

Ocean acidification and aragonite saturation compounding anthropogenic stressors on marine life

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Abstract

Background: Ocean acidification is usually reported as annual or global means, yet marine organisms respond to the saturation state they actually meet, which in cold and productive waters is the winter minimum. We recomputed the aragonite saturation state (Ω) of winter casts at long carbonate time-series sites from the primary measurements, and we compared the mapped winter field of the OceanSODA-ETHZ product for 1982 to 2024 with zone-specific ecological reference thresholds.

Results: In the Iceland Sea, the subarctic North Pacific and the Southern Ocean, winter Ω already sits at or below 1.6, the threshold for sensitive aragonite calcifiers, and the Iceland Sea record declined by $0.0046 \pm 0.0007 \Omega$ per year before 2014. About 44% of the mapped ocean surface was below its winter threshold in 2022 to 2024, a figure between 37 and 52% under every zonation scheme tested, and extending each cell's own 43-year trend carries it to about 57% by 2045. The water below its threshold coincides with the upwelling and high-nutrient regions that support most of the marine food web, where pteropods, bivalve larvae, oyster hatcheries and juvenile crabs already show responses at the saturation and pH levels now reached. An openly documented index of published declines places marine animal life at about 35 to 54% of its 1850 level, so acidification is acting on a system that fishing, whaling, habitat loss, pollution and climate disruption had already depleted.

Conclusions: We also set out, as a testable hypothesis, how a falling pH may alter colloidal chemistry, micro-viscosity and iron availability. We conclude that ocean acidification should be treated now as an active part of cumulative marine risk, that reporting should use winter minima alongside annual means, and that redox potential, zeta potential and particle measurements should be added to existing time-series stations.

Keywords: ocean acidification; aragonite saturation state; winter exposure; ecological thresholds; calcifying plankton; pteropods; cumulative stressors; marine defaunation; regime shifts

1 Background

The aragonite saturation state, Ω , is calculated from measured properties of seawater, including the partial pressure of carbon dioxide, pH, total alkalinity, calcium concentration, salinity and temperature [1]. It describes how easily marine animals can build and keep shells and skeletons of

aragonite, which is a form of calcium carbonate. Aragonite dissolves below $\Omega = 1$, a shell forms readily above about $\Omega = 1.6$, and sensitive calcifiers begin to suffer in the marginal zone between those two values (Section 4.2).

Saturation is usually reported as an annual mean, and in cold water an annual mean is always higher than the winter reading that marine life actually meets. The ocean acidification planetary boundary is a clear example, since it is expressed as a global annual mean of Ω 2.75, which is 80% of the pre-industrial value of 3.44 [2, 3]. That threshold was chosen to keep high-latitude surface water, the first to approach undersaturation, above the point of dissolution and to protect most coral systems. The difficulty is not that the framework ignores cold water, but that a single global annual mean cannot show when individual cold basins cross the line in winter. A recent reassessment raised the pre-industrial baseline to Ω 3.51, found that by 2020 the global mean had entered the uncertainty range of the 20% boundary and that four of seven ocean regions, the Arctic among them, had crossed the boundary, and argued for a stricter 10% boundary that the whole surface ocean passed by 2000 [4].

This study addresses two questions about the present state of the acidifying ocean. First, how much of the ocean already sits below the saturation at which its own calcifying organisms respond, when exposure is judged at the winter minimum rather than the annual mean? Second, what state was marine life already in when that chemistry began to change? To answer the first question, we recomputed the winter casts of the long carbonate time series of the Iceland Sea, the Irminger Sea, the subarctic North Pacific and the Southern Ocean from the primary measurements, and we compared the mapped winter field of the OceanSODA-ETHZ product [5] with zone-specific ecological reference thresholds. To answer the second question, we compiled the published record of marine animal declines since 1850 into an openly documented index. We then set out, as a clearly labelled hypothesis, how a falling pH may act on plankton through colloidal chemistry, viscosity and iron, beyond its effect on shells, and we report one satellite test of that hypothesis.

2 Methods

2.1 Data sources and their roles

Two kinds of measurement play fixed and separate roles throughout this study. The gridded OceanSODA-ETHZ product [5, 6] supplies the spatial and global evidence, because only a mapped field covers the whole ocean surface, while discrete ship-based casts supply independent regional validation and direct winter measurements at selected sites. Neither is used in the role of the other, and no global figure rests on the discrete sites alone. The discrete casts come from the SPOTS time-series synthesis [7], cross-checked against GLODAPv2.2022 [8] and CODAP-NA [9]. Every primary dataset used in this study is public and is listed in Table 1 with its accession or citation.

Table 1 Data sources used in this study

Dataset	Variable(s) used	Coverage	Source
OceanSODA-ETHZ v2025	omega_ar (aragonite saturation), omega_ar_uncert	1×1°, monthly, 1982–2024, global	Gregor & Gruber [5]; NOAA NCEI OCADS accession 0220059, https://doi.org/10.25921/m5wx-ja34 ; landing page: https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0220059
SPOTS time-series synthesis	DIC, total alkalinity, pCO ₂ , temperature, salinity, silicate, phosphate (discrete casts)	Iceland Sea, Irminger Sea, Station K2, Munida	Lange et al. [7]
GLODAPv2.2022	Interior/surface DIC, total alkalinity, nutrients (quality-control cross-check for discrete casts)	Global ocean interior compilation	Lauvset et al. [8]
CODAP-NA	Discrete inorganic carbon, oxygen, and nutrients (North American margin cross-check)	North American ocean margins	Jiang et al. [9]
MODIS-Aqua Kd ₄₉₀ and chlorophyll-a (Station ALOHA optics)	Diffuse attenuation coefficient Kd ₄₉₀ and chlorophyll-a (Section 2.6, Station ALOHA)	4 km monthly, 2003–2021, box of 6° latitude by 8° longitude around Station ALOHA	NASA OBPG R2018.0 products served by NOAA OceanWatch ERDDAP (aqua_kd490_monthly_2018_o, aqua_chla_monthly_2018_o)
ESA Ocean Colour CCI v6.0	Total absorption coefficient at 443 nm (Section 2.6, Station ALOHA)	4 km annual, 1998–2025, Station ALOHA box	Plymouth Marine Laboratory THREDDS server (oceancolour.org)

Every primary dataset used in this study, with the variables taken from it, its coverage and its accession or citation; all of these datasets are public.

2.2 Carbonate chemistry of the discrete casts

The aragonite saturation state of the discrete casts was computed with PyCO₂SYs v1.8 [10] from the primary SPOTS measurements [7]. Dissolved inorganic carbon was paired with measured total alkalinity where alkalinity exists, from 2014 onwards, and with the partial pressure of carbon dioxide (pCO₂) for the Iceland Sea and Irminger Sea records before 2014, when alkalinity was not measured at those stations. Every calculation used measured in-situ temperature, salinity, silicate, phosphate and pressure, the constants of Lueker et al. [11], Dickson [12] and Uppström [13] on the total pH scale, and samples from the shallowest 25 dbar (Additional file 1, Table S1). The two input pairs give Ω values that are not fully consistent, and the disagreement is largest in cold water [14, 15], so the step at 2014 in Figure 1 is a change in the analysis rather than in the ocean, and no slope is fitted across that change. Winter was taken as January to March in the Northern Hemisphere and July to September in the Southern Hemisphere.

Recomputing every cast from the primary data identified a processing error in an earlier version of this analysis. From 1995 the archived pCO₂ at these stations appears to be reported at a fixed laboratory equilibration temperature of 4 °C rather than at in-situ temperature, and treating that value as the measurement temperature introduced a spurious step at 1995 of about +0.28 Ω in the Iceland Sea and -0.22 Ω in the Irminger Sea. The stored-sample protocol introduced in mid-1993 is described by Ólafsson et al. [16], and the interpretation of 4 °C is inferred from internal evidence (Additional file 1, Note S1). Taking the archived value at in-situ temperature removes the step and brings the implied alkalinity into agreement with the alkalinity measured from 2014, with an alkalinity-to-salinity ratio of 65.9 against a measured 65.7. The corrected casts also lie within about 0.12 Ω of the independent gridded field in every period. Trends before 2014 were fitted by least squares against time alone and, for comparison with the published record, by multivariate regression on time and temperature, and the results are insensitive to surface cutoffs from 10 to 30 dbar.

2.3 Zonal ecological reference thresholds

A single global threshold cannot serve every ocean, because coral reefs and polar pteropods respond at very different saturation states. Each cell of the winter field was therefore compared with the threshold of its own latitude zone. Poleward of 50°, the threshold is Ω 1.6, set at the upper edge of the biological marginal zone of about Ω 1.2 to 1.5, in which bivalve larvae show a response [17] and pteropods are considered to be negatively affected [18], and consistent with the low saturation already measured in these waters [19]. Equatorward of 30°, the threshold is Ω 3.3, the saturation at which net carbonate accretion on reefs approaches zero [20]. Between those bands the threshold is Ω 2.4, the midpoint of the two anchored values, which is a stated choice rather than a measurement, because the temperate band holds a mixed calcifier community with no single measured threshold. This zonation is scheme A, which is the scheme shown in Figure 2. Scheme B moves the band boundaries poleward to 55° and 35°, and scheme C restricts the reef threshold to within 23.5° of the equator, so that the three schemes together give the structural range of the estimate.

2.4 Winter threshold analysis and projections

The winter field was built from the OceanSODA-ETHZ aragonite saturation [5] as the February value north of the equator and the August value south of the equator for each of the 43 years from 1982 to 2024, on the native 1° grid, and the mean of the 2022–2024 winters is the reference present state. The single coldest month is used because this analysis classifies exposure, the saturation that an organism meets at the seasonal minimum, rather than fitting a trend. Repeating the classification on a three-month winter mean lowers the share of the ocean below its threshold from 43.7% to 42.6%, a difference of 1.1 percentage points, and lowers the share at each projected date by 0.3 percentage points or less. The mapped winter field agrees with the discrete winter casts to within about 0.01 to 0.12 Ω where both exist (Additional file 1, Note S1).

A linear trend was fitted in every cell by ordinary least squares against year, using 43 points per cell and excluding cells with any missing winter value. The projections to 2035, 2045 and 2055 apply that trend to the reference field over 9, 19 and 29 years counted from 2026, which omits about three years of trend and therefore understates the change, and no acceleration or deceleration is assumed. Areas are weighted by the cosine of latitude in every calculation of this kind. Seasonally ice-covered cells are not mapped by the product and carry no fitted trend, so for the polar and subpolar zone we report the measured present state rather than a projection restricted to that zone.

2.5 Statistical analysis and uncertainty

Three independent sources of uncertainty were quantified for the percentage of mapped ocean below its zonal threshold. Measurement uncertainty was propagated from the product's own per-cell reported uncertainty by Monte Carlo simulation, using 500 Gaussian perturbations of the 2022–2024 mean field. Spatial sampling uncertainty was obtained by a block bootstrap of 10° by 10° blocks with 5,000 resamples, so that spatially correlated neighbouring cells are not treated as independent evidence. Structural uncertainty is the range across zonation schemes A to C, and we quote this range in the text because it is the widest of the three. Per-cell winter trends were tested against a null slope of zero, and significance was also assessed on a spatially thinned subsample of every fifth cell in latitude and longitude, which gives 1,329 quasi-independent cells at roughly 5° spacing, with a Wilcoxon signed-rank test of the median trend. Percentages are quoted to the nearest whole point, with 57.5% given as 57% so that the projection is not overstated. The whole classification pipeline was independently re-implemented and reproduces every reported point estimate exactly.

2.6 Light attenuation and absorption at Station ALOHA

To test one prediction of the hypothesis set out in Section 4.5, we examined satellite optics at Station ALOHA, an oligotrophic site in the North Pacific subtropical gyre where surface chlorophyll shows no trend in three decades of water samples [21]. Monthly 4 km products of the diffuse attenuation coefficient K_d490 and of chlorophyll-a from MODIS-Aqua (NASA R2018.0, served by NOAA OceanWatch ERDDAP) were averaged as geometric means over a box of 6° latitude by 8° longitude around the station, using all months. Trends over 2003 to 2021 were fitted by ordinary least squares, with p values corrected for first-order autocorrelation. Total absorption at 443 nm was taken for the same box from the ESA Ocean Colour CCI v6.0 annual product of inherent optical

properties over 1998 to 2025. Satellite attenuation and chlorophyll are derived from the same blue-green reflectance ratio, so attenuation adds information only where it departs from chlorophyll, and for that reason the test uses a site with no chlorophyll trend.

2.7 Biocurve construction

No census of global marine animal life exists, either for today or for 1850, and none is in prospect. We therefore built an openly documented index, the biocurve, as a weighted mean of the fraction of each animal group remaining against an 1850 baseline of 100%, $\text{Nature}(t) = \Sigma(w_i \cdot r_i) / \Sigma w_i \times 100\%$, with every r_i equal to 1 in 1850. Thirteen groups enter with the importance weights and documented fractions listed in Additional file 1, Table S4, and each fraction is referenced to its published source in Table 2. The importance weighting gives most weight to apex, structural and calcifying groups, and equal weights and a production weighting were computed as alternatives (Additional file 1, Table S5). The index covers animal life in the upper 200 m and excludes the mesopelagic zone, an exclusion that runs in one direction, because counting the deep layer would raise the index.

The 1850 value is definitional, and the present value is the only point computed directly from data. The 1900, 1950 and 1985 values are an interpolation positioned by the periods of the documented declines, drawn from 1950 as $R(t) = 69 - 33.6 \times ((t - 1950)/73)$ raised to the power 1.4, in which the exponent is a stated choice. Groups whose records begin after 1850 are treated as though their published decline were the whole decline, so the index overstates what remains and should be read as an upper bound on surviving structure. The full construction and its sensitivity tests are given in Additional file 1, Note S3.

2.8 Grading of evidence

Because the argument combines measurement, established chemistry and inference, we grade every claim in four tiers. Established claims rest on direct measurement or on chemistry that is not in dispute. Demonstrated claims are shown in engineered seawater systems but not yet at the scale of the ocean. Hypothesised claims follow from established chemistry but have not been observed in the open ocean. Scenarios follow from ecological theory rather than from measurement, and they are labelled as scenarios wherever they appear.

2.9 Use of artificial intelligence

The authors used Claude (Anthropic), a large language model, as an assistant for compiling published values, processing the OceanSODA-ETHZ and SPOTS data, recomputing the carbonate system, preparing figures and checking consistency. Every numeric claim was checked against its primary source or re-derived from the primary data, and the authors directed, verified and approved all analyses and conclusions and take full responsibility for the content of this study.

3 Results

3.1 Winter saturation at the cold-water time-series sites

The Iceland Sea holds the longest carbonate record of the cold-water basins considered here. Ólafsson et al. [22] measured a decrease in winter surface Ω of 0.0072 ± 0.0007 per year between 1985 and 2008, from about 1.6 to about 1.5, with winter surface pH falling by 0.0024 ± 0.0002 units per year. The OSPAR assessment [23] extends these results, with an Iceland Sea trend of about 0.006Ω per year over 1985 to 2020 and an Irminger Sea trend of about 0.012Ω per year over 1983 to 2020. It records Iceland Sea Ω at or around 1.5 in the 1980s, with seasonal minima reaching about 1.3 since 2015, while the Irminger Sea has only started to reach values below 1.5 seasonally over the past decade.

Over the internally consistent record before 2014, the recomputed Iceland Sea winter series declines at $-0.0046 \pm 0.0007 \Omega$ per year on a simple fit against time ($n = 57$, $p < 10^{-8}$), while the Irminger Sea is statistically flat over the same period ($-0.0014 \pm 0.0009 \Omega$ per year, $n = 51$, $p = 0.13$; Figure 1). The flat Irminger record shows that the fitting method does not manufacture declines, so the significant trend in the Iceland Sea belongs to the water rather than to the method. With the multivariate regression on time and temperature, the recomputed 1985–2008 casts reproduce the published temperature-adjusted Iceland Sea trend of $-0.0072 \pm 0.0007 \Omega$ per year [22] within the combined uncertainty (Additional file 1, Note S1).

Of the four cold-water basins, the Iceland Sea, the subarctic North Pacific and the Southern Ocean already sit at or below Ω 1.6 in winter, while the warmer Irminger Current water sits just above that threshold. The subantarctic site at Munida, off New Zealand, reads about Ω 2.0 in water about 9°C warmer than the polar sites, which is consistent with the relation across the neighbouring mapped cells of about 0.08Ω per degree Celsius (Additional file 1, Note S1). Station K2 and Munida have too few winter casts to support a fitted trend, so their long-term rates come from the mapped product [24, 25] (Additional file 1, Table S3).

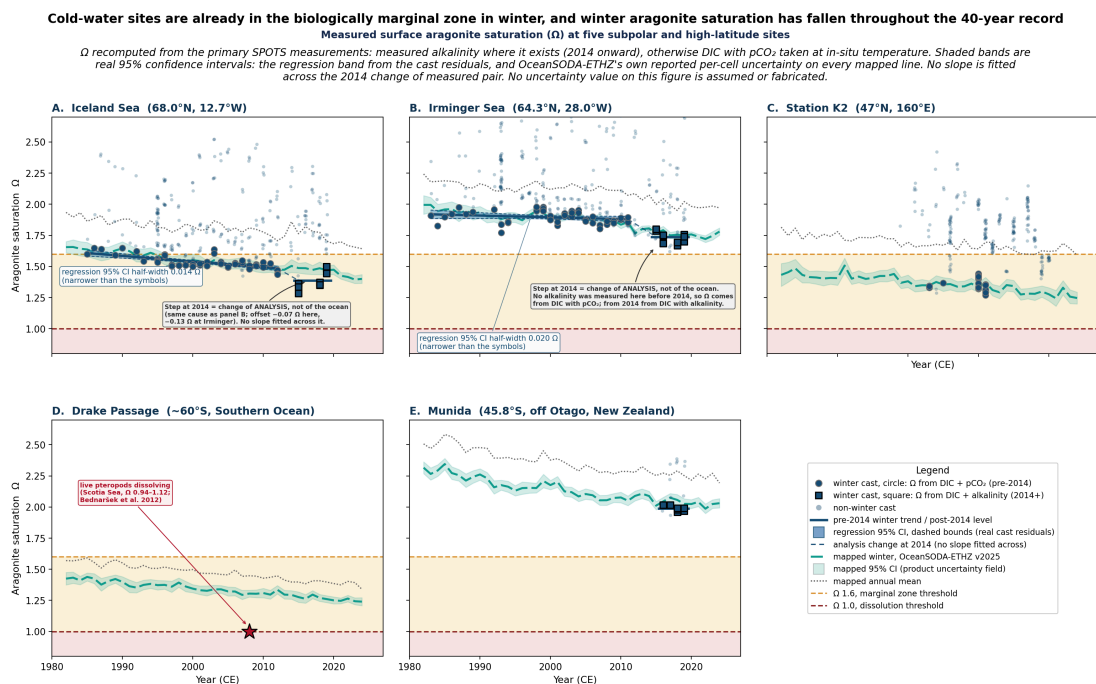


Figure 1 Measured winter surface aragonite saturation at five subpolar and high-latitude sites

Panels show the Iceland Sea (A), the Irminger Sea (B), Station K2 (C), Drake Passage (D) and Munida (E). Circles show discrete winter casts before 2014, computed from dissolved inorganic carbon with the partial pressure of carbon dioxide; squares show casts from 2014 onwards, computed from dissolved inorganic carbon with measured alkalinity. Dark blue shows the winter regression before 2014 with its 95% confidence band and the mean level after 2014; no slope is fitted across 2014, because the change of input pair introduces an analytical offset. Teal dashed lines show the mapped OceanSODA-ETHZ winter mean with its 95% band [5], grey dotted lines show the mapped annual mean, and faint small circles show casts outside winter. Winter is January to March in the Northern Hemisphere and July to September in the Southern Hemisphere. Drake Passage has no sustained discrete record, so only the mapped product is shown there. Methods and cast counts are given in Additional file 1, Note S1.

3.2 Share of the winter ocean below its ecological threshold

Under scheme A, 43.7% of the mapped ocean surface, or about 44%, was below its zonal threshold in the 2022–2024 winters (Figure 2). The Monte Carlo interval on this figure is 43.7 to 43.9% and the bootstrap interval is 39.6 to 47.8%, against a structural range of 36.9 to 52.5% across the three zonation schemes (Additional file 1, Table S2). Scheme C lowers the present figure to 37% and scheme B raises it to 52%, so the finding that two-fifths to one-half of the winter ocean surface is at or near its threshold does not depend on where the lines are drawn, although the exact percentage varies within that range. Extending each cell's own 43-year trend, an estimated 49% will be below its threshold by 2035, 57% by 2045 and 65% by 2055, with bootstrap half-widths of about 4 percentage points at every horizon.

Poleward of 50°, 79.1% of the cosine-weighted area was below Ω 1.6 in the 2022–2024 winters, and poleward of 55° the share was 88.0%. Because that water is already below its threshold, it will have been below for more than a decade by 2035, with no extrapolation required.

Winter saturation declined in almost every cell of the ocean over 1982 to 2024. In the thinned subsample, 99.8% of cells show an individually significant negative trend ($p < 0.05$), and a Wilcoxon signed-rank test rejects a zero median trend ($p < 0.001$). The area-weighted mean trend is -0.073Ω per decade and the median is -0.072Ω per decade, consistent with the global trend of $-0.071 \pm 0.006 \Omega$ per decade over 1982 to 2021 that Ma et al. [26] obtained from an earlier version of the same product.

The water below its threshold is not randomly distributed across the ocean surface. At every latitude it coincides with the productive upwelling and high-nutrient regions, namely the eastern equatorial Pacific, the Arabian Sea, the eastern boundary systems and the subpolar basins, while the unproductive gyre cores remain above threshold. The two persistent high-nutrient, low-chlorophyll regions, in the Southern Ocean and the subarctic North Pacific, lie within this low-saturation water, where iron deficiency limits primary production and leaves nutrients unused [27, 28].

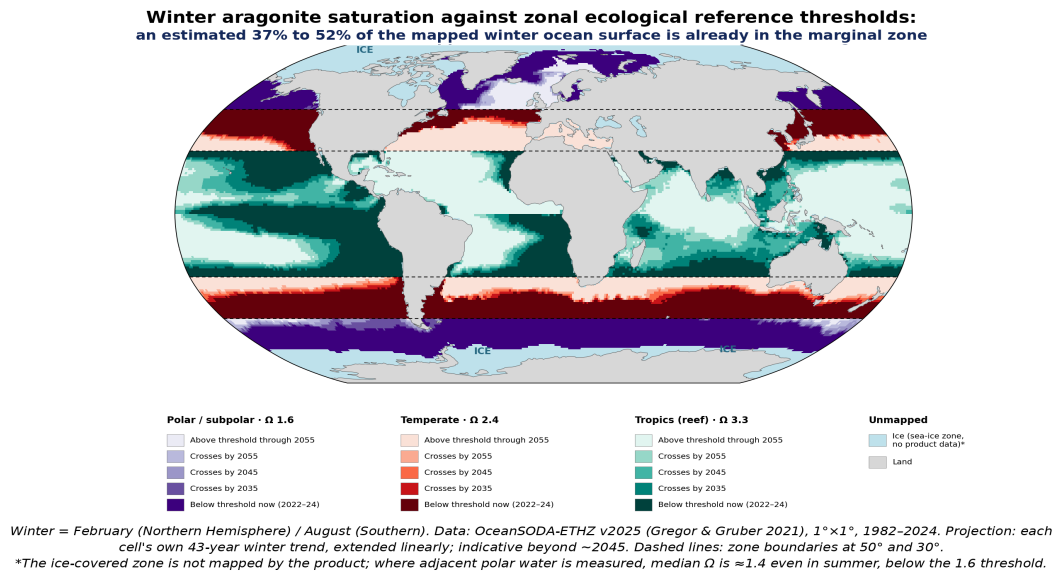


Figure 2 Winter surface aragonite saturation compared with zonal ecological reference thresholds

The colour family gives the zone and its threshold: purple for polar and subpolar water (Ω 1.6) [19], red for temperate water (Ω 2.4, a stated interpolation) and blue-green for tropical reef water (Ω 3.3) [20]. Shading gives status, from below the threshold in the 2022–2024 winters (darkest), through the projected decade of crossing (2035, 2045, 2055), to above the threshold through 2055 (palest), from the 1982–2024 winter trend of each cell [5]. Winter is February in the Northern Hemisphere and August in the Southern Hemisphere. Pale blue marks the sea-ice zone that the product does not map; where adjacent polar water is measured, its median Ω is about 1.4, even in summer. Projections are linear and should be read as indicative beyond about 2045.

3.3 Documented declines and the biocurve

Table 2 lists the documented declines in marine animal life and calcifiers since 1850, each a published measurement or indicator. Wild marine mammals are down by about 70%, to roughly 30% of their 1850 level [29]. Fishing has cut the biomass of exploited marine fish by roughly half since pre-industrial times, leaving about 47% across large marine ecosystems by the time of peak catch [30]. Predatory fish of high trophic level declined by about two-thirds between 1880 and 2007 [31], oceanic sharks and rays by 71% between 1970 and 2018 [32], and monitored seabirds by about 70% between 1950 and 2010 [33]. Since the 1950s, living coral cover has halved, at least 63% of reef-associated biodiversity has declined, and catch per unit effort on reefs has fallen by 60% [34]. North Atlantic krill have roughly halved since 1958, mainly through warming and a squeezed habitat rather than acidification [35]. The marine Living Planet Index fell by 56% between 1970 and 2020 [36].

Table 2 Documented declines in marine animal life and calcifiers since 1850

Species / group	Approx. location	Time frame	Documented change (loss of nature)	Biocurve value at end of record (% of 1850). [†]	Reference
Predatory fish (trophic level ≥ 3.5)	Global	1880–2007	–67% (two-thirds)	45	[31]; cf. [37]
Planktonic foraminifera (calcite)	Global (Challenger→Tara)	1870s–2011	Shells thinner in every modern specimen: 48–76% in <i>N. dutertrei</i> , up to ~30% in <i>G. ruber</i> (4 scans, eastern equatorial Pacific, 1875 vs 2011).	43	[38]
Coral reefs (coverage, biodiversity, catch per effort)	Global tropics	1950s–2015	Cover ~–50%; biodiversity –63%; CPUE –60%	40	[34]
Exploited fish biomass (10 g–100 kg)	Large marine ecosystems	pre-industrial–1990s	To ~47% of pre-industrial (roughly halved)	52	[30]
Antarctic krill	SW Atlantic, Southern Ocean	1976–2003	38–81% per decade reported; contested (no significant decline 1976–2016).	48	[39, 40]; cf. [41]
Krill (euphausiids)	North Atlantic (subpolar)	1958–2017	–50%	39	[35]
Coccolithophore calcification	Gulf of Maine	2001–2018	0.4→0.2 mg C m ^{–3} d ^{–1} , ~–50% over 2001–2018 (coincides with a water-mass change and rising Ω ; not attributed to acidification)	39	[42, 43]
Pteropods (habitat suitability)	California Current System	1984–2019	Modelled exposure to $\Omega < 1.5$ water rose 9% → 49% (hindcast indicator)	38	[18]
Wild marine mammals	Global	1850–2020	To ~30% of 1850 (–70%)	37	[29]
Marine vertebrates (Living Planet Index)	Global	1970–2020	–56%, 1970–2020 (contested)	37	[36]; cf. [44]
Snow crab	E. Bering Sea	2018–2021	> 10 billion lost (starvation after marine heatwave)	37	[45]

Species / group	Approx. location	Time frame	Documented change (loss of nature)	Biocurve value at end of record (% of 1850). [†]	Reference
Oceanic sharks & rays	Global	1970–2018	–71%	39	[32]
Seabirds	Global	1950–2010	–70% (monitored populations)	43	[33]
Coastal & estuarine systems	12 estuarine/coastal systems	historical–late 20th C	>90% of formerly important species depleted, >65% of seagrass and wetland habitat destroyed; oyster reefs –85% globally [46].	49	[47]

Documented declines in marine animal life and calcifiers since 1850, ordered by the start of each record. Every row reports a published measurement or indicator; rows marked as indicators are calcification or habitat-suitability measures rather than abundance counts, and contested figures are cited with their counter-evidence. The fifth column gives the whole-ocean biocurve value (Section 2.7) at the date the record ends, not a property of that group. [†] The biocurve value is the weighted mean of the fraction of the 1850 level remaining across all documented groups (Additional file 1, Note S3), plotted in Figure 3. It is an interpretive synthesis of separately documented declines rather than a census, and the present value lies between about 35% (importance-weighted) and 54% (tonnage-weighted) of the 1850 level.

On the importance weighting, the biocurve stands at 35.4% of the 1850 level in about 2023, with a band of 28.5 to 44.7%; it is 48% with equal weights and 54% on a production weighting (Figure 3; Additional file 1, Table S5). The spread between those weightings reflects a real feature of the ocean, which now holds more raw weight of life than working structure, because the dominant zooplankton pool has declined by about half while apex and structural groups have lost two-thirds to three-quarters. Varying the exponent of the interpolation from 1.2 to 1.8, or replacing the power law with a straight line, moves the 1985 value only between 53 and 60%. Removing the coastal compartment and renormalising the weights moves the present value from 35.4 to 38.5%.

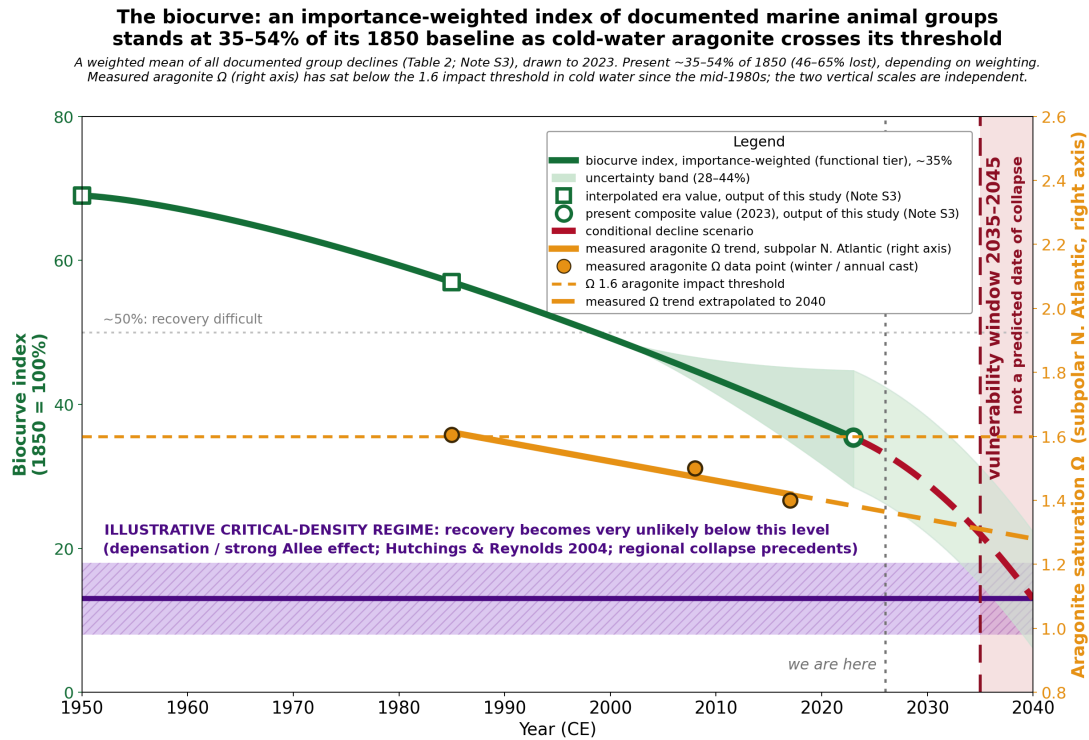


Figure 3 The biocurve, an index of documented declines in marine animal life since 1850

The index is expressed relative to its 1850 level of 100% and is drawn to about 2023 (Table 2; Additional file 1, Note S3), with subpolar North Atlantic aragonite saturation and the Ω 1.6 threshold on an independent right-hand axis. The curve is an interpretive synthesis rather than a census: open squares mark interpolated era values, the open circle marks the present composite, and the shaded band carries the uncertainty of the importance weighting. Filled orange points are measured aragonite casts, the solid orange line is their least-squares trend, and the dashed orange line extends that trend linearly to 2040, reaching about Ω 1.28. The red line is a scenario rather than a projection: it shows the direction that the theory of Section 4.6 permits if present pressures continue, and its entry into the illustrative critical-density regime (purple) is a stated choice rather than a computed value. The vertical band from 2035 to 2045 marks the period in which 49 to 57% of the mapped ocean is projected to be below its winter threshold (Figure 2); it is not a predicted date of collapse.

3.4 Light attenuation at Station ALOHA

At Station ALOHA, light attenuation in the MODIS-Aqua record rose by 3.1% over 2003 to 2021 ($p = 0.002$), while chlorophyll did not change significantly (+2.1%, $p = 0.61$), and the chlorophyll change accounts for about one fifth of the rise in attenuation. The merged ESA record shows no trend in total absorption at 443 nm at this site over 1998 to 2025, so coloured dissolved organic matter is not the cause of the darkening, and particulate backscatter is the only optical term that rose, although that rise is not itself statistically significant. A small change in attenuation at the surface compounds through the water column, and the fitted rise removes about 4% of the light at 50 m, 8% at 100 m and 11% at 150 m.

4 Discussion

4.1 Winter exposure and the limits of annual means

Biological thresholds are point-exposure relationships between the saturation that an organism meets and its response, established from animals in their natural water rather than from annual climatologies. The correct quantity to compare with them is therefore the saturation actually experienced, which in cold basins is the winter minimum, and comparing thresholds with an annual mean understates exposure. The point is practical rather than technical, because the change from one season to the next in these basins is as large as the underlying trend over several decades. In the Iceland Sea, the fitted trend explained 89% of the variance of the winter pH series but only 38% when all seasons were combined [22].

The measured winter state agrees with the wider literature on surface saturation. Poleward of about 60° north and south, many areas have surface Ω below 1.5, while between 40°N and 40°S the surface stays above 2.0 [48]. The Southern Ocean is the front line, where a shallow saturation horizon is projected to emerge suddenly this century [49, 50], shell dissolution is already observable in polar and upwelling waters [19, 51], and live pteropods have been observed to dissolve as Ω approaches 1.0 [52].

The coincidence of low saturation with productive water (Section 3.2) reflects one mechanism rather than chance, because upwelled deep water supplies both the nutrients that make these regions productive and the respired carbon dioxide that lowers their saturation. The waters that sustain the food web are therefore, everywhere, the closest to their biological limits. In the open equatorial upwelling, water below Ω 3.3 indicates this coupling rather than direct harm to reefs, which are coastal. The subpolar North Atlantic also holds the one region that has cooled while the rest of the ocean warmed, a pattern attributed to a weakening of the overturning circulation [53], and colder water sits at lower saturation, so part of the low baseline of that region is thermal. The anomaly extends well below the surface layer [54], which matters for the many plankton that spend the daylight hours in deeper, colder and more corrosive water than no surface product records.

4.2 Biological thresholds and calcifier responses

The link between reduced calcification and falling saturation has been recognised since Kleypas et al. [55], and the dissolution point, $\Omega = 1.0$, is not in dispute. In the California Current System, a strong upwelling region, a model hindcast shows the exposure of shelled pteropods to water below Ω 1.5 rising from 9% to 49% between 1984 and 2019 [18]. The measured biology matches that exposure, since 53% of pteropods sampled onshore show severe shell dissolution, against 24% offshore, in proportion to the undersaturated fraction of the water column [51]. When the same corrosive upwelled water entered Pacific Northwest oyster hatcheries from 2007, larval survival tracked the saturation of the intake water so closely that the industry now buffers and treats its seawater before use [56]. This evidence supports the use of Ω 1.6 as the threshold for polar and subpolar water in Figure 2.

Reef corals decline at a much higher saturation, with net carbonate accretion approaching zero around Ω 3.3 [20]. About a quarter of the sea-floor calcifiers studied already live in water that is undersaturated for their own skeletal mineral [57], and some authors contend that Ω is a proxy for

the true driver, the ratio of bicarbonate to hydrogen ions [58].

Skeletal mineralogy sets the likely order in which calcifying groups become vulnerable. The modern ocean is a high-magnesium aragonite sea, with a molar magnesium-to-calcium ratio of about 5.2, near the highest of the past 250 million years [59, 60], and a calcium content of about 10 mmol kg⁻¹, less than half of the Cretaceous value [61]. High-magnesium calcite, used by coralline algae and sea urchins, dissolves more readily than aragonite, and aragonite dissolves more readily than low-magnesium calcite [62, 63]. The expected order is therefore high-magnesium calcite builders first, aragonite builders next and calcite-shelled plankton last. We offer that order as a mechanistic expectation rather than a fitted relationship, because physiology often overrides mineralogy and some species calcify more under elevated carbon dioxide [63].

A threshold alone cannot capture the whole biological risk, because harm also depends on the duration of exposure and on the life stage exposed. Bednaršek et al. [19] project pteropod shell dissolution with thresholds that account for both the magnitude and the duration of exposure, for the early and middle life stages whose survival governs the population. Two waters with the same winter minimum are therefore not equivalent, since exposure during reproduction, settlement or moulting does more damage than exposure at a tolerant stage, and a month below the threshold does more damage than a week.

The eastern Bering Sea shows that duration and season are not abstract concerns. Its shelf ranks among the most productive and corrosive seas, because the decomposition of its large summer production, together with river runoff, removes carbonate from the bottom water [64]. A model hindcast for 1970 to 2022 finds that bottom water acidifies about twice as fast as surface water, that its pH has fallen to about 7.8, the level at which juvenile crabs begin to show symptoms in the laboratory, and that the shelf area with bottom water below that value grew from 5 to 10% before 2005 to more than half of the shelf by 2022 [65]. Surface water on the inner shelf is undersaturated for about half of the year [66, 67]. Juvenile red king crab (*Paralithodes camtschaticus* (Tilesius, 1815)) and Tanner crab (*Chionoecetes bairdi* Rathbun, 1924) reared at reduced pH show lower survival and growth [68], and juvenile snow crabs (*Chionoecetes opilio* (Fabricius, 1788)) held at pH 7.5 suffer about 40% higher mortality than at present-day pH [69]. The Bering Sea snow crab population then collapsed, with the loss of more than ten billion animals between 2018 and 2021, mainly through a marine heatwave and starvation rather than acidification [45]. The collapse is nonetheless a clear case of a productive cold-water fishery pushed past a biological limit in a sea where acidification has reached levels shown to harm the same animals.

4.3 Calcifying plankton

Planktonic foraminifera provide supporting evidence from a comparison that spans more than a century. Comparing shells from an 1875 Challenger station with 2011 Tara Oceans material from the eastern equatorial Pacific, Fox et al. [38] found every modern specimen thinner, by up to 76% in *Neogloboquadrina dutertrei* and by up to about 30% in *Globigerinoides ruber*. The comparison is a single before-and-after pair, but foraminifera build low-magnesium calcite, one of the most acidification-resistant biominerals, so a signal of carbonate stress there suggests that even the hardiest plankton are affected.

Coccolithophores show why a single record must be read with care. Their occurrence in the North Atlantic rose roughly tenfold, from about 2% to over 20% of Continuous Plankton Recorder samples between 1965 and 2010, a rise tentatively linked to rising carbon dioxide [70]. Where calcification itself has been measured over decades, in the Gulf of Maine, it fell from about 0.4 to about 0.2 mg C per cubic metre per day between 2001 and 2018 [42, 43]. That decline, however, coincided with a change in the water entering the gulf, as warm and salty slope water displaced cooler and fresher water, and aragonite saturation rose over the seven years with carbonate data, so the record shows that calcification can fall steeply within decades without being evidence of acidification harming calcifiers. Tropical coccolithophore calcification has been found to be independent of carbonate chemistry [71], and some strains calcify more under high carbon dioxide [72].

4.4 Acidification in an already depleted ocean

Acidification is not arriving in an intact ocean, and the record of loss is long (Table 2). Some widely quoted figures are disputed, and we use the cautious ones. The often-quoted 90% loss of large predatory fish [37] is widely considered too high [73–75]. A few fast-declining populations can pull the Living Planet Index down [44], while others argue that many populations are still in real decline [76]. A synthesis of formal stock assessments places the decline in the adult biomass of tunas and their relatives at 52% over 1954 to 2006 [77]. Reported falls in Antarctic krill (*Euphausia superba* Dana, 1850) of 38 to 81% per decade in the southwest Atlantic sector [39] are challenged as partly a sampling artefact [41, 78], although a circumpolar reanalysis still finds a decline in the Atlantic sector [79] and a later analysis reports a southward contraction of the range [40]. None of these disputes changes the direction of travel, because biomass models, stock assessments, mammal counts and plankton records all show a clear decline in marine animal life.

Direct human pressure, rather than acidification, caused most of these losses through industrial fishing, whaling, bottom trawling, the destruction of coral reefs, oyster reefs and mangroves, and widespread pollution. Climate disruption has added a growing share of the loss in recent decades, through ocean warming, marine heatwaves, coral bleaching and the loss of oxygen from the ocean [20, 80, 81]. Warming is the main driver of the halving of North Atlantic krill [35], and the collapse of the Bering Sea snow crab followed a marine heatwave and the starvation that came with the heatwave [45]. Coastal and estuarine systems carry the heaviest historical losses, with more than 90% of formerly important species depleted and more than 65% of seagrass and wetland habitat destroyed [47], and oyster reefs have declined by about 85% worldwide [46]. Removing the largest fish also weakens the biological carbon pump, because the carbon held in their bodies and sinking waste no longer reaches the deep sea [82, 83]. Acidification is therefore acting on communities already thinned by other pressures, and that is the condition in which its effects must be judged.

The biocurve is offered in this context as an interpretive baseline rather than a census. Declining to synthesise is not a neutral choice, because it leaves no quantified baseline against which later change can be read, and that is how each generation comes to accept a depleted state as normal [84]. Every input to the index is referenced to its source, and every value that is derived rather than measured is labelled as such. Our own field observations from a sailing passage of eighteen days across the tropical North Atlantic in the winter of 2022, which are anecdotal rather than systematic, are reported in Additional file 1, Note S4.

4.5 A hypothesised chemical cascade beyond the carbonate system

Aragonite saturation also tracks chemistry that sets the physical character of seawater, including its clarity and the ease with which a larva can move and feed. This section is a hypothesis, graded in the tiers of Section 2.8, and we set it out together with the observations that would confirm or refute the hypothesis. Two terms from colloid chemistry recur throughout the argument in this section. Zeta potential is the effective surface charge on particles, which decides whether they repel one another and stay suspended or coagulate and settle, and redox potential is the net tendency of the water to oxidise or reduce.

The established part of this argument is not in dispute in the chemical literature. Rising carbon dioxide lowers pH and carbonate ion concentration and consumes buffer capacity [85], and dissolved organic matter and inorganic colloids undergo pH-dependent charge neutralisation, coagulation and flocculation. As carbon dioxide diffuses through the surface microlayer, which can reduce gas transfer by up to about a third [86], pH falls, the zeta potential of suspended particles becomes less negative and metal solubility rises, while total alkalinity is unchanged. Because marine particles already sit close to the coagulation threshold in high-ionic-strength seawater, even a modest shift in charge can have an effect.

The demonstrated part of the argument comes from engineered seawater systems and aquaria. Ferric coagulation of organic matter and colloids is run at industrial scale in desalination pretreatment, where the high ionic strength of seawater compresses the electrical double layer [87], and the coagulation of dissolved organic matter improves as pH declines [88]. In our own unpublished operating records from public aquaria holding 20 million litres, these reactions accelerate over about ten hours when buffering is lost, with measurable declines in water quality and animal condition unless alkalinity, oxygen and redox potential are raised promptly. Aquaria are enclosed and intensively managed, so they show that the chemistry is real, fast and reversible, but they cannot show the rate or scale at which the same reactions would proceed in open water.

The hypothesised part is that a falling pH raises the colloidal load and the micro-viscosity of open-ocean water by an amount that matters for plankton. In a sea with an active organic cycle, bacterial respiration of organic matter lowers oxygen and pH together and consumes buffer capacity further [89], and the expected response of calcium-bridged marine gels [90] has not yet been measured at open-ocean pH. The final link of the chain has been confirmed in the laboratory, where a modest rise in viscosity at constant temperature slows the swimming and the feeding currents of planktonic larvae and small zooplankton [91, 92]. The link from falling pH to a higher colloidal load in the open ocean remains to be demonstrated, and no sustained ocean observing programme that we could identify records redox potential, zeta potential or particle size.

Iron is the element that links these chemical pathways most directly to productivity. It limits growth across the high-nutrient, low-chlorophyll regions that lie inside the low-saturation water [27], it is one of the most effective natural flocculants, and its chemical speciation is acutely sensitive to pH [93]. Acidification lowers the iron available to phytoplankton [94], while falling pH also speeds the reduction of ferric iron by dissolved polyphenols, so that reduced iron persists for longer [95]. A recent review concludes that the net direction for iron, copper and zinc depends on which pH-controlled pathway dominates [96], and the response of the whole photochemical iron cycle of the sunlit layer [97, 98] still needs dedicated study.

Coastal dead zones show where this sequence of reactions can end when it runs to completion. The world has more than 500 of them [80, 99], and where their carbonate chemistry has been measured, the hypoxic water is also acidified. Respiration of the eutrophication-driven organic load lowers the subsurface pH in the northern Gulf of Mexico and the East China Sea [89], and in Chesapeake Bay the bottom water reaches a pH of about 7.45 with aragonite saturation well below 1 [100]. Nutrient loading has crossed its own planetary boundary, at about three times the boundary for nitrogen and about twice the boundary for phosphorus [2]. The cascade also favours still water, and stratification has strengthened and ventilation weakened over the past half-century [101], while the oxygen content of the ocean has fallen [80, 81].

Satellite records offer a first and indirect test of the hypothesis. About 21% of the ocean darkened between 2003 and 2022, particularly in polar regions [102], and about 40% of the ocean changed colour over two decades [103], but at productive sites the darkening cannot be separated from greening, because satellite attenuation and chlorophyll share the same blue-green band ratio. The rise in attenuation at Station ALOHA without a matching rise in chlorophyll or absorption (Section 3.4) points to particles rather than dissolved matter. The particles are not identified, and a rise in biological supply is an equally plausible cause [21], so the observation is consistent with the hypothesis without confirming the hypothesis.

The hypothesis makes three testable predictions that existing programmes could check at modest cost. Adding redox potential, zeta potential, particle size and turbidity to the existing carbonate time-series stations would be inexpensive relative to the chemistry already collected there. A laboratory measurement of the coagulation response of natural seawater particles to a pH change of the size already recorded would test the central link directly. Over the coming decade, ocean-colour records can also test whether high-nutrient, low-chlorophyll conditions spread as saturation declines, which the hypothesis predicts but which has not yet been observed, since those regions have contracted at the poles since 2010 while chlorophyll there has risen [28].

4.6 Abrupt change and regional precedents

Three well-tested ideas explain why a sudden and lasting change of state is plausible in a thinned food web. Below a critical density, a strong Allee effect makes a population decline faster rather than more slowly [104, 105]. Diversity steadies fluctuating systems, so a food web that loses diversity also loses its buffer [106–108], even though complexity alone can destabilise a randomly assembled community [109]. Systems near a tipping point can shift abruptly, sometimes with early-warning signals that are hard to read [110, 111]. None of this makes such a change certain, but it means that a stressed food web may not simply continue its present trend.

One regional end state is what Jackson [112] called the rise of slime, a simplified, microbially dominated system with blooms of toxic dinoflagellates and jellyfish, in which the large animals are greatly reduced. This end state has already appeared regionally in several ocean basins. Off Namibia, the Benguela sardine (*Sardinops sagax* (Jenyns, 1842)) stock collapsed under overfishing and was replaced by jellyfish and the bearded goby (*Sufflogobius bibarbatus* (von Bonde, 1923)), a state that has persisted for decades even after fishing was sharply reduced [113, 114, 115]. In the Black Sea, pollution, overfishing and an invading comb jelly (*Mnemiopsis leidyi* A. Agassiz, 1865) turned the open water to jelly in the 1980s [116, 117], with only partial recovery after pollution fell

and a second invader reduced the comb jelly [118]. When Northwest Atlantic cod (*Gadus morhua* Linnaeus, 1758) collapsed in the early 1990s, forage fish, snow crab and shrimp took their place on the eastern Scotian Shelf [119], and like most collapsed fish stocks they showed little recovery within fifteen years [120, 121]. Recovery is sometimes possible, since North Sea herring (*Clupea harengus* Linnaeus, 1758) rebuilt after the fishery was closed and carefully managed [121, 122].

These precedents are regional, and a worldwide rise of jellyfish is not supported, since the available synthesis shows roughly twenty-year oscillations rather than a steady global increase [123, 124]. No mechanism is yet established by which regional shifts would propagate into a single global transition. A United Kingdom national security assessment published in 2026 nonetheless concludes, with high analytical confidence, that at current rates of biodiversity loss every critical ecosystem is on a pathway to collapse, while stating that it is not a scientific report and that its judgements on timing carry low confidence [125].

4.7 Limitations

Several limitations bound these results, and several of them would make the true exposure larger rather than smaller. The projections are linear extensions of 43-year trends, and they should be read as indicative beyond about 2045. The zonal thresholds are ecological reference values rather than lethal limits, and the temperate value is an interpolation, which is why we quote the structural range rather than a single figure. The analysis uses surface saturation, whereas many plankton spend the daylight hours in deeper and more corrosive water, and the sea-ice zone is not mapped, although adjacent polar water already lies below its threshold, so both omissions tend to understate exposure. Station K2 and Munida have too few winter casts for a fitted trend of their own. The biocurve is an interpretive synthesis of separately documented declines rather than a census, and its interpolated era values rest on a stated choice of curve. Finally, the chemical cascade of Section 4.5 remains a hypothesis, and the single optical result at Station ALOHA is consistent with the hypothesis without confirming the hypothesis.

5 Conclusions

The cold, productive waters that feed most of the marine food web are acidifying at rates that have persisted for four decades, and in winter they already sit at or below the threshold at which sensitive calcifiers respond. Judged at the winter minimum rather than the annual mean, about 44% of the mapped ocean surface is below its own ecological reference threshold, between 37 and 52% under every zonation scheme tested, and on the measured trends more than half will be below by 2045. The water nearest its biological limit is, everywhere, the water that sustains the food web.

This chemistry is acting on a marine system that fishing, whaling, habitat destruction, pollution and climate disruption had already reduced to roughly 35 to 54% of its 1850 level, on our interpretive synthesis. Acidification did not cause those losses, but it now adds to them in communities with little capacity to spare, where the mechanisms of abrupt change are present vulnerabilities rather than distant possibilities.

We draw four practical conclusions for monitoring, reporting and management from this study. First, ocean acidification should be treated as an active component of cumulative marine risk now, not solely as a future concern. Second, saturation should be reported at the winter minimum and

with the duration of the corrosive season, alongside annual means, because biological thresholds are defined by exposure. Third, redox potential, zeta potential and particle measurements should be added to existing carbonate time-series stations, so that the hypothesised chemical cascade can be tested rather than argued. Fourth, because reversal becomes a matter of rebuilding once critical densities are crossed, the protection and restoration of productive cold-water and coastal systems should begin while recovery remains possible. It is no longer sufficient to do no harm, and the systems that remain now need active restoration.

Abbreviations

CCI: Climate Change Initiative

CODAP-NA: Coastal Ocean Data Analysis Product in North America

ERDDAP: Environmental Research Division's Data Access Program

ESA: European Space Agency

GLODAP: Global Ocean Data Analysis Project

JAMSTEC: Japan Agency for Marine-Earth Science and Technology

Kd490: diffuse attenuation coefficient at 490 nm

MODIS: Moderate Resolution Imaging Spectroradiometer

NCEI: National Centers for Environmental Information

NOAA: National Oceanic and Atmospheric Administration

OCADS: Ocean Carbon and Acidification Data System

pCO₂: partial pressure of carbon dioxide

SPOTS: Synthesis Product for Ocean Time Series

Ω: aragonite saturation state

Declarations

Ethics approval and consent to participate

Not applicable, because the study used only published and publicly archived data.

Consent for publication

Not applicable, because the manuscript contains no data from any individual person.

Availability of data and materials

The datasets supporting the conclusions of this article are available in the NOAA National Centers for Environmental Information repository, OceanSODA-ETHZ v2025, accession 0220059, <https://doi.org/10.25921/m5wx-ja34>, and in the Zenodo repository,

<https://doi.org/10.5281/zenodo.21970808>. The Zenodo deposit holds the recomputed cast-level saturation values, the winter threshold grids, the uncertainty ensembles and all analysis and figure code under a CC BY 4.0 licence. Every other primary dataset used in this study is public and is listed in Table 1 with its accession or citation.

Competing interests

The authors declare that they have no conflict of interest. Both authors are affiliated with the GOES Foundation, a non-profit marine science and conservation organisation. Howard Dryden founded Dryden Aqua Ltd and is the inventor of AFM activated filter media; he retired from the company in 2022 and has since sold his entire shareholding, so he holds no financial interest in the company. That background in water treatment is the source of the colloid and coagulation chemistry applied in this study.

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Authors' contributions

Howard Dryden and Diane Duncan jointly conceived and designed the study reported here. Howard Dryden compiled and analysed the data, computed the saturation values, built the figures and the biocurve, and drafted the manuscript. Diane Duncan contributed the biological interpretation and revised the manuscript, and both authors approved the final version.

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