA's Aqua MODIS satellite (hereafter “current SST”) (Supplementary Material: Fig. S1) to capture the average climate conditions experienced by whale sharks, rather than acute temperature fluctuations. Observed SST from satellites was used in preference to Optimum Interpolation SST, which is a mix of observation from various platforms and interpolation. These spatial datasets were standardised to a 0.25° grid using bilinear interpolation via the ‘resample’ function in the *raster* R package (Hijmans, 2022).

2.3. Future thermal and prey-availability conditions

For estimates of future SST and ZB, we used outputs from five CMIP6 ESMs that included the required zooplankton variable (Petrik et al., 2022): CanESM5-CanOE, CNRM-ESM2-1, GFDL-ESM4, IPSL-CM6A-LR, and UKESM1-0-LL (see Supplementary Material: Table S1 and Fig. S2), under three Shared Socioeconomic Pathways (SSPs; SSP1–2.6, SSP3–7.0 and SSP–58.5). SSP1–2.6 represents an optimistic scenario, characterized by a shift to a more sustainable economy and a reduction in socioeconomic inequality, resulting in a peak in radiative forcing of 2.6 W m^{-2} before 2100. SSP3–7.0 represents a medium-high scenario, with regional economic rivalry and a stabilization of radiative forcing levels at $\sim 7 \text{ W m}^{-2}$ by 2100. SSP5–8.5 is characterized by a continued increase

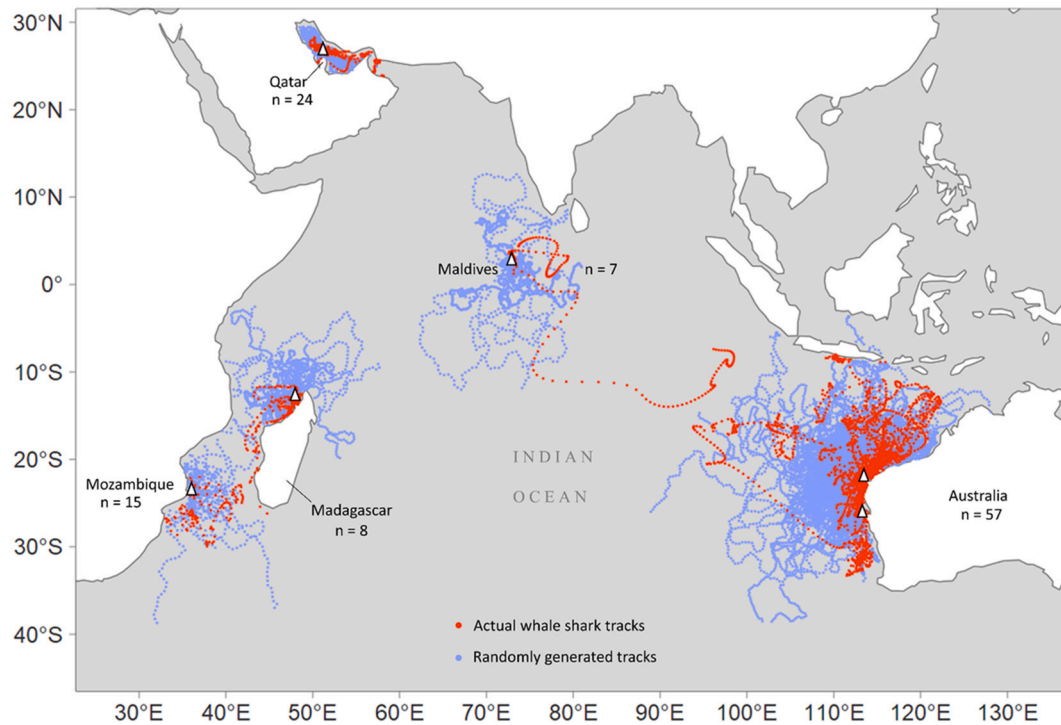


Fig. 1. State-space modelled (SSM) movement tracks of 111 whale sharks *Rhincodon typus* satellite-tracked from five countries around the Indian Ocean between 2010 and 2018 (actual tracks (in red)) and tracks of correlated random walks (randomly generated tracks (in blue)) generated from the SSM tracks - five for each individual shark's actual track. Actual tracks were used as presence data and randomly generated tracks used as pseudo-absence data in generalised additive mixed models. White triangles show tagging locations.

of greenhouse gas emissions resulting from a fossil-fuel-based economy and increased energy demand, with a radiative forcing $>8.5 \text{ W m}^{-2}$ by 2100, rising thereafter (Masson-Delmotte et al., 2021).

Not all ESMs have the same size-resolved zooplankton fields. We have used the “zooc” field, which is the sum of the zooplankton components that are available for each model. These zooplankton fields are related to primary production using various empirical equations (Kearney et al., 2021). We used the bias correction method to estimate future ZB, but did not for SST because it is the most robustly estimated variable in ESMs (Schoeman et al., 2023), whereas ZB is relatively poorly estimated (Petrik et al., 2022). This entails calculating the difference for ZB from the ESM outputs now and in the future, and adding this difference to current data. Specifically, for each ESM, under each SSP, we first regridded from the native grid to a uniform 1° spatial grid using an area-weighted bilinear interpolation in the Climate Data Operators (CDO) software (Schulzweida, 2021). We then extracted SST and ZB data from the surface layer for each ESM under each SSP. A decadal mean value for each grid cell was calculated from each of the five ESMs under each SSP for the end of the historical period (2005–2014) and for the last decade of the future projections (2091–2100). Although it is common to use multi-decadal means for assessing ESM data from different time periods (Schoeman et al., 2023), we used a 10-yr time period so it was consistent with the whale shark telemetry data (2010–2019). To account for variation in projections from the five ESMs (see Supplementary Material: Fig. S2), their decadal means were averaged and these ensemble means used in all analyses. Each 1° cell was then split into four cells (of 0.25° each) with the same value, to match the spatial resolution of the grids representing current climate conditions. The relative change in SST and ZB in each grid cell from the historical to the future ESMs under each of the three climate change scenarios was then calculated using the two decadal means for each SSP, and applied to the current SST and ZB to produce projected future values of SST and ZB across the Indian Ocean.

Due to large differences between zooplankton observations and the

ESM outputs, we calculated the proportional change in biomass from the historical to future decades, rather than using the more commonly used delta method for absolute change, as:

$$ZB_{future(i,j,k)} = ZB_{Stromberg(i)} * \left(\frac{(Mn_{future(i,j,k)} - Mn_{hist(i,j)})}{Mn_{hist(i,j)}} \right)$$

where $ZB_{future(i,j,k)}$ is the future ZB for grid cell i , in model j for SSP k , $ZB_{Stromberg}$ is the current estimated ZB, Mn_{future} is the mean future ZB (2091–2100) from the ESMs, and Mn_{hist} is the mean historical ZB (2009–2014) from the ESMs.

For SST, this change was calculated using the delta method, as we were more confident in absolute measure of temperature in the ESM output:

$$SST_{future(i,j,k)} = SST_{MODIS(i)} + (Mn_{future(i,j,k)} - Mn_{hist(i,j)})$$

where $SST_{future(i,j,k)}$ is the future SST for grid cell i , in model j for SSP k , SST_{MODIS} is satellite derived current SST, Mn_{hist} is the mean historical SST from the ESMs (2009–2014) and Mn_{future} is the mean future SST (2091–2100) from the ESMs.

Current and future projections of SST and ZB under each of the three SSPs were matched to locations along the actual and random tracks of the whale sharks using the *raster* R package. This represented SST and ZB conditions that the whale sharks encountered or could encounter in the future if they continue to use the same areas of the Indian Ocean. The current and future (in 2100 under each SSP) minimum, mean (\pm SD) and maximum SST and ZB were determined for each region of the Indian Ocean.

2.4. Effects of warming on energetic costs of whale sharks

To investigate how energetic costs of whale sharks change with increasing body size and temperature, we estimated standard metabolic

rate (SMR, ml O₂ h⁻¹) for whale sharks using the equation:

$$SMR = aM^b$$

where a is the scaling coefficient, b is the mass scaling exponent, and M is the mass of the animal (kg). This estimates the metabolic rate required to keep the animal alive but does not account for other energetic costs such as movement, growth or reproduction. SMR was chosen as a conservative measure due to the difficulty and uncertainty in estimating total (TMR) or active metabolic rate (AMR) in this large and highly mobile marine ectotherm.

Body mass (M , kg) was calculated for the range of TLs of sharks in this study using:

$$M = 12.1 \times TL^{2.862}$$

where TL is total length (m) (Hsu et al., 2012).

The scaling exponent and coefficient of SMR vary widely among species, and are temperature-dependent for fish (Killen et al., 2010), but are unknown for whale sharks. Therefore, we estimated the scaling exponent and coefficient using a phylogenetic mixed modelling approach, based on data for related species, and their phylogenetic relationships with whale sharks (Garland et al., 2000). Metabolic rate data were collated from published studies on 170 fish species (White et al., 2022) and the effect of temperature on the scaling exponent (b) and the log₁₀-transformed scaling coefficient (log₁₀ a) were analysed using phylogenetic mixed models (Lynch, 1991; Housworth et al., 2004; Hadfield and Nakagawa, 2010) run using the *phyr* R package (Ives et al., 2020). The tree used for analysis was downloaded from the Open Tree of Life (<https://tree.opentreeoflife.org>, Hinchliff et al., 2015) using the *rotl* R package (Michonneau et al., 2016). Branch lengths were set using the arbitrary method of Grafen (1989), and relationships between temperature and log₁₀ a and between temperature and b for the whale shark were estimated by analysing the data with the tree rerooted at the node that gives rise to a three-way polytomy of the whale shark, its sister species in the data set (zebra shark, *Stegostoma tigrinum*), and the lineage containing all other species in the data set. This specifies the whale shark's placement on the phylogenetic tree and increases the accuracy and precision of the predictions made for the SMR parameters of species (Garland et al., 2000). These relationships were used to predict values of a and b for whale sharks at temperatures relevant to this study, and these predicted coefficients and exponents were used to estimate the SMR of whale sharks across the range of sizes of the tagged sharks in this study at current and projected future sea surface temperatures.

SMR in ml O₂ h⁻¹ was converted to grams of O₂ h⁻¹ (1 ml O₂ = 1.43 mg O₂ at standard atmospheric pressure) and then to kJ day⁻¹ using the general oxy-calorific coefficient of 14.14 (J mg⁻¹ O₂ consumed) (Elliott and Davison, 1975), which gives the energy required each day to satisfy the shark's SMR.

The amount of prey needed to fulfil this minimum daily calorific requirement was estimated using the mean calorific content of zooplankton prey (1357 kJ kg⁻¹) at a whale shark feeding site in Mexico (Motta et al., 2010), assuming all calories ingested are converted to energy.

Values of a and b were predicted from the phylogenetic models for the SST (current and in 2100 under each SSP) in each grid cell across the extent of the Indian Ocean covering the movement tracks of all tagged sharks. From these, the SMR of a 7 m TL whale shark (the median- and modal-sized shark in our study, see Results) was calculated for each grid cell and plotted to map the energetic landscape of whale sharks in the Indian Ocean currently, and in the future under each SSP (Supplementary Material: Fig. S3). The SMR at each location along the movement track of shark A-496, a 7 m (TL) male whale shark tracked from Ningaloo Reef in 2017, was used to calculate the mean daily amount of zooplanktonic prey, and the total amount of prey A-496 would have to consume along its entire movement track to satisfy this SMR under current climate conditions, and in 2100 under each SSP. We also

determined the mean daily intake of prey required to satisfy SMR by the largest shark in this study (10 m TL, see Results) at the current mean temperatures for each region of the Indian Ocean and in 2100 under each SSP.

2.5. Extent of suitable habitat for whale sharks

To examine how the extent of suitable whale shark habitat might shift under future climate scenarios, we constructed two telemetry-based habitat models based on the presence and pseudo-absence of tagged whale sharks. We chose four physical and environmental variables that may influence the presence of whale sharks for inclusion as predictors in generalised additive mixed models (GAMMs): SST (°C); ZB (mg C m⁻³) (current SST and ZB as described above; Supplementary Material: Fig. S1); bathymetry (ocean depth; m) and slope (angle of the seafloor; °); (Supplementary Material: Fig. S4). The General Bathymetric Chart of the Oceans (GEBCO) 2019 Grid at 15 arc-second resolution (GEBCO Compilation Group, 2019) provided data on the depth of the seafloor. The slope of the seafloor was calculated from the bathymetry data using the 'terrain' function in the *raster* R package (Hijmans, 2022). Environmental variables that have been shown to influence the occurrence of whale sharks include SST, bathymetry and bathymetric slope, and chlorophyll- a concentration as an indication of productivity and a proxy for zooplanktonic prey availability (Sequeira et al., 2012; Rohner et al., 2013b; Reynolds et al., 2017; Copping et al., 2018). However, we include ZB from the observational model (Strömberg et al., 2009) and the ESMS as an improvement on using chlorophyll- a as a proxy.

Non-linear relationships between whale shark presence/pseudo absence and current environmental variables were estimated using GAMMs (binomial distribution logit link) in the *mgcv* R package (Wood, 2011). To create a 'region-based' model, we included the region of the Indian Ocean in which the shark was tracked (RegionIO) as a fixed effect and as an interaction term, allowing the intercept and smooth of the relationships between whale shark presence/absence and the predictors to vary by region. This model assumes that sharks from different regions could have different preferences for environmental variables, allowing exploration of potential differences that can arise from models built at different spatial scales. In contrast, our 'whole-species' model excluded RegionIO completely, forcing consistent relationships across regions and thus assuming that preferences are the same for all whale sharks. Both our 'region-based' and 'whole-species' models included individual identity (SharkID) as a random effect to account for repeated measurements from the same individuals. We used cubic regression splines for the smoothing functions for the physical and environmental covariates rather than the default thin plate splines in the *mgcv* R package because cubic regression splines can be less prone to overfitting (Wood, 2017). Varying the number of knots changes the wiggleness of the spline curves. Using the default number of knots ($k = 10$) for each predictor produced biologically implausible relationships, suggesting overfitting of the data. We thus used a lower number of knots ($k = 3$) to constrain the relationships and reduce the likelihood of overfitting. Relationships from the two models were used to predict the likelihood of occurrence of whale sharks in the four regions of the Indian Ocean under current conditions, and under changes to SST and ZB projected in 2100 under the three SSPs. The relative habitat suitability for whale sharks (on a scale of 0–1) under current conditions, and the change in relative habitat suitability between current and future conditions, were mapped to each region of the Indian Ocean at a resolution of 0.25°.

3. Results

Satellite-tracked whale sharks ranged 3–10 m TL, with a mean of 6.7 ± 1.3 m (all means reported ± SD), and a median and mode of 7 m TL. After removing sharks tracked for <4 days, tracking duration ranged between 4 and 290 days (the latter for A-496, a 7 m TL male from Australia; see Fig. 4). Based on estimates of whale shark TL, body mass

ranged from 281 kg for a 3 m shark (hereafter “small shark”), to 8806 kg for a 10 m shark (hereafter “large shark”). For more information on the tagged whale sharks and how their size and the extent of their movements varied across aggregations, see Reynolds et al. (2022).

Temperature had a significant effect on both the scaling coefficient (a) ($p = 0.0035$) and exponent (b) ($p = 0.0005$) in the mass-scaling equation for whale sharks, and consequently influenced estimates of their SMR (Fig. 2). Estimates of a ranged 0.140–0.600 and b from 0.749 to 0.806 at 13.4 °C and 33.4 °C respectively (the minimum and maximum temperatures in this study) (Supplementary Material: Fig. S5).

3.1. Current thermal and prey-availability conditions

The current SST in waters used by and available to tracked sharks ranged from a minimum of 13.2 °C in SEIO, to a maximum of 31.2 °C in the Arabian Gulf. The means ranged from 24.9 ± 1.8 °C in SEIO to 28.8 ± 0.3 °C in CIO (Fig. 3A) and the mean SST across all the regions was 25.6 ± 1.7 °C. The current ZB found in waters of the four regions of the Indian Ocean ranged from a minimum of 1.2 mg C m⁻³ in SEIO, to a maximum of 82.8 mg C m⁻³ in the Arabian Gulf. The mean ZB ranged from 5.3 ± 6.2 mg C m⁻³ in SEIO to 31.4 ± 16.4 mg C m⁻³ in the Arabian Gulf, over 5.5 times greater than the next largest mean ZB (5.7 ± 4.5 mg C m⁻³ in CIO) (Fig. 3B). The mean ZB across all the regions was

8.2 ± 11.3 mg C m⁻³.

3.2. Future thermal and prey-availability conditions

Ensemble mean SSTs from the five ESMs used in this study are projected to rise by 2100 in all four regions of the Indian Ocean under all three SSPs. Under the high-emissions scenario (SSP5–8.5) by 2100, SST is projected to range from a minimum of 16.3 °C (in SEIO) to a maximum of 33.4 °C (in the Arabian Gulf) and mean SST is projected to increase from current means by between 3.4 °C (from 24.9 ± 1.8 °C to 28.3 ± 2.0 °C) in SEIO, and 4.9 °C (from 27.4 ± 0.4 °C to 32.3 ± 0.7 °C) in the Arabian Gulf (Fig. 3A). The mean SST in all four regions combined is projected to increase from current temperatures by 3.6 °C to 29.2 ± 2.1 °C under SSP5–8.5. Ensemble mean ZB is projected to decrease from current levels by 2100 in each region under each of the three SSPs, except in SEIO where, under SSP5–8.5, mean ZB will increase from current levels by 4.2 %. (for the full range of zooplankton in the five ESMs under each emission scenario, see Supplementary Material: Fig. S2).

The largest decreases are projected in the Arabian Gulf, where ZB is projected to decrease by 20.9 %, 25.3 % and 27.5 % under SSP1–2.6, SSP3–7.0 and SSP5–8.5 respectively (Fig. 3B).

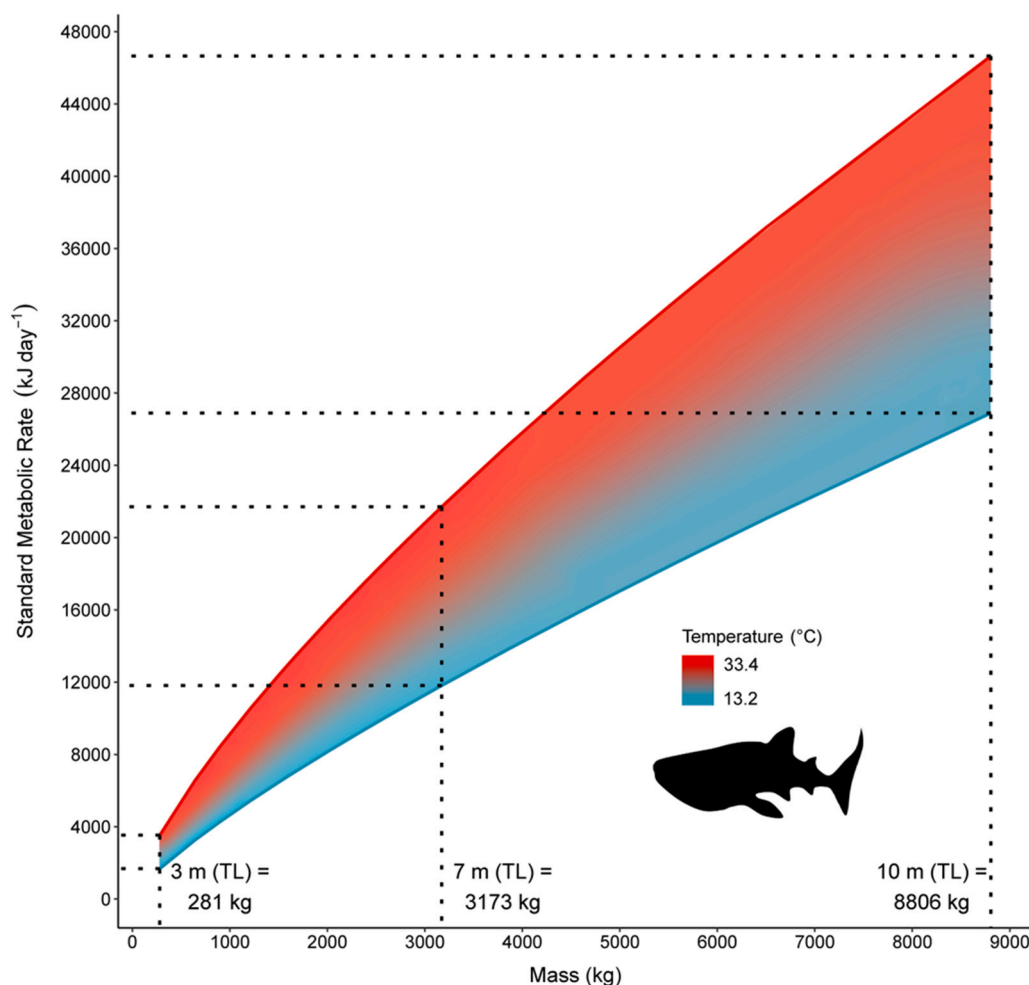


Fig. 2. Standard metabolic rate (SMR) for whale sharks *Rhincodon typus* at the range of body sizes tracked from five countries in the Indian Ocean. Temperatures are the minimum (13.2 °C) sea surface temperature (SST) under current climate conditions, and maximum SST (33.4 °C) in 2100 under a future climate change scenario, Shared Socio-economic Pathway 5–8.5, in waters used, or that could potentially be used in the future by whale sharks from these areas. Dotted lines show the mass and corresponding SMRs of the smallest (3 m), median-sized (7 m) and largest (10 m (all total lengths)) whale sharks in this study. From the minimum to the maximum temperature, SMR increases by 109.7 %, 83.7 % and 73.5 % for the small, median and large sharks respectively.

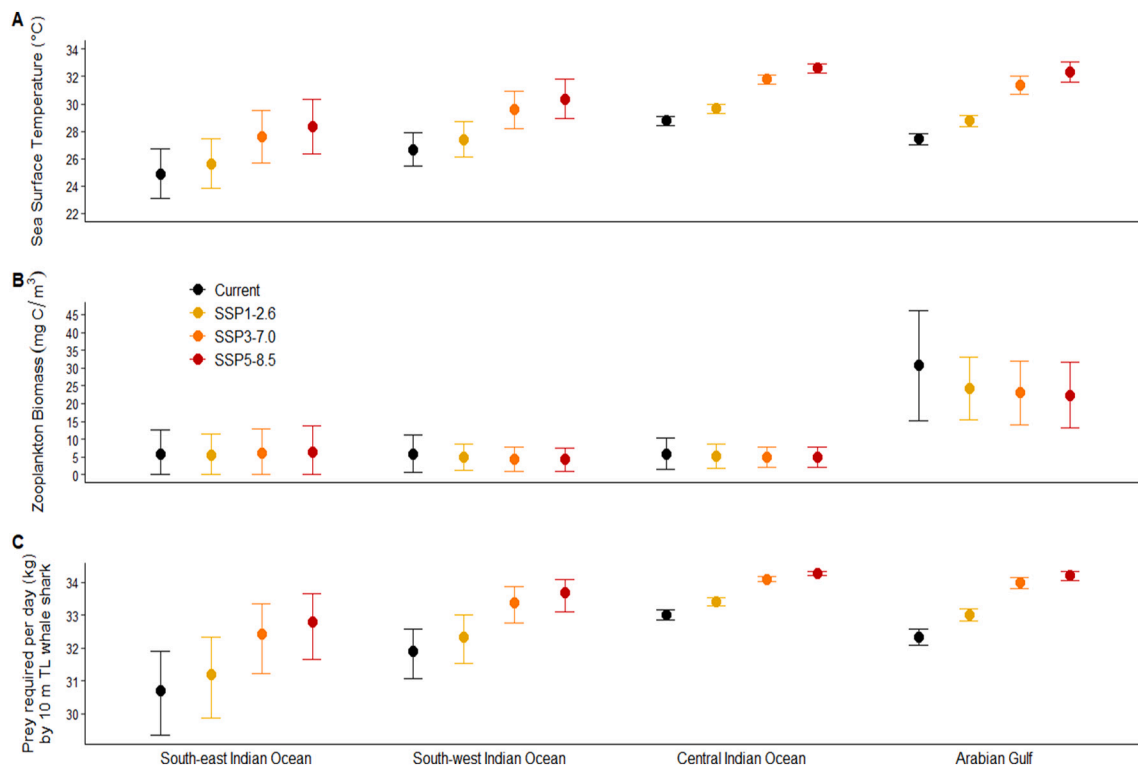


Fig. 3. A Mean Sea Surface Temperature and B mean Zooplankton Biomass in waters used by whale sharks (*Rhincodon typus*) in four regions of the Indian Ocean, under current climate conditions (Current) and in 2100 under three different climate change scenarios (Shared Socio-economic Pathways (SSP1–2.6, SSP3–7.0, SSP5–8.5)). C Mean amount of prey required per day to satisfy standard metabolic rate of a 10 m total length whale shark at the SSTs shown in A). All error bars show standard deviation.

3.3. Energetic costs of whale sharks

Future increases in SST projected across all four regions of the Indian Ocean produced a corresponding increase in SMR and energetic requirements of whale sharks (Figs. 2, 3C, 4; Supplementary Material: Fig. S3). Across the range of body masses (281–8806 kg) and SSTs (13.2–33.4 °C), SMR ranged from 1676 to 3529 kJ day⁻¹ for small (3 m TL) sharks, and 26,891 to 46,652 kJ day⁻¹ for large (10 m TL) sharks (Fig. 2). Although the greatest absolute increases in SMR are projected for large sharks (e.g., an increase of 19,761 kJ day⁻¹ for a 10 m TL shark), the SMR of a small shark is expected to more than double between these two temperatures (an increase of 109.7 %). An increase in SST from 25.6 °C (the mean temperature encountered by sharks from all regions under current climate conditions) to 29.1 °C (mean in 2100 under SSP5–8.5), results in an expected 9.9 and 6.3 % increase in SMR for small and large sharks respectively. These estimates of SMR across the SST range (13.2–33.4 °C), indicated temperature coefficient (Q₁₀) values for whale sharks ranging from 1.31 in large sharks to 1.45 in small sharks.

For A-496 (7 m TL), SMR ranged from 15,566 kJ day⁻¹ at the minimum temperature along its movement track (19.0 °C under current climate conditions) to 21,000 kJ day⁻¹ at the maximum temperature (30.6 °C in 2100 under SSP5–8.5). Based on the current temperatures encountered along its movement track, mean SMR of A-496 was 18,135 ± 1294 kJ day⁻¹ and this rose by 2.0, 6.9 and 8.5 % under SSP1–2.6, SSP3–7.0 and SSP5–8.5 respectively (Fig. 4). This equates to an average minimum daily requirement of 13.4 ± 1.0 kg of prey under current conditions, rising to 14.5 ± 0.8 kg of prey required under conditions in 2100 projected by SSP5–8.5. The total amount of prey required by A-496 to satisfy SMR throughout his total duration of tracking (290 days) was 3782 kg under current conditions, rising to 3858 kg, 4044 kg and 4103 kg under SSP1–2.6, SSP3–7.0 and SSP5–8.5 respectively.

3.4. Extent of suitable habitat for Indian Ocean whale sharks

Our region-based model (deviance explained 30.9 %), and our whole-species model (deviance explained 27.1 %) showed marked differences in the relationships between SST and whale shark presence/absence, while relationships for the other environmental variables and whale shark presence/absence were more similar (Fig. 5). The region-based model showed bell-shaped relationships for SST, typical of thermal performance curves, but only for SWIO and the Arabian Gulf. The probability of whale shark presence increases with temperature in SEIO, but decreases steeply with temperature for CIO, although the range of SSTs these sharks encountered was quite different. In contrast, the whole-species model assumes that whale sharks as a species have the same temperature preferences and suggests a truncated bell-shaped curve across all regions, with highest probability of occurrence between 26 and 28 °C (Fig. 5).

In both models, there was generally a dome-shaped relationship between the probability of finding whale sharks and zooplankton biomass, with highest whale shark occurrences at intermediate zooplankton biomass levels (Fig. 5).

Both models predicted higher likelihood of occurrence of whale sharks in shallow waters (< 200 m depth), but also in very deep waters (> 1000 m depth), similar to the relationship between whale shark presence and bathymetry found in a previous study which used data from only SEIO (Reynolds et al., 2017) (Fig. 5). The exception is the relationship predicted for sharks in the Arabian Gulf and the CIO by the region-based model.

The whole-species model predicted increasing probability of whale shark presence with bathymetric slope, although the region-based model produced unexpected variation in the relationships between whale shark presence and slope for sharks in different regions. The probability of presence increased with slope for SEIO, but the relationship curve for the Arabian Gulf was a leptokurtic, high-peaked bell-

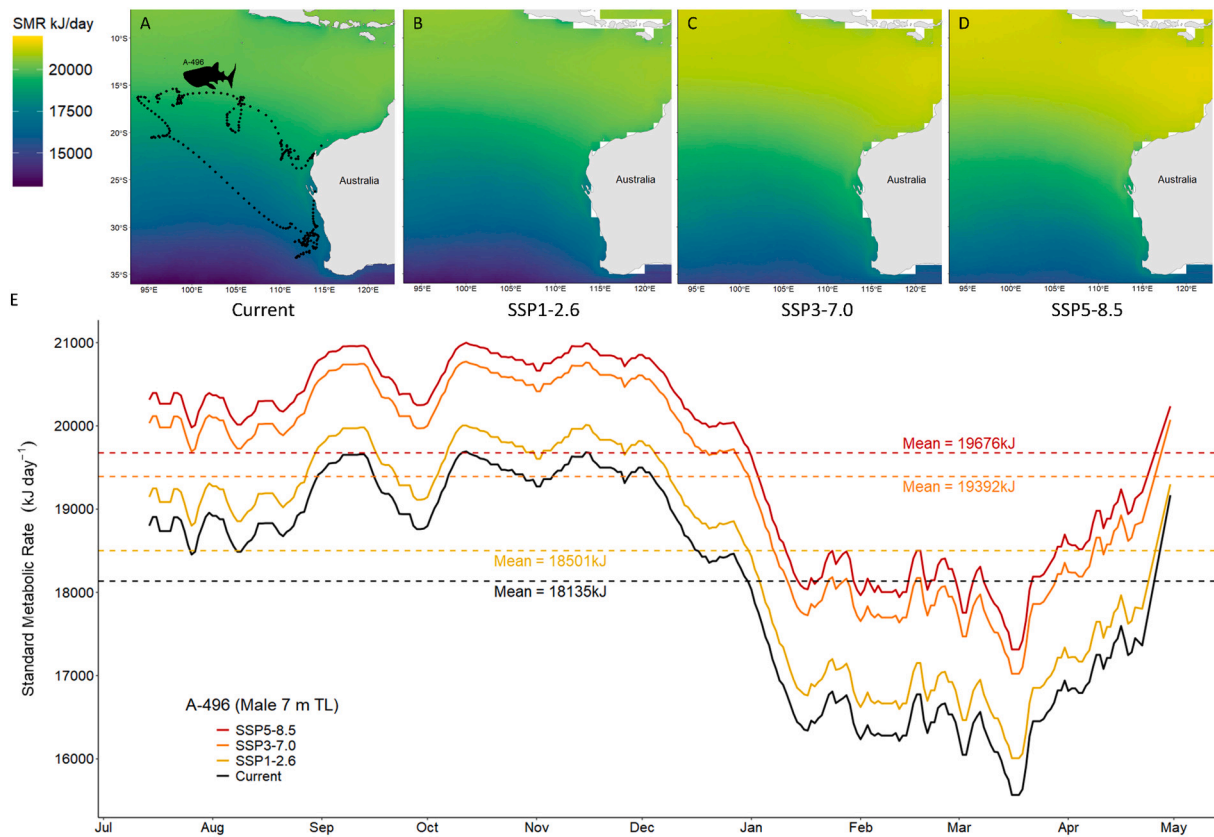


Fig. 4. Energetic landscape maps of South-east Indian Ocean showing standard metabolic rate (SMR, kJ day^{-1}) for 7 m total length (TL) whale sharks *Rhincodon typus* (the median-sized shark in our study), calculated using the mass scaling equation and sea surface temperatures under A current conditions (black dots show the satellite-tracked movement path of A-496, a 7 m TL male shark tracked from Ningaloo Reef, Australia in 2017); and by 2100 under three future climate change scenarios, Shared Socioeconomic Pathways (SSP): B SSP1-2.6; C SSP3-7.0; and D SSP5-8.5. E SMR of shark A-496 at each location along its movement path under current climate conditions (Current) and if the same path was used in 2100 under three SSPs (SSP1-2.6, SSP3-7.0 and SSP5-8.5).

shape, and for CIO and SWIO was an almost flat line, close to one and zero respectively (Fig. 5).

The region-based model appears to overfit the relationships between sharks and the four variables in some of the regions (curves that display large standard error ribbons). The region in which the most sharks were tagged, the SEIO ($n = 57$), has the best model fit for each variable, with the small sample size for the other regions perhaps contributing to the overfitting (Fig. 5A).

The region-based and whole-species GAMMs resulted in different predictions of the relative suitability of habitat for whale sharks in the waters of the four regions of the Indian Ocean under current conditions, and corresponding projections by 2100 under each of the three SSPs. Predictions of current suitable habitat from the two models were relatively similar for SEIO and SWIO, but the region-based model showed higher relative values for some areas of CIO and the Arabian Gulf, most notably around the equator and outside the Strait of Hormuz respectively (Fig. 6; Supplementary Material: Fig. S6).

When future relative habitat suitability was predicted from the two models, the outcomes in some areas varied markedly. Both models projected that suitable habitat in the SEIO will remain fairly stable, with slight decreases in habitat suitability in some areas, but increases in others (Fig. 6; Supplementary Material: Fig. S6). The whole-species model showed a similar trend to this across all four regions under all three SSPs (with slightly more areas of increased habitat suitability for the Arabian Gulf under SSP5-8.5). However, in comparison to the whole-species model, the region-based model showed slightly more areas where relative habitat suitability decreased in SWIO and large decreases in suitability across broad areas in CIO and the Arabian Gulf under all three SSPs. Again, the small sample size in CIO and overfitting

of the region-based model is contributing to the large differences seen between the projections from the two models in some of the regions (Fig. 6; Supplementary Material: Fig. S6).

4. Discussion

Our study used three future climate change scenarios from CMIP6 to investigate how ocean warming (SST) and changes to food availability (ZB) could affect the physiology and distribution of the world's largest marine ectotherm, the endangered whale shark. Our results show that SMR of whale sharks increases with temperature and body mass, and therefore the energetic requirements of whale sharks will increase in the future with projected ocean warming. These increasing metabolic demands caused by rising temperatures might not be easily met by feeding, as zooplankton biomass is generally projected to decline in the future, by up to 27.5 % in some places. The combination of rising metabolic demands and declining prey availability could have detrimental consequences for the energetic balance of whale sharks. Despite projected SST increases of up to 4.9 °C from current temperatures, and contrary to previous studies which found contractions of potential future distributions of whale sharks (Sequeira et al., 2014) and other elasmobranch species (Diaz-Carballido et al., 2022), our whole-species model projected relative habitat suitability would remain comparatively stable in the future under all three SSPs (Fig. 6B). Conversely, projections from our region-based model (in which relationships between whale shark presence and environmental predictors were allowed to differ across regions of the Indian Ocean where whale sharks are spatially segregated (Prebble et al., 2018; Reynolds et al., 2022)) were more variable. While SEIO and SWIO remained relatively stable, projections for CIO and the

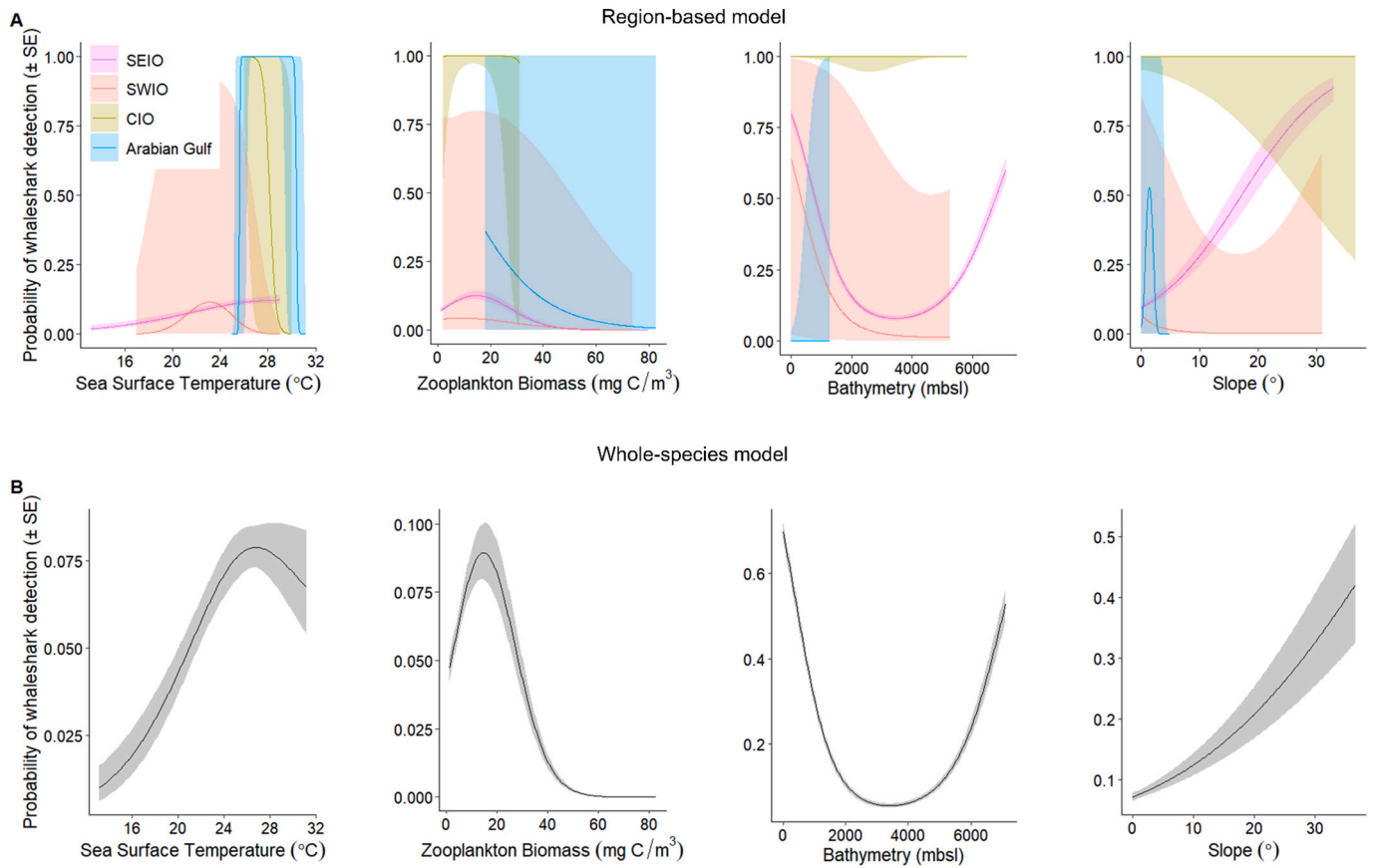


Fig. 5. Results from binomial generalised additive mixed models (GAMM) showing the effects of four variables (Sea surface temperature (°C); Zooplankton biomass (mg C/m³); Bathymetry (metres below sea level); and Slope of the seafloor (°)) on the probability of whale shark *Rhincodon typus* occurrence in four regions of the Indian Ocean in which whale sharks were tracked. A Region-based model that allows the preferences for the variables in the models of sharks from different areas to vary and B Whole-species model in which the preferences for the variables are assumed to be consistent across sharks from all areas. Ribbons show \pm standard error.

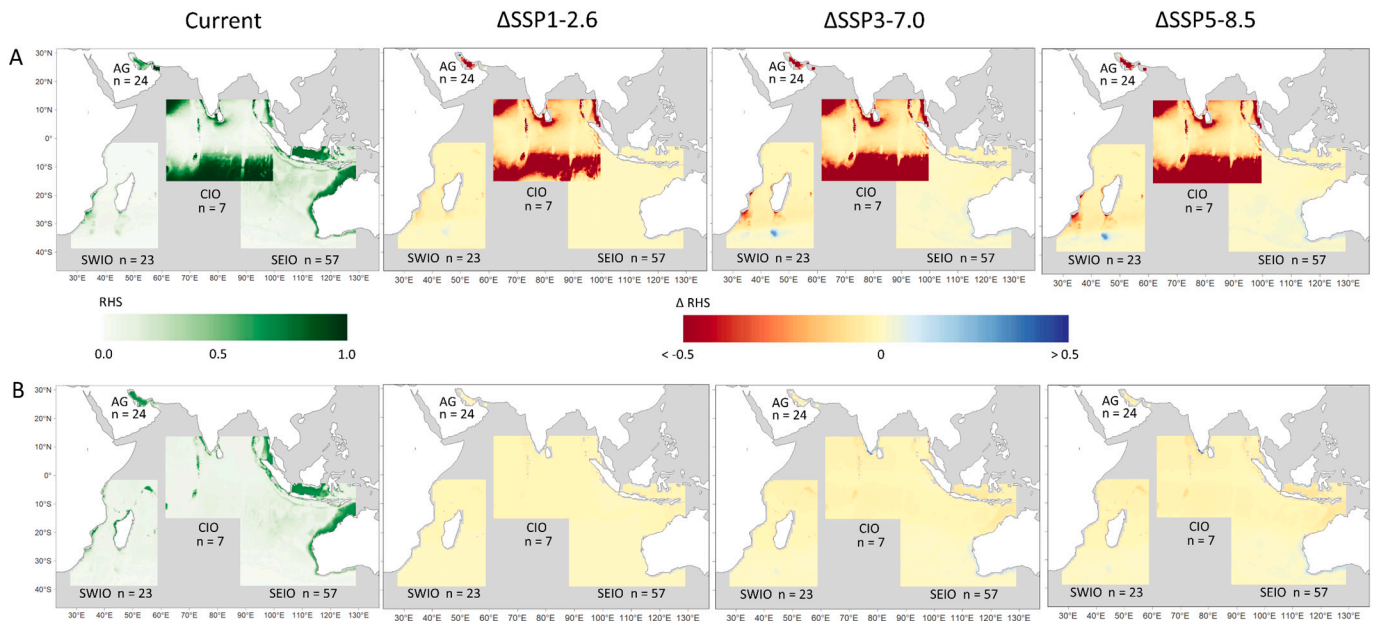


Fig. 6. Projections of relative habitat suitability (RHS) for whale sharks *Rhincodon typus* in four areas of the Indian Ocean in which sharks were satellite-tracked (Arabian Gulf (AG), central Indian Ocean (CIO), south-west Indian Ocean (SWIO) and south-east Indian Ocean (SEIO)), under current climate conditions and the change in RHS (Δ RHS) from current by 2100 under three future climate change scenarios, Shared Socioeconomic Pathways (SSP) generated from two generalised additive mixed models: A region-based model that allows the preferences for the variables in the models of sharks from different regions to vary and B whole-species model in which the preferences for the variables is assumed to be consistent across sharks from all regions.

Arabian Gulf were more pessimistic, with projected decreases in relative habitat suitability over broad areas (Fig. 6A). However, the results from the region-based model may be more an artefact of the small sample size from some regions contributing to the overfitting of the models, rather than a reflection of any intraspecific differences in whale shark preferences for the modelled variables. Our results indicate that although including data from regions that a species inhabits where they encounter differing environmental and physical variables may be valuable for species distribution modelling, care must be taken when interpreting models, especially when sample sizes are limited.

4.1. Thermal tolerance and species distribution modelling

Whale sharks in these four regions of the Indian Ocean experience different thermal environments due to their spatial segregation (Prebble et al., 2018; Reynolds et al., 2022). Although genetic studies suggest a single stock in the Indo-Pacific (Castro et al., 2007; Schmidt et al., 2009; Vignaud et al., 2014), which could preclude local adaptation, it is possible that phenotypic plasticity and/or local acclimatisation may have resulted in intraspecific variation in their thermal limits and preferences. The sharply defined temperature preferences identified by our region-based model (Fig. 5) are what we would expect if there was some intraspecific variation in thermal limits. However, this could also be an artefact of the range of temperatures in each region being only a subset of the range of temperatures found across all regions. Region-based and whole-species distribution models make differing assumptions about whether animals have different thermal tolerances regionally or not (Bennett et al., 2019), but the lack of explicit knowledge in this regard can lead to spurious predictions of species distributions (Hällfors et al., 2016). Our results also highlight the limitations of building species distribution models with environmentally or geographically restricted data that do not capture the full range of the variables that influence the distribution of a species (Nazzaro et al., 2021). The thermal tolerance limits of whale sharks are not well understood, nor is the degree to which they may be locally acclimatised or phenotypically plastic. The differing predictions of suitable habitat for whale sharks from our two models and how this may change in the future, exemplify why caution is warranted when projecting future risk for species in which detailed knowledge of thermal tolerances is lacking and if sample sizes are small (Hällfors et al., 2016).

The conventional approach of combining data from different regions within a species' distribution, which often have no known connectivity, as for whale sharks in the Indian Ocean, can underestimate the amount of local adaptation in populations. However, parameterising local models can also suffer from having insufficient data to answer the question of whether local populations are truly different; a paucity of data can make it appear that there is local adaptation when there might not be. The collection of more data in the future (particularly in regions where whale sharks are known to occur but are underrepresented in this dataset) will help resolve the issue of whether the variation arises from local adaptation.

Introducing the physiology of a species into distribution modelling is valuable and can account for heterogeneity in the physiological responses of different populations of a species that can arise from local adaptation or acclimatisation (Harishchandra et al., 2022). Correlative species distribution or habitat selectivity modelling, such as we have done here, uses a species' relationship to its environment to predict its distribution. Correlative models are relatively simple and do not require consideration of biological parameters such as physiology, behaviour, or food web dynamics (Peck et al., 2018). This can lead to overly simplistic model projections, especially for widely-ranging marine species that may have broad environmental tolerances (Muhling et al., 2017). Mechanistic models incorporate biological parameters into distribution modelling, attempting to make model predictions more biologically realistic. However, in species for which physiological parameters are not well-known (and cannot be measured directly, such as whale sharks),

these must be estimated or extrapolated from other species, which also introduces uncertainty into model predictions (Muhling et al., 2017). Although we do not attempt to incorporate physiology into our habitat suitability modelling, our study provides a first step towards the goal of making correlative models more mechanistic and defining thermal tolerance curves for whale sharks.

If whale sharks in some areas, such as the Arabian Gulf, are already operating at the limits of their thermal tolerance, we would expect them to retreat from these areas under future warming. However, the upper thermal limit for whale sharks is unknown. No decline in their swimming activity was observed in temperatures of 28 °C (Nakamura et al., 2020), they have been recorded actively feeding in waters ~33 °C (Robinson et al., 2013), and temperatures in surface waters of the Arabian Gulf, which hosts a large aggregation of whale sharks, regularly exceed 35 °C (Robinson et al., 2017). Whale sharks are generally described as a tropical species (Rowat and Brooks, 2012) but they appear to tolerate a large thermal range (at least acutely). They make deep dives, to a recorded 1928 m, experiencing water temperatures as low as 3.4 °C (Tyminski et al., 2015), and they have been reported in temperate waters at high latitudes (e.g., the Bay of Fundy, Canada (Turnbull and Jackie, 2006), the Sea of Okhotsk, Japan (Tomita et al., 2014), the Southern Ocean coast of Western Australia (Norman et al., 2016) and the north-east coast of New Zealand (Duffy, 2002)). The low values of Q_{10} implied by our phylogenetic modelling (1.3–1.4) suggest low thermal sensitivity, which could be an advantage for whale sharks, because changes in temperature would have limited consequences as they move through different thermal regimes. Whale sharks appear to use behavioural thermoregulation, spending time in warm surface waters to increase body temperature after time at depth (Thums et al., 2013) or to assimilate nitrogen from prey more efficiently (Wyatt et al., 2019) — or conversely in very warm waters such as the Arabian Gulf, diving to cooler waters to slow their metabolism (Thums et al., 2013; Tyminski et al., 2015; Robinson et al., 2017; Araujo et al., 2020). Our models used surface ocean temperatures to infer changes to the horizontal distribution of whale sharks. However, because they are not confined to surface waters for feeding (Rohner et al., 2013a), it is possible that surface warming could also change the vertical distribution of whale sharks, causing them to spend more time at depth where waters are cooler. These behaviours, their large body size providing thermal inertia (Nakamura et al., 2020), and their high mobility may allow whale sharks to cope with future ocean warming, as long as sufficient zooplankton prey remains available to maintain their energetic balance.

4.2. Energetic requirements

The distribution, phenology, abundance and community structure of zooplankton are already being affected by climate change (Richardson, 2008) and the CMIP6 models project a future decrease in ZB in the four regions of the Indian Ocean (except SEIO under SSP5–8.5). Our estimates of SMR suggest that the mean daily energetic requirement for a 7 m TL whale shark tagged in Australian waters will rise from ~18,100 kJ day⁻¹ under current temperatures along its movement track, to a projected ~19,700 kJ day⁻¹ in 2100 under SSP5–8.5, which equates to an increase in zooplankton required from 13.4 kg to 14.5 kg. These estimates were made using the temperature-dependent values of a and b in the mass-scaling equation for whale sharks predicted by the phylogenetic modelling, revealing a Q_{10} of approximately 1.3–1.4. This is at the lower end of the range of Q_{10} values reported for sharks i.e., 1.3 for epaulette sharks (*Hemiscyllium ocellatum*) (Chapman et al., 2011) to 2.9 for sandbar sharks (*Carcharhinus plumbeus*) (Dowd et al., 2006). An alternative method for estimating SMR for whale sharks would have been to use typical values of Q_{10} for fishes of between 2 and 3 (Carlson et al., 2004), which would have increased our estimates of SMR as temperature increased. The phylogenetic modelling approach was chosen as a means of reducing uncertainty and more accurately predicting SMR of whale sharks based on their phylogenetic relationships to other

species for which SMR has been directly measured.

SMR represents the minimum energy required by the organism to survive and does not incorporate other energetic requirements such as movement. Total metabolic rate includes basic living costs, plus the energy required for growth, reproduction, and any activity over and above this minimum (active metabolic rate (AMR)) and is more ecologically relevant (Halsey et al., 2015). The inclusion of estimates of AMR in whale sharks would therefore have increased our estimates of their energetic requirements. However, measuring or even estimating AMR in large, highly mobile marine ectotherms is complex (Lawson et al., 2019; Watanabe and Goldbogen, 2021) and varies between species depending on behavioural and physiological factors (Halsey et al., 2015). Extrapolating total metabolic rate from SMR is also complicated by the fact that the relationship between AMR and temperature is not necessarily the same as the relationship between SMR and temperature and therefore it cannot be assumed that the effect of temperature on total metabolic rate will be the same as its effect on SMR (Halsey et al., 2015). We therefore chose to use SMR as it is a widely accepted metric in physiology, is more readily estimated and involves less uncertainty than attempting to estimate AMR or total metabolic rate. It is also important to understand the minimum energetic requirements of a species, and our use of the phylogenetic modelling approach provides a conservative estimate of this for whale sharks. The food intake required to satisfy the total energetic requirements of whale sharks will therefore be higher than our estimates e.g., 13.4–14.5 kg required to satisfy the SMR of our 7 m TL whale shark. Rations fed to captive whale sharks as a percentage of body mass are estimated at 0.3–0.5 % at Georgia Aquarium (Dove et al., 2022) and ~ 1 % at Okinawa Churaumi Aquarium (Matsumoto et al., 2017) and equate to estimates by Motta et al. (2010) of prey ingested by wild individuals (Dove et al., 2022). This suggests that for our 7 m TL whale shark, daily food intake could be ~31 kg and for the largest whale shark in this study (10 m TL/8806 kg), could be as high as ~88 kg.

Although we expected that whale shark occurrence would be positively related to increasing ZB, the highest probability of whale shark occurrence was at intermediate ZB levels. This relationship may be a consequence of several factors, including the model output underestimating high zooplankton abundances in time and space; species or sizes of zooplankton preferred by whale sharks not following total zooplankton biomass produced by the Strömberg et al. (2009) model and ESMs; or that highly productive river plumes might be unsuitable in some way, or too shallow for whale sharks. Zooplankton are extremely patchy, and can increase by several orders of magnitude under bloom conditions (Suthers et al., 2019). By contrast, the statistical model of ZB we used from Strömberg et al. (2009) estimates the climatological mean ZB and has a relatively coarse spatial scale (0.25° resolution). This might be a reasonable estimate of zooplankton biomass over long temporal and large spatial scales but will miss the huge, fine-scale, spatial and temporal variation in zooplankton density at local scales (McGillcuddy and Franks, 2019). Whale sharks are likely to have “feeding thresholds”, as seen in basking sharks *Cetorhinus maximus* (Sims, 1999) and manta rays *Mobula alfredi* (Armstrong et al., 2016), such that they feed only when prey density is high enough to make it energetically worthwhile (Nelson and Eckert, 2007; Gleiss et al., 2013; Rohner et al., 2015). Indeed, values of densities of zooplankton measured at observed whale shark feeding events are orders of magnitude higher than values from the ZB model. For example, we estimated mean zooplankton biomass in the four regions of the Indian Ocean between 0.0053 and 0.0314 gC m⁻³ from the ZB model, whereas it was estimated to be 0.34 gC m⁻³ off the Yucatan Peninsula (Mexico) (from Motta et al. (2010) and using a conversion of 0.4 for carbon from wet weight (Postel et al., 2000), and 0.19 for dry weight from wet weight (Omori, 1969)) and ~ 58.52 gC m⁻³ at Ningaloo Reef (Australia) (from calculations in Gleiss et al. (2013) on data reported by Wilson et al. (2001) and using the conversions above). Models often underestimate extreme values, and ESMs with a 1° resolution can be considered to average biomass values over an area of ~12,225 km² at

the equator. Our estimates also use a relatively low value of calorific content of prey (Motta et al., 2010) and some prey items of whale sharks may be 2–3 times higher in calorific content (e.g., Euphausiids (Wyatt et al., 2019) and other crustaceans (Grémillet et al., 2017 and references therein)). The assimilation efficiency of whale sharks is unknown, and our calculations assume that all calories consumed are converted to energy, whereas in reality only a proportion of calories ingested will be available for use by consumers. Also, we have assumed that whale sharks eat only zooplankton and our models provide only estimates of surface zooplankton. However, whale sharks in some areas target tuna spawn (Heyman et al., 2001; Robinson et al., 2013) and small fishes (Duffy, 2002; Diamant et al., 2021), are able to digest macroalgae (Meekan et al., 2022), and also feed at depth (Rohner et al., 2013a). Prey distribution and abundance are major drivers of whale shark foraging behaviour. Further work to elucidate the thermal tolerances of other prey (or prey-producing) species, such as tuna (the spawn of which supports two of the largest whale shark aggregations in the world (Heyman et al., 2001, Robinson et al., 2013)), would help to project future whale shark distributions based on potential shifts in prey distributions. Although ZB is projected by the ensemble means of the climate models to decrease in the future, whale sharks may still be able to target high-density patches of diverse prey with high calorific content and maintain their energy balance by maximising energy intake and minimising energy output.

4.3. Survival in a warming world

Species such as whale sharks that have evolved in stable tropical conditions and have long lifespans, slow growth rates and later maturation are thought to be more vulnerable to the effects of climate change (Perry et al., 2005; Tewksbury et al., 2008). However, the capacity for thermal acclimation is greater in animals from more stable environments, and increases with decreasing latitude (Seebacher et al., 2015). Differences between the hottest temperatures that individuals experience locally and those experienced across the global range of the species suggest that individuals from some areas may be able to survive in temperatures much warmer than those they typically experience (Bennett et al., 2019). Therefore, even if whale sharks in areas such as the Arabian Gulf are approaching the thermal limits of the species, sharks from other areas may be able to cope with warmer conditions than they are currently experiencing. Evidence from the fossil record suggests that whale sharks have remained relatively unchanged and occupied a similar ecological niche for at least the last 20 million years (Maisch and Becker, 2021), and our study provides cause for cautious optimism that whale sharks will be able to survive in the future SST and ZB conditions projected by the latest climate models.

However, the current and future SST data we used are long-term averages, giving the current mean climate, and the potential future mean climate. This results in the future mean and even maximum temperatures in our study regions from these models being within the range of acute temperatures in which whale sharks have been recorded. Nevertheless, with projections of more frequent and extreme marine heatwaves (Oliver et al., 2019), whale sharks may encounter future acute water temperatures across their range that push them beyond their thermal tolerance limits. There are also many other factors that could negatively affect their fitness and survival, as well as those of the species they rely on for food. These include other consequences of climate change beyond the scope of this study, such as deoxygenation (Oschlies et al., 2018), ocean acidification (Kroeker et al., 2013) (which will negatively impact carbonate-producing species of the whale sharks' zooplanktonic prey), degradation of coral reefs (Hoegh-Guldberg, 1999), as well as other anthropogenic impacts on our oceans, such as shipping, fishing and pollution (Reynolds et al., 2022). Large body size also appears to be a disadvantage for marine ectotherms during periods of global warming and reductions in size are already being seen in some species (Messmer et al., 2017; Martins et al., 2023). The absolute

energetic costs of large sharks will be higher than smaller sharks under future warming (Fig. 2). This may slow growth rates and reduce size-at-age, causing selective pressure for smaller body size (Messmer et al., 2017), and could lead to a reduction in body size of the world's biggest fish. As data collection in the marine realms improves, such considerations can be incorporated into future models of habitat suitability and future risk for vulnerable taxa.

4.4. Conclusion

Understanding both the changes in suitable habitat and the effects on physiology provide insights into the complex responses of species to climate change. For whale sharks, our lack of knowledge of the thermal tolerance limits of the species is hampering our ability to project changes in the extent of their suitable habitat. By comparing whole-species and region-based models, we explore possible outcomes and highlight the need for further research into the thermal physiology of whale sharks from areas with differing environmental ranges. Investigating the effects of temperature on the future energetic requirements of the species revealed how individuals will be differentially affected by climate change, depending on their body size and the region they inhabit. Our study provides the first step in defining the relationship between temperature, body mass and metabolic rate in whale sharks. The development of more complex bioenergetics models for the species and a better understanding of intraspecific variation in thermal tolerances are needed to provide further insights into the complex effects of climate change on the world's largest ectotherm.

CRediT authorship contribution statement

Samantha D. Reynolds: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Craig E. Franklin:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. **Bradley M. Norman:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Anthony J. Richardson:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Jason D. Everett:** Writing – review & editing, Visualization, Methodology, Formal analysis. **David S. Schoeman:** Writing – review & editing, Visualization, Methodology, Formal analysis. **Craig R. White:** Writing – review & editing, Methodology, Formal analysis. **Christopher L. Lawson:** Writing – review & editing, Visualization, Methodology. **Simon J. Pierce:** Writing – review & editing, Investigation, Data curation. **Christoph A. Rohner:** Writing – review & editing, Investigation, Data curation. **Steffen S. Bach:** Writing – review & editing, Investigation, Data curation. **Francesco G. Comezzi:** Writing – review & editing, Investigation, Data curation. **Stella Diamant:** Writing – review & editing, Investigation, Data curation. **Mohammed Y. Jaidah:** Writing – review & editing, Investigation. **David P. Robinson:** Writing – review & editing, Investigation, Data curation. **Ross G. Dwyer:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

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authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Ethics statement

All appropriate ethics and other approvals were obtained for the research.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.175832>.

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