Title: Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels

Short title: Hemispheric seabird productivity

One sentence summary: Seabird breeding productivity tracks hemispheric asymmetry in ocean climate change.

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Abstract: Climate change and other human activities are causing profound effects on marine ecosystem productivity. We show that the breeding success of seabirds is tracking hemispheric differences in ocean warming and human impacts, with strongest effects on fish-eating, surface-foraging species in the north. Hemispheric asymmetry suggests the need for ocean management at hemispheric scales. For the north, tactical climate-based recovery plans for forage fish resources are needed to recover seabird breeding productivity. In the south, lower-magnitude change in seabird productivity presents opportunities for strategic management approaches, such as large marine protected areas to sustain food webs and maintain predator productivity. Global monitoring of seabird productivity enables detection of ecosystem change in remote regions and contributes to understanding of marine climate impacts on ecosystems.

Main Text: Earth's environments and biological systems are changing at unprecedented rates. An under-appreciated emergent property of global change is differences, or asymmetries, in the responses of marine ecosystems in the northern and southern hemispheres to anthropogenic influences. In the northern hemisphere, ecosystem change is thought to be more pronounced because humans have been exploiting marine resources at industrial levels there over longer periods of time (*1*). Further, greater land mass in the north may amplify rates of anthropogenic global warming (*2*). In contrast, the vast oceanic domains of the southern hemisphere are believed to more efficiently buffer the effects of greenhouse gas emissions on ocean temperatures. The remoteness of marine systems in the south also has limited human access and some associated impacts (whaling being one major exception), until recently (*3*).

Analysis of temperature trends, velocity of ocean warming (*4*), and indices of marine heatwaves confirms hemispheric differences in climate change impacts for the upper ocean (Fig. 1). The variety and scope of human impacts on marine ecosystems (*3*) are greater in the northern hemisphere, but have expanded faster in the southern hemisphere over the period 2003 to 2013 (Fig. 1I-L; *3, 5*).

To date, global syntheses of marine ecosystem change have not explicitly considered hemispheric variation in ocean climate change (*6*). Moreover, by necessity, most assessments have been based on disparate taxon-specific response variables, such as calcification rates in corals, range and distributional shifts of fish, timing and intensity of plankton blooms, or vital rates of marine vertebrates (*6, 7*). The use of dissimilar response variables across species and trophic levels limits synthesis to simplified, often binary metrics of effects (e.g., "consistency"

with predictions of climate change), which hampers comparisons across marine ecosystems (*8, 9*). To avoid these issues, a unified approach is required in which analogous and interpretable variables are considered at the scale of large marine ecosystems (*10*). A good example of an overarching metric to assess marine ecosystem change has recently emerged in the form of estimates of "breeding productivity" of marine predators, i.e., the number of young produced per female per year (*11, 12*).

Here, we test the hypothesis that the breeding productivity of seabirds is tracking hemispheric asymmetry in ocean climate change and human use. Due to the availability of global-scale data on breeding productivity, seabirds stand out among marine vertebrates, with numerous multi-decadal datasets in both hemispheres (e.g., Crozet, Pribilof, and Farallon islands; *13, 14*, Tables S1–S3, Figs. S1, S2). The accumulation of long-term datasets among hemispheres is remarkably similar, although there are fewer data overall in the south (Fig. S1). During breeding, seabirds provision themselves and offspring on a wide variety of food resources spanning copepods to small pelagic fish and thereby provide an integrated response to climate change across trophic levels (*7*). Seabird breeding productivity is known to reflect non-linear numerical responses to mesozooplankton and small fish availability in the epipelagic zone (*15–18*). Notably, seabirds, which breed in colonies but forage at sea during reproduction, may be particularly vulnerable to ocean change as their breeding sites are static in space while the availability of their food resources is spatially and temporally dynamic.

We predicted greater declines in northern hemisphere seabird breeding productivity than southern. To test this hypothesis, we compiled 122 time series of annual breeding productivity (proportionate change from the long-term mean) for 66 seabird species, representing 3,586 annual data points across the globe over the period 1964 to 2018 (Tables S1–S3, Fig. S2). We used these data to conduct an analysis of seabird breeding success in relation to hemispheric asymmetry in ocean warming (*19*).

To evaluate possible hemispheric variation in reproductive trends associated with seabird ecology, we categorized each species' trophic level based on their primary diet during the breeding season on the resolution of decades (*19*). Trophic level is a key ecological characteristic because the effect of climate change on marine top predators often acts mechanistically through food resources (*7*). For this investigation, we categorized species as 1) planktivores that primarily consume mesozooplankton and larval fishes, 2) piscivores that primarily consume small pelagic fish, and 3) omnivores that consume both plankton and fish. After considering trophic level, we further dissected species' foraging characteristics by examining whether species feeding in the upper water column ("surface-foraging") are more vulnerable to ocean changes than species foraging at depths > 10 m ("sub-surface foraging"). Feeding depth co-varies with other life-history traits in seabirds, such as body size and foraging range (*20*). Whereas over 47% of the planktivores and 59% of the piscivorous species included in our study were sub-surface foragers, only 9 (33%) of the 27 omnivorous species foraged at depth (Table S2).

Trends in seabird breeding productivity varied by trophic level; within each trophic level, they also varied by hemisphere, but we found no overall effect of foraging depth on productivity (Fig. 2A, Table S4, Fig. S3). Omnivorous species, many of which provision young with small pelagic

fish (Table S2), showed the most substantial changes in both hemispheres, with larger decreasing trends in normalized breeding productivity in the north (1.00 ± 0.17 to -0.53 ± 0.09 (point estimates from the start to the end of the study period, respectively, $\pm$ standard error) than in the south (0.3 ± 0.22 to -0.13 ± 0.11). Breeding productivity of piscivorous species declined in the north (0.30 ± 0.14 to -0.17 ± 0.07), but increased in the south (-0.43 ± 0.31 to 0.21 ± 0.16). In contrast, planktivorous seabirds showed increasing productivity trends in the north (-0.54 ± 0.27 to 0.21 ± 0.13) and stable productivity in the south (0.18 ± 0.30 to -0.1 ± 0.16).

To ascertain whether decreasing productivity is related to an increasing rate of breeding failure, potentially associated with the increasing frequency of marine heatwaves in both hemispheres (Fig. 1C,D), we examined the probability of breeding failure, defined as breeding success < 10% relative to the mean for each time series (*19*). Trends in the probability of breeding failure corroborated observations of normalized breeding success, with significant effects varying by hemisphere, trophic level, and foraging depth (Fig. 2B, Table S5). Overall, the probability of breeding failure increased for piscivores in both hemispheres, and for omnivores in the north. For piscivores, probability of breeding failure was significantly higher in the northern hemisphere, and it was also elevated for surface-foraging species in both hemispheres, especially in recent years. Surface-feeding omnivores in the north followed a similar pattern, with the probability of breeding failure escalating rapidly after 2000. Breeding failure was relatively uncommon for planktivores and omnivores in the southern hemisphere, where trends were weak.

Thus far, global analyses of seabirds have shown inconsistent responses to climate change in terms of their phenology (i.e., timing of reproduction, *21*), though trends in vital rates have been more consistently negative (*6, 7*). By using seabird breeding productivity as a unified variable to sense change at the global scale, we observed greater consistency in identified responses to ocean warming (Figs. 1, 2), though hemispheric variation in the magnitude and rate of the warming apparently impacted fish-eating species the most. We could not include temperature change directly in our models since temperature increased with time and would confound the effect of hemisphere. Moreover, as rates of change in temperature, velocity of ocean warming, and marine heatwaves vary strongly by hemisphere (Fig. 1), using hemisphere as a covariate in models is a proxy for these metrics of anthropogenic climate change. We nevertheless conducted sensitivity tests that omitted hemisphere as a fixed effect, in which we found evidence of declining breeding success with increasing rate of ocean warming or velocity of ocean warming (*19*). The variance explained by our models was low, so other variables that may play a role in determining productivity, such as short-term local weather events (*22*) or other factors that may affect food resources (e.g., fisheries) or density-dependent mechanisms (e.g., *23*), should be considered in future analyses. Even with the substantial global dataset we compiled, we were unable to address all competing factors that drive variation in seabird breeding productivity.

Our study provides important insights for ecosystem monitoring and management. First, because seabirds accumulate and integrate, in a statistical sense, climatic, oceanographic, and food web variation, they provide immediate signals of changes in ecosystems that are difficult to observe directly, particularly in remote regions of the world (*24*). The signals provided by seabird breeding productivity could easily be used to assess global change in marine ecosystems on an annual timeframe with relatively simple coordination and data sharing of governmental

monitoring programs. Second, most global climate models predict increasing ocean stratification owing to ocean warming (*9, 25*), which may limit nutrient input into the epipelagic zone and thereby affect meso-zooplankton and forage fish populations (*26*). The dwindling productivity of seabirds across the north, with its greater rate of warming, suggests that realized increasing stratification may already be affecting marine ecosystems there (*27, 28*), though other confounding human impacts on surface-foraging species (e.g., plastics pollution, *29*), may also partly explain increases in probability of breeding failures. Relatedly, the significant effect of foraging depth on trends in probability of breeding failure across trophic levels suggests that access to sub-surface foraging habitats, regardless of trophic level or hemisphere, confers some resilience to sub-surface feeding seabirds, such as penguins and puffins. In contrast, surface-feeding albatrosses, petrels, and terns may be most susceptible to warming-related changes in food resources. Third, while the rate of change in human use and impacts is increasing more rapidly in the south, the overall impacts of humanity on marine ecosystems, including the combined effects of climate change, fisheries, and other forms of marine resource exploitation, and pollution is considerably greater in the northern hemisphere (*3, 9*).

Our study indicates that the prognosis for sustained breeding productivity of northern-hemisphere fish-eating and omnivorous breeding seabirds is poor, unless availability of food resources is improved. One approach to increase functional seabird predator-prey interactions could include enhancing food-web redundancies and connectivity through management targeting prey diversity, promoting a greater portfolio of forage fish populations. An obvious factor that needs continuing attention is temporal or spatial management of fisheries that target small pelagic fish or large zooplankton (e.g., krill) and may compete with seabirds for food, especially near colonies during the reproductive period (*30*); time-area fisheries closures may be an effective strategy for improving seabird productivity in the northern hemisphere (*31*).

Implications of our study for southern hemisphere seabirds and their ecosystems demonstrate less urgency, although there are regional exceptions, especially in the Southern Ocean (*32*). Generally, however, our results portend opportunity in the southern hemisphere, where implementation of longer-term ecosystem-based approaches could be effective in mitigating impending human impacts (*3, 32*) and those predicted by the latest suite of Earth-system models (*9*). While compelling effects on seabird breeding productivity have been realized for fisheries closures near seabird colonies (*31*), establishment of large marine protected areas (*33, 34*) could enhance seabird and other predator foraging opportunities and communities year-round. If foraging opportunities can be managed, even relatively small changes in breeding productivity over the long-term could enhance population stability and recovery (*31*).

In conclusion, the disparity between central-place foraging seabirds breeding at fixed points in space relative to spatially and temporally dynamic ocean habitats and prey resources (*35, 36*) places seabirds at particular risk from ocean climate change, especially in combination with other human-induced perturbations such as pollution and fisheries. The changes in seabird breeding productivity related to hemispheric variation in ocean warming and human uses documented by this paper calls out the need to sustain long-term monitoring programs, some of which are threatened, illustrates the critical role that seabirds play as sentinels of global marine change, and highlights the need for policies that reduce climate change impacts on the world's marine ecosystems.

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Supplementary Materials:
Materials and Methods:
      Seabird breeding productivity
      Variation in trends between species
      Hemispheric differences in warming
      Statistical model
Supplemental Text:
      Sensitivity tests for models including hemisphere as a fixed effect
      Additional data collection acknowledgements
Figs. S1–S3
Tables S1–S5
References 37–54

Fig. 1: Maps and kernel density plots showing hemispheric differences in indices of marine climate change and human use in the upper ocean. (A,B) Rate of warming and (C,D) velocity of ocean warming based on HadISST1 data over the 50-year period 1968–2019; trends over the period 1968–2017 for (E,F) cumulative number of marine heat-wave days and (G,H) trends in cumulative marine heatwave intensity based on NOAA OISST; and (I,J) cumulative human impacts in 2003 (e.g., fishing, shipping, contamination as defined by Halpern *et al*. (*3*)) and (K,L) rate of change in human impacts from 2003–2013. All maps are overlaid with 45 locations across the world where seabird breeding biology was studied (white circles). For kernel density plots (and summary statistics), data equatorward of 15° and poleward of 75° in both hemispheres (lightly shaded polygons on the maps) were excluded to avoid bias by extreme values or seasonally missing data. None of our sample sites were within these areas. All data presented were re-gridded onto equal-area hexagons (~0.5° at the equator) for computation and visual representation to avoid latitudinal bias in grid area. Resulting data are summarized for each kernel density plot (tables in B, D, F, J, L) by median, 10th and 90th percentiles by hemisphere (Hemi) and sites within hemisphere (Sites).

Fig. 2: Modeled trends and standard errors of seabird breeding productivity and probability of breeding failure. (A) Normalized breeding productivity of seabirds by trophic level and hemisphere (north: red, and south: blue ± s.e.) as a function of time. Trends in individual time series (dashed lines) are shown as background. See Material and Methods for model details. (B) Modeled trends in the probability of breeding failure by trophic level,

foraging depth (surface or sub-surface), and hemisphere. Observations of breeding success or failure are provided as background points, colored by hemisphere.