Emergence of climate change signals in marine ecosystem thermal niches

Yeray Santana-Falcón (✉ yeraysf@gmail.com)

CNRM-Météo France <https://orcid.org/0000-0002-2627-1947>

Roland Seferian

CNRM <https://orcid.org/0000-0002-2571-2114>

Article

Keywords:

Posted Date: December 9th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-1060043/v1>

License: This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Nature Climate Change on September 29th, 2022. See the published version at <https://doi.org/10.1038/s41558-022-01476-5>.

Emergence of climate change signals in marine ecosystem thermal niches

Yeray Santana-Falcón*¹ and Roland Séférian¹

¹CNRM, Université de Toulouse, Météo-France, CNRS, Toulouse, France

Temperature is one of the most important drivers of global ocean patterns of biodiversity^{1,2,3}, shaping thermal niches through thresholds of physiological thermal tolerance⁴. Because of anthropogenic global warming, lower and upper thermal niche bounds are predicted to change affecting the future distribution of marine species^{5,6}. Current working hypotheses suggest an expansion of ectotherms toward their poleward boundaries^{7,8}. Nonetheless, the knowledge of the timing and extent of these rearrangements across latitude and depth remains limited. Here, using daily data across the water column from both Ocean Sites network observations and novel Earth System Model, we track the emergence of thermal niches whose lower bound is warmer than their current upper bound, potentially disrupting marine habitats. We show that these developments will emerge by ~2030 in subsurface waters (~50 – 1000 m) if anthropogenic emissions continue to rise, whereas they delay several decades if emissions are substantially reduced. By 2100, thermal niches will be warmer than current counterparts. However, we further show that depending on the vertical level, concomitant changes in both boundaries will result in wider or narrower thermal niches. These results suggest that the redistribution of marine species might differ across depth, shedding light upon a much more complex picture of the impact of climate change on marine habitats.

Anthropogenic climate change fingerprints in the world's oceans by warming significantly their upper layers^{9,10}. This increase in heat content is projected to alter long-term well defined thermal niches driving species redistribution at a global scale^{11,12}. These changes are already affecting goods and services provided by the oceans¹³, and are projected to be amplified with rising greenhouse gases emissions. A close coupling between marine organisms' physiological thermal tolerances and environmental temperature^{14,15} suggests that distributional shifts can be predicted by tracking changes on the lower and upper bounds of the ecosystems' thermal niches⁶. Few studies have yet considered the vertical structure of temperature in the ocean (e.g., ref. 16), thus current understanding on how and when climate change will drive changes in marine habitats is restricted to the ocean surface (e.g., ref. 12,17,18). However, the surface is

just the tip of the iceberg of an ocean at change under anthropogenic pressure, and the general extent to which species distribution will be affected by changes in ecosystems' thermal niches below the surface remains an open question.

Predicting changes in the distribution of marine ecosystems due to variations in environmental temperature relies on the assumption that species' tolerance ranges reflect the magnitude of the local temperature variability^{15,19}. Marine organisms tend to occupy the extension at which environmental temperatures lie within their tolerances²⁰, perhaps owing to oxygen limitation of these tolerance ranges²¹. We thus consider the lower and upper limits of the thermal niches to be represented by the environmental temperature minimum (Tmin) and maximum (Tmax). At each depth, Tmin and Tmax correspond to the annual 1st and 99th percentile as computed using the statistical distribution of daily records, respectively. Though this approach encompasses most of the range of temperature variability, it can yield conservative projections as tolerance ranges can be wider than environmental thermal niches^{22,23}, and as ectotherms display some plasticity to adapt to environmental temperatures that challenge their tolerance limits^{24,25}. Nonetheless, there is limited capacity of acclimation when long-term heating occurs²⁶, especially for tropical species²⁷ and during reproductive stages²⁸. In this regard, our overarching objective is to understand how and when global warming-induced changes in thermal niches over the water column will take place in the future affecting current marine ecosystems.

We take advantage of comprehensive data sets of daily three-dimensional ocean temperatures from both the long-term Ocean Sites (OS) network and a state-of-the-art Earth System Model (ESM). This novel data set and its exploitation represents a major novelty to improve our understanding of how future climate change will impact marine ecosystems. To provide a reliable framework upon which to derive the future evolution of lower and upper thermal niche bounds, we select six OS stations for which at least seven years of daily temperature observations from the surface to ~1000 m depth are available (Table S1). We map them into polar, temperate, and tropical ocean domains, and determine the surface area of ocean domains informed by the OS stations by computing the level of similarity in daily temperature profiles using a p-value analysis (Fig. 1a, see Methods). A pattern of alternation of cooling and warming periods is seen over the time of available observations (Fig. 1b). In general, these episodes last a few years though they last longer at the northernmost stations. Though measurements' coverage is not complete along depth and time for some stations, we consider

they allow us to confidently compute annual Tmin and Tmax, and extract trends to compare with the ESM simulation (see Supplementary Material).

Three-members ensemble simulations were performed with CNRM-ESM2-1²⁹ (see Methods) encompassing the historical period (1850-2014) followed by two future projections (2015-2100) that explore very contrasted emission pathways³⁰ developed for the sixth Coupled Model Inter-comparison Project³¹ (CMIP6); a low (SSP1-2.6) and a high (SSP5-8.5) emission pathways. To overlap observations with the model, observations were daily resampled, and remapped into the simulation's vertical levels. At each OS location, we extract a subsample of the historical + SSP5-8.5 simulation that matches the period of the observations. Comparison between both data sets (Fig. S1) show simulation deviates from observations at the northernmost stations, especially at station FRAM at which observations show a warming period before 2010 that can be originated from an anomaly advection of North Atlantic waters northwards³². This anomalous episode can also be behind the positive anomaly at station CIS-1.

Figure 1: Overview and geophysical properties of the six long-term Ocean Sites (OS) stations. (a) Map illustrating the geographic location and period of the six available long-term OS stations. Colour code indicates how the OS stations are grouped into polar (blue), temperate (green) and tropical (orange) ocean domains according to their geographical coordinates. The shading indicates the ocean domains that are informed by each OS station. These domains are determined by assessing the level of similarity between daily profiles using a statistical p-value analysis (see Methods). (b) Depth-time hovmoller plots of daily ocean temperature anomalies from the surface to 1000 m. Anomalies are computed from the full observational records by removing the daily climatological temperature to daily temperature. Red (blue) colours indicate warmer (cooler) daily temperature variations with respect to the daily climatological temperature.

Observations and model data are then used to compute profiles of Tmin and Tmax over the available period. We derive the anomalies of the lower and upper thermal range boundaries by removing the mean temperature profile from Tmin and Tmax profiles. These profiles are then employed to determine the magnitude of the thermal range across depth (Fig. 2), informing of the vertical structure of current ecosystems' thermal niches. As expected, thermal ranges decrease toward high and low latitudes^{15,28} being wider at temperate domains, and toward deeper layers as temperature variability does. The largest amplitude of the thermal range takes place in the first 200 m of the water column where most of the biota lives³³. This sheds light on a more complex picture of the temperature profiles, which have been overlooked by previous studies (e.g., ref. 17,18).

temperature (T_{midpoint}) is computed as the arithmetic mean of T_{min} and T_{max} . The shape of thermal niches is mostly symmetric with a wider breadth above 50 m that narrows rapidly with depth. Modelled thermal niches (in grey) are in agreement with observed counterparts (in orange), except for an underestimation at station FRAM. Excluding station FRAM, the agreement is further corroborated by T_{midpoint} profiles ($R^2 > 0.8$). At MBARI, simulated thermal ranges as well as the T_{midpoint} profile are warmer than derived from the observations, maybe due to the difficulties of CNRM-ESM2-1 to reproduce the cold waters off the California upwelling (see ref. 29).

Emergence of changes in current thermal niches

With the shape of current thermal niches established, we track when and where concomitant changes in the lower and upper boundaries of the thermal range will take place. Concomitant changes in T_{min} and T_{max} can be seen as a compound event³⁴ since they can result in several developments of the thermal niches, possibly leading to a redistribution of marine ecosystems or driving to their collapses (Fig. S2). Thermal niches will shift toward warming or cooling temperatures if both the temperature of the lower and upper bounds of the thermal range increases or decreases, respectively. In addition, thermal niches can also expand if T_{max} warms more rapidly than T_{min} , or narrow if T_{min} warms more rapidly than T_{max} . As depicted by the observations and as simulated by CNRM-ESM2-1, trends in T_{min} and T_{max} over the recent years (Fig. S3 and S4) lead to various developments in thermal niches. In general, warming trends were stronger than cooling trends thus resulting in warmer thermal niches. The pace at which these changes occurred varies between stations, but it has been shown to push marine organisms to acclimate to a warmer environment^{11,35,36} (see Supplementary Material). Overlapping to this warming, an imbalanced warming of T_{max} results in wider thermal niches. These expanded thermal niches may host more marine species generating interspecific competition for resources and space. By contrast, excess warming of T_{min} shrinks the thermal range, possibly leading to the loss of ecosystems' habitability. Though the responses of marine organisms to these changes can be difficult to predict³⁷, as global warming trends are likely to increase^{16,38,39}, it is key to understand the time at which these changes may occur.

To assess how and when future thermal niches may emerge from warming-induced changes in the thermal range bounds, we modify the canonical approach of the Time of Emergence⁴⁰ (ToE). We track the evolution of T_{min} across the water column under two contrasted scenarios, i.e., SSP5-8.5 and SSP1-2.6, with respect to the current (1990 to 2020

mean period) $T_{midpoint}$ and T_{max} , considered as key thresholds for marine ecosystems. When T_{min} surpasses a first threshold ($T_{midpoint}$), we consider that the shift of the thermal range may represent a *warning* to current ecosystems since $T_{midpoint}$ has been observed to align well with the temperature of maximum ecological success of a specific species (see ref. 5). Furthermore, when an ecosystem will be exposed to a T_{min} that is warmer than the current T_{max} , we consider that organisms should deal with a completely *new thermal niche* (see Fig. 3a).

Figure 3: Emergence of climate change signals in thermal ranges. (a) Schematic explaining how the evolution of the lower bound of the thermal range (T_{min}) may result in the emergence of changes in marine thermal niches pending on when and where T_{min} is warmer than current $T_{midpoint}$ or T_{max} . (b) Vertical profiles of the timing of when future T_{min} will be warmer than current

Tmidpoint and Tmax at each OS station. Current period is considered as the average between 1990 to 2020. At each depth level, this timing is considered as the year at which a spline for the whole period simulation (1850 to 2100) time-series of Tmin surpasses a threshold based on the spline for the current period time-series of Tmidpoint (gold lines) or Tmax (dark red lines). Further details are available in the Methods section. Solid (dashed) lines represent the timing computed as simulated for SSP5-8.5 (SSP1-2.6). Dashed horizontal lines demarcate the water column into upper epipelagic (surface – 50 m), lower epipelagic (50 – 200 m) and mesopelagic (200 – 1000 m) layers.

Considering the approach discussed above, we find a rather good agreement across all OS stations in the first 200 m of the water column (Fig. 3b), with only noticeable changes in the thermal range within lower epipelagic waters (50 – 200 m). This feature results from both the shape of the current thermal ranges (Fig. 2), and the rather homogeneous warming of the ocean in these layers (see Fig. S3). The responses in mesopelagic waters (200 – 1000 m) are more contrasted. In the four northernmost stations, the emergence of these warnings delay in the deepest layers (> 700 m) as the rate of change of Tmin decreases. At BATS station, at which Tmin and Tmidpoint are close across the mesopelagic layer, Tmin crosses this threshold as early as the present decade. Small rates of change in the thermal ranges preclude this warning to emerge during this century at the mesopelagic layer of HOT (see Figure S5), though they appear by ~2040 below 700 m depth as Tmin warms more rapidly.

The emergence of Tmin crossing current Tmax follows a similar profile of that for Tmidpoint, but with a delay of about two to four decades. Still, it comes up above 200 m depth before 2080 in all domains. Below 200 m, it emerges before 2070 following a high emission pathway, appearing sooner in the tropics than in northern stations. Consistently across all stations, emergence times are delayed by several decades when a low emission pathway is considered (dashed lines).

End-of-the-century thermal niches

We now focus on the changes in thermal ranges by the end of the century (2080 – 2100). This analysis is relevant for tracking the impact of climate change on marine ecosystems as the lower and the upper boundaries of the thermal range will continue to change even after crossing ecosystems thresholds. As changes in thermal range boundaries can take place in both directions and at different pace because of physical and dynamical ocean processes, they can result in complex rearrangements of the thermal niches by the end of the century.

Under the high emission scenario, end-of-the-century thermal niches differ from those estimated over the historical period (1990 – 2014) (Fig. 4 and S6). In general, both the lower and upper

181 bounds of the thermal niches will be warmer (red shading) across the water column. Situations
 182 in which end-of-century Tmin will be warmer than historical Tmax occur at all stations within
 183 either the epi- or mesopelagic, or in both layers, in agreement with emergence times shown in
 184 Fig. 3. The only exceptions are found in the deepest levels of the station FRAM, and in most
 185 parts of the mesopelagic layer of the station HOT-01, where Tmax and Tmin are predicted to be
 186 slightly cooler than the historical period. Such features may result from seasonal changes in
 187 deep water mass flow or in subtropical cells, redistributing heat across ocean layers.

188

189 **Figure 4: End-of-the-century thermal ranges resulting from concomitant changes in their lower and upper bounds in**
 190 **response to climate change.** Vertical profiles illustrate temperature anomalies for Tmin and Tmax with respect to the mean over
 191 last years of the historical simulation (taken as the 1990 to 2014 average) for the historical (1990 – 2014; light lines) and end-of-the-
 192 century (2080 – 2100) periods. Vertical profiles for the future period are only given for the high emission scenario (SSP5-8.5).
 193 Reddish (bluish) shading areas indicate ocean layers where the lower (Tmin) and the upper (Tmax) boundaries of the end-of-the-
 194 century thermal range are warmer (cooler) than the current period. Dashed horizontal lines demarcate the water column into upper
 195 epipelagic (surface – 50 m), lower epipelagic (50 – 200 m) and mesopelagic (200 – 1000 m) domains. Right-hand sided boxes

indicate how the resulting changes in both boundaries have reshaped the vertical structure of the thermal ranges. Shrinking of the thermal range will result if T_{min} increases and T_{max} either decreases or increases slower. Expanding of the thermal range will result if T_{max} increases and T_{min} either decrease or increase slower. A warmer (cooler) thermal range will result if both T_{min} and T_{max} increases (decreases) at comparable paces. All changes are rounded to 0.05°C consistent with estimates of the internal climate variability of the thermal range across the water column. Boxes are given for both high emission (SSP5-8.5) and low emission (SSP1-2.6) scenarios.

Consequently to these changes, complex thermal niche developments take place (Fig. 4). Depending on the station and the layer considered, end-of-the-century thermal niches will be warmer and narrower as a result of a quicker warming of T_{min} (yellow rectangles), or warmer and wider as T_{max} warms more rapidly than T_{min} (violet rectangles). In the former case, new conditions will challenge local adaptation of inhabitant organisms. In the latter, possible spread of species from neighbour habitats may generate additional stresses by changing species interaction¹². Wider thermal niches will result above 200 m at all stations under a high-emission scenario with the only exception at station CIS-1 due to an excess warming of T_{min} (Fig. S6a). Below 200 m, the pace of warming of both bounds are comparable, generating both wide or narrow thermal niches depending on the station. Considering a low emission scenario, more heterogeneous developments appear. All stations show warming anomalies (Fig. S6b), except at station CIS-1 where both bounds will generally be cooler than the historical mean. Only developments at stations FRAM and K276 are consistent across emission scenarios.

Concluding remarks

Marine ecosystems are already being threatened by numbers of anthropogenic stressors like fishing⁴¹, acoustic pollution⁴² or plastics⁴³. Climate change exacerbates their degradation by pushing organisms to adapt to a less-oxygen warmer ocean⁴⁴. In addition, extreme events like marine heatwaves⁴⁵ are expected to increase as a consequence of global warming⁴⁶ with devastating effects on marine ecosystems. Because of these climatic impact drivers, the current working hypotheses suggest an expansion of ectotherms like fish toward their poleward boundaries^{7,8}. The novel data employed here demonstrates the added-value of scrutinizing climate change perturbations on ecosystem thermal niches across the water column with respect to surface data. We find that ongoing climate change will generate changes across the water column in the upper and lower thermal range bounds on six OS stations. If anthropogenic emissions continue to rise, we project that the lower bound of thermal ranges may cross the upper limit of current thermal niches as early as ~2030 in subsurface waters (~50 – 1000 m), potentially affecting their habitability. These changes can be delayed several decades with

immediate emission reduction consistent with a high mitigation scenario. In response to ocean warming, the shape of thermal niches will also change. We project that by 2100, depending on the vertical layer, thermal niches will be warmer and wider, potentially increasing the interspecific pressure; or warmer and narrower, forcing organisms to adapt to new local conditions or migrate. Assuming organisms are adapted to current environmental conditions, such changes may lead to rearrangements of marine habitats in the decades to come across latitude and, if possible, depth⁴⁷. These results shed light on a much more complex picture (see Fig. S7) of the impacts of climate change to ecosystems by adding the vertical dimension.

References

1. Edgar, G. J. *et al.* Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. *Sci. Adv.* **3**, e1700419 (2017).
2. Beaugrand, G., Rombouts, I. & Kirby, R. R. Towards an understanding of the pattern of biodiversity in the oceans. *Glob. Ecol. Biogeogr.* **22**, 440–449 (2013).
3. Tittensor, D. P. *et al.* Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101 (2010).
4. Pörtner, H. O., Bock, C. & Mark, F. C. Oxygen- & capacity-limited thermal tolerance: Bridging ecology & physiology. *J. Exp. Biol.* **220**, 2685–2696 (2017).
5. Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**, 88–92 (2015).
6. Stuart-Smith, R. D., Edgar, G. J. & Bates, A. E. Thermal limits to the geographic distributions of shallow-water marine species. *Nat. Ecol. Evol.* **1**, 1846–1852 (2017).
7. Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. Ecology: Climate change and distribution shifts in marine fishes. *Science* (80-.). **308**, 1912–1915 (2005).
8. Chaudhary, C., Richardson, A. J., Schoeman, D. S. & Costello, M. J. Global warming is causing a more pronounced dip in marine species richness around the equator. *Proc. Natl. Acad. Sci. U. S. A.* **118**, e2015094118 (2021).
9. Levitus, S. *et al.* Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems. *Geophys. Res. Lett.* **36**, n/a–n/a (2009).
10. Barnett, T. P. *et al.* Ocean science: Penetration of human-induced warming into the world's oceans. *Science* (80-.). **309**, 284–287 (2005).
11. Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Chang.* **3**, 919–925 (2013).

- 262 12. Garciá Molinos, J. *et al.* Climate velocity and the future global redistribution of marine
263 biodiversity. *Nat. Clim. Chang.* **6**, 83–88 (2016).
- 264 13. Free, C. M. *et al.* Impacts of historical warming on marine fisheries production. *Science*
265 (80-.). **363**, 979–983 (2019).
- 266 14. Hughes, N. F. & Grand, T. C. Physiological ecology meets the ideal-free distribution:
267 Predicting the distribution of size-structured fish populations across temperature
268 gradients. *Environ. Biol. Fishes* **59**, 285–298 (2000).
- 269 15. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and
270 latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* **278**, 1823–1830 (2011).
- 271 16. Kwiatkowski, L. *et al.* Twenty-first century ocean warming, acidification, deoxygenation,
272 and upper-ocean nutrient and primary production decline from CMIP6 model projections.
273 *Biogeosciences* **17**, 3439–3470 (2020).
- 274 17. Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future
275 vulnerability of marine biodiversity compared with contemporary and past changes. *Nat.*
276 *Clim. Chang.* **5**, 695–701 (2015).
- 277 18. Trisos, C. H., Merow, C. & Pigot, A. L. The projected timing of abrupt ecological
278 disruption from climate change. *Nature* **580**, 496–501 (2020).
- 279 19. Janzen, D. H. Why Mountain Passes are Higher in the Tropics. *Am. Nat.* **101**, 233–249
280 (1967).
- 281 20. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution
282 of animals. *Nat. Clim. Chang.* **2**, 686–690 (2012).
- 283 21. Pörtner, H. O. Oxygen- And capacity-limitation of thermal tolerance: A matrix for
284 integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* **213**, 881–
285 893 (2010).
- 286 22. Araújo, M. B. *et al.* Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206–1219 (2013).
- 287 23. Deutsch, C. A. *et al.* Impacts of climate warming on terrestrial ectotherms across latitude.
288 *Proc. Natl. Acad. Sci. U. S. A.* **105**, 6668–6672 (2008).
- 289 24. Seebacher, F., White, C. R. & Franklin, C. E. Physiological plasticity increases resilience
290 of ectothermic animals to climate change. *Nat. Clim. Chang.* **5**, 61–66 (2015).
- 291 25. Hoffmann, A. A. & Sgró, C. M. Climate change and evolutionary adaptation. *Nature* **470**,
292 479–485 (2011).
- 293 26. Sandblom, E. *et al.* Physiological constraints to climate warming in fish follow principles of
294 plastic floors and concrete ceilings. *Nat. Commun.* **7**, 11447 (2016).
- 295 27. Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Ecology: Putting the heat on tropical
296 animals. *Science* (80-.). **320**, 1296–1297 (2008).

- 297 28. Dahlke, F. T., Wohlrab, S., Butzin, M. & Pörtner, H. O. Thermal bottlenecks in the life
298 cycle define climate vulnerability of fish. *Science (80-.)*. **369**, 65–70 (2020).
- 299 29. Séférian, R. *et al.* Evaluation of CNRM Earth System Model, CNRM-ESM2-1: Role of
300 Earth System Processes in Present-Day and Future Climate. *J. Adv. Model. Earth Syst.*
301 **11**, 4182–4227 (2019).
- 302 30. Gidden, M. J. *et al.* Global emissions pathways under different socioeconomic scenarios
303 for use in CMIP6: A dataset of harmonized emissions trajectories through the end of the
304 century. *Geosci. Model Dev.* **12**, 1443–1475 (2019).
- 305 31. Eyring, V. *et al.* Overview of the Coupled Model Intercomparison Project Phase 6
306 (CMIP6) experimental design and organization. *Geosci. Model Dev.* **9**, 1937–1958
307 (2016).
- 308 32. Beszczynska-Möller, A., Fahrbach, E., Schauer, U. & Hansen, E. Variability in Atlantic
309 water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES J.*
310 *Mar. Sci.* **69**, 852–863 (2012).
- 311 33. Sutton, T. T. Vertical ecology of the pelagic ocean: Classical patterns and new
312 perspectives. *J. Fish Biol.* **83**, 1508–1527 (2013).
- 313 34. Leonard, M. *et al.* A compound event framework for understanding extreme impacts.
314 *Wiley Interdiscip. Rev. Clim. Chang.* **5**, 113–128 (2014).
- 315 35. Calosi, P., Bilton, D. T. & Spicer, J. I. Thermal tolerance, acclimatory capacity and
316 vulnerability to global climate change. *Biol. Lett.* **4**, 99–102 (2008).
- 317 36. Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. & Levin, S. A. Marine taxa track
318 local climate velocities. *Science (80-.)*. **341**, 1239–1242 (2013).
- 319 37. Donelson, J. M., Munday, P. L., McCormick, M. I. & Pitcher, C. R. Rapid
320 transgenerational acclimation of a tropical reef fish to climate change. *Nat. Clim. Chang.*
321 **2**, 30–32 (2012).
- 322 38. Bopp, L. *et al.* Multiple stressors of ocean ecosystems in the 21st century: Projections
323 with CMIP5 models. *Biogeosciences* **10**, 6225–6245 (2013).
- 324 39. Cheng, L., Abraham, J., Hausfather, Z. & Trenberth, K. E. How fast are the oceans
325 warming? *Science (80-.)*. **363**, 128–129 (2019).
- 326 40. Hawkins, E. & Sutton, R. Time of emergence of climate signals. *Geophys. Res. Lett.* **39**,
327 n/a–n/a (2012).
- 328 41. Jackson, J. B. C. *et al.* Historical overfishing and the recent collapse of coastal
329 ecosystems. *Science (80-.)*. **293**, 629–637 (2001).
- 330 42. Duarte, C. M. *et al.* The soundscape of the Anthropocene ocean. *Science (80-.)*. **371**,
331 eaba4658 (2021).
- 332 43. Rochman, C. M. & Hoellein, T. The global odyssey of plastic pollution. *Science (80-.)*.

333 **368**, 1184–1185 (2020).

334 44. Brierley, A. S. & Kingsford, M. J. Impacts of Climate Change on Marine Organisms and
335 Ecosystems. *Curr. Biol.* **19**, R602–R614 (2009).

336 45. Frölicher, T. L. & Laufkötter, C. Emerging risks from marine heat waves. *Nat. Commun.* **9**,
337 2015–2018 (2018).

338 46. Frölicher, T. L., Fischer, E. M. & Gruber, N. Marine heatwaves under global warming.
339 *Nature* **560**, 360–364 (2018).

340 47. Jorda, G. *et al.* Ocean warming compresses the three-dimensional habitat of marine life.
341 *Nat. Ecol. Evol.* **4**, 109–114 (2020).

342 **Methods**

343 **Ocean Sites observations**

344 The *Ocean Sites* (OS) network constitutes a worldwide effort to monitor ocean parameters
345 through high-quality data extracted from long-term, high-frequency observations at several
346 locations of the World ocean. Six OS stations, listed in Table S1, were selected because of the
347 availability of continuous daily measurements of ocean temperature and salinity across the
348 water column for more than seven years, allowing a robust computation of thermal range
349 boundaries (see below). All of the six stations provide data from the surface to about 1000 m
350 depth, that have been resampled daily at each depth, and then interpolated into the vertical grid
351 of CNRM-ESM2-1.

352 Observational data is accessible through [http://tds0.ifremer.fr/thredds/catalog/CORIOLIS-](http://tds0.ifremer.fr/thredds/catalog/CORIOLIS-OCEANSITES-GDAC-OBS/DATA/)
353 [OCEANSITES-GDAC-OBS/DATA/](http://tds0.ifremer.fr/thredds/catalog/CORIOLIS-OCEANSITES-GDAC-OBS/DATA/). Last accessed was in October 2020.

354 **Simulations**

355 This work exploits simulations from a state-of-the-art Earth system model, CNRM-ESM2-1²⁹,
356 that has been developed by the CNRM-CERFACS climate group for the sixth phase of the
357 Coupled Model Inter-comparison Project (CMIP6³¹). The ocean component of CNRM-ESM2-1 is
358 NEMOV3.6⁴⁸, which resolves ocean dynamics on an eORCA1 grid⁴⁹ with 75 vertical z-coordinate
359 levels. This grid offers a horizontal resolution of about 1° with a grid refinement up to 0.3° in the
360 tropics.

361 In this study, we performed four simulation with CNRM-ESM2-1: a 250 year-long pre-industrial
362 control simulation (without anthropogenic forcing) to estimate the model's internal variability;
363 and a historical simulation from 1850 to 2014 followed by two future scenarios from 2015 to
364 2100, which are used to derive present and future variations in temperature minimum and
365 maximum.

366 These simulations were produced using the external forcing as recommended by CMIP6 for the
367 pre-industrial state and the historical period. For the future scenarios we used contrasting
368 pathways: a low (SSP1-2.6) and high (SSP5-8.5) emission pathways as described in ref. 30.

369 All simulations provide daily outputs from the ocean surface to 4000 m for ocean temperature
370 and salinity as well as oxygen, pH and net primary productivity. Here, we exploit only the first 47
371 vertical layers for ocean temperature and salinity in order to describe the first 1000 m depth of
372 the water column. Finally, to ensure both observations and model data (historical + SSP5-8.5
373 simulation) cover exactly the same period, model data was selected to begin and end at the
374 same date as observations.

375 **Ocean domains informed by Ocean Site stations**

376 Though OS networks are located throughout the World ocean, our selection of OS stations is
377 disproportionately located in the North Atlantic and North Pacific oceans (see Fig. 1 and Table
378 S1). To assess how large is the surface area of ocean domains informed by our six selected OS
379 stations, we compute the level of similarity between daily profiles as provided by observations
380 and the model hindcast over the current period (1990-2020) using the statistical approach
381 presented in ref. 50. This approach compares simultaneously the mean and the daily variations
382 of OS daily profiles with a neighbour grid-point model profile using a Chi-squared-based test.
383 The test consists in comparing the cumulative sum of the Welch's t_z^{251} across depth levels to an
384 empirical Chi-squared distribution with 47 degrees of freedom (i.e., the number of depth levels).
385 We use 10,000 random samples of this Chi-squared distribution to estimate the empirical
386 distribution of the Chi-squared law. The distribution is then used to compute an empirical
387 'integrated' p-value that represents an objective metric to determine how far the two profiles are
388 consistent between each other within the depth interval.

389 The empirical 'integrated' p-value allows us to quantify the match between profiles. We establish
390 a threshold of 0.90 to consider a profile over a grid-cell consistent with the OS profile. For

391 further analysis, stations were grouped into three ocean domains: polar, temperate and tropical
392 waters.

393 **Estimation of thermal niche boundaries**

394 The working definition of the thermal niche employed in this work assumes that the species'
395 tolerance ranges reflect the magnitude of the local temperature variability^{15,19}. As a
396 consequence, we infer the vertical structure of the thermal niche from the lower and upper limits
397 of the thermal range that is captured by the minimal and maximal environmental temperature
398 across the water column.

399 Thanks to high-frequency data, we provide a robust yearly estimate of these bounds using the
400 annual first (p01, Tmin) and last (p99, Tmax) percentiles of both model and observation
401 temperature time-series at each depth level. In order to minimize the influence of the internal
402 climate variability when comparing model and data results, we estimate model annual
403 percentiles by grouping the three ensemble members. Thus, model percentile for thermal range
404 is derived from a $365 \times 3 = 1095$ sample of daily outputs at each depth.

405 The breadth of thermal ranges are estimated as the difference between Tmax and Tmin at each
406 depth level. Midpoint temperatures (Tmidpoint) correspond to the arithmetic mean of Tmin and
407 Tmax, thus assuming normality in the distribution of Tmin and Tmax.

408 **Tmin crosses thermal niche thresholds**

409 To track future changes in the thermal range boundaries, we employed a method inspired from
410 the well-established Time of Emergence (ToE) approach (see Supplementary Material). As for
411 the ToE approach, our method requires estimates of a climate change signal (S). We estimate it
412 using daily model outputs from 1850 to 2100 for an ensemble of three realizations from CNRM-
413 ESM2-1 that has been run following historical and low emission SSP1-2.6 and high emission
414 SSP5-8.5 pathways. For each pathway, we define S as the smooth spline (four degrees of
415 freedom) of the variation of Tmin during the full simulation. In general, the ToE approach is
416 defined as the first year at which S surpasses twice the standard deviation of the internal
417 climate variability. Here, in contrast, we make use of different thresholds that have a meaning
418 for ecosystem functioning, which represent key characteristics of the thermal range, Tmidpoint
419 and Tmax. These two thresholds are defined as the average of a smooth spline (four degrees of

420 freedom) of the variation of Tmidpoint and Tmax during the past 30 years from today (1990 to
421 2020); a period considered to be representative of the current period.

422 For illustration purposes, we illustrate how our approach works for four depth levels of HOT-01
423 station (Fig. S5).

424 **End-of-the-century thermal niches**

425 End-of-the-century thermal niches provide a snapshot of the concomitant changes in thermal
426 range boundaries resulting from climate change. We compute the end-of-the-century thermal
427 niche from daily data over the 2080-2100 period. Fig. 4 displays the end-of-the-century thermal
428 range anomalies of both Tmin and Tmax with respect to the mean over 1990-2014,
429 corresponding to the last years of the historical simulation. To compare with the historical
430 profiles, we also include their anomalies. At each depth level, we assess the magnitude of the
431 changes between the end-of-the-century and the historical profiles.

432 As changes in thermal range boundaries can evolve in both directions, and with a different
433 pace, they may result in a re-arrangement of the vertical shape of the thermal range. To track if
434 end-of-the-century thermal niches are also wider or narrower, we compute the difference
435 between Tmax and Tmin anomalies at each depth level (Fig. S6). If the difference is positive,
436 thermal niches will be wider, i.e., Tmax warms more rapidly. If the difference is negative,
437 thermal niches will be narrower, i.e., Tmin warms more rapidly. If differences are $< 0.05\text{ }^{\circ}\text{C}$ (i.e.,
438 level of uncertainty informed from the analysis of the internal variability of thermal range profiles
439 in Fig. S4), we consider no changes in the shape of thermal niches will take place, i.e., only
440 shifting toward warming or cooling is projected. Both emission pathways are displayed in Fig.
441 S6.

442 In Fig. 4 we have assigned a colour code for each of these developments. A depiction of these
443 developments is provided in Fig. S2.

444 **Model internal variability**

445 As a consequence of the chaotic nature of processes in the Earth systems being simulated
446 (ocean-atmosphere-land-biosphere-cryosphere), one of the main sources of uncertainties in
447 climatic future projections is their internal variability⁵². One way to isolate these uncertainties is

to generate an ensemble of model realizations⁵³. Here we make use of an ensemble of three members in order to minimise the influence of the internal variability in our computation. Each realization starts from different initial conditions of the model of Dec 31st 1980 (member 1), 1900 (member 2), and 2000 (member 3), sampling different states of the model climate.

References (methods):

15. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* **278**, 1823–1830 (2011).
19. Janzen, D. H. Why Mountain Passes are Higher in the Tropics. *Am. Nat.* **101**, 233–249 (1967).
29. Séférian, R. *et al.* Evaluation of CNRM Earth System Model, CNRM-ESM2-1: Role of Earth System Processes in Present-Day and Future Climate. *J. Adv. Model. Earth Syst.* **11**, 4182–4227 (2019).
30. Gidden, M. J. *et al.* Global emissions pathways under different socioeconomic scenarios for use in CMIP6: A dataset of harmonized emissions trajectories through the end of the century. *Geosci. Model Dev.* **12**, 1443–1475 (2019).
31. Eyring, V. *et al.* Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geosci. Model Dev.* **9**, 1937–1958 (2016).
48. Madec, G. *et al.* *NEMO ocean engine*. <https://www.earth-prints.org/handle/2122/13309> (2017) doi:10.5281/zenodo.3248739.
49. Mathiot, P., Jenkins, A., Harris, C. & Madec, G. Explicit representation and parametrised impacts of under ice shelf seas in the z*- coordinate ocean model NEMO 3.6. *Geosci. Model Dev.* **10**, 2849–2874 (2017).
50. Middag, R. *et al.* Intercomparison of dissolved trace elements at the Bermuda Atlantic Time Series station. *Mar. Chem.* **177**, 476–489 (2015).
51. Welch, B. L. The Generalization of 'Student's' Problem when Several Different Population Variances are Involved. *Biometrika* **34**, 28 (1947).
52. Dai, A. & Bloecker, C. E. Impacts of internal variability on temperature and precipitation trends in large ensemble simulations by two climate models. *Clim. Dyn.* **52**, 289–306 (2019).
53. Deser, C., Phillips, A., Bourdette, V. & Teng, H. Uncertainty in climate change projections: The role of internal variability. *Clim. Dyn.* **38**, 527–546 (2012).

481

482 **Data availability** Interpolated data presented in the paper will be available through the Zenodo
483 repository.

484 **Acknowledgements** We thank L. Kwiatkowski, S. Berthet and E. Sánchez for comments on
485 pre-submission drafts of the manuscript. This work was supported by the European Union's
486 Horizon 2020 research and innovation program with the TRIATLAS project under the grant
487 agreement No 817578, the COMFORT project under the grant agreement No 820989 and the
488 ESM2025 project under the grant agreement No 101003536.

489 **Author Contributions** Y.S.F. and R.S. conceived the study, developed the data sets,
490 performed the computations and wrote the manuscript.

491 **Competing interests** The authors declare no competing interests.

492 **Materials & Correspondence** yeray.santana@meteo.fr

493

494

495

496

497

498

499

500

501

502

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SantanaFalconSeferianSupplMat.pdf](#)