

Recurrent jellyfish blooms are a consequence of global oscillations

Robert H. Condon^{a,1}, Carlos M. Duarte^{b,c}, Kylie A. Pitt^d, Kelly L. Robinson^{a,e}, Cathy H. Lucas^f, Kelly R. Sutherland^g, Hermes W. Mianzan^h, Molly Borgeberg^a, Jennifer E. Purcellⁱ, Mary Beth Decker^j, Shin-ichi Uye^k, Laurence P. Madin^l, Richard D. Brodeur^m, Steven H. D. Haddockⁿ, Alenka Malej^o, Gregory D. Parry^{p,2}, Elena Eriksen^q, Javier Quiñones^r, Marcelo Acha^h, Michel Harvey^s, James M. Arthur^d, and William M. Graham^t

^aDauphin Island Sea Laboratory, Marine Environmental Sciences Consortium, Dauphin Island, AL 36528; ^bUniversity of Western Australia Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia; ^cDepartment of Global Change Research, Instituto Mediterráneo de Estudios Avanzados, Universidad de las Islas Baleares y el Consejo Superior de Investigaciones Científicas, 01790 Esporles, Spain; ^dAustralian Rivers Institute and Griffith School of Environment, Griffith University, Gold Coast Campus, QLD 4111, Australia; ^eDepartment of Marine Sciences, University of South Alabama, Mobile, AL 36688; ^fNational Oceanography Centre Southampton, University of Southampton, Southampton SO14 3ZH, United Kingdom; ^gDepartment of Biology, University of Oregon, Eugene, OR 97403; ^hConsejo Nacional de Investigaciones Científicas y Técnicas de Argentina, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata B7602HSA, Argentina; ⁱShannon Point Marine Center, Western Washington University, Anacortes, WA 98221; ^jDepartment of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520; ^kDepartment of Environmental Dynamics and Management, Hiroshima University, Higashi-Hiroshima 739-8528, Japan; ^lWoods Hole Oceanographic Institution, Woods Hole, MA 02543; ^mNorthwest Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries, Newport, OR 97365; ⁿMonterey Bay Aquarium Research Institute, Moss Landing, CA 95039; ^oMarine Biology Station Piran, National Institute of Biology, 6330 Piran, Slovenia; ^pDepartment of Primary Industries, Victorian Fisheries, Queenscliff 3225, VIC, Australia; ^qInstitute of Marine Research, 5817 Bergen, Norway; ^rLaboratorio Costero de Pisco, Instituto del Mar del Perú, Paracas, 11550 Ica, Peru; ^sDirection des sciences océaniques et de l'environnement, Institut Maurice-Lamontagne, Pêches et Océans Canada, Mont-Joli, QC, Canada G5H 3Z4; and ^tDepartment of Marine Science, University of Southern Mississippi, Stennis Space Center, MS 39529

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A perceived recent increase in global jellyfish abundance has been portrayed as a symptom of degraded oceans. This perception is based primarily on a few case studies and anecdotal evidence, but a formal analysis of global temporal trends in jellyfish populations has been missing. Here, we analyze all available long-term datasets on changes in jellyfish abundance across multiple coastal stations, using linear and logistic mixed models and effect-size analysis to show that there is no robust evidence for a global increase in jellyfish. Although there has been a small linear increase in jellyfish since the 1970s, this trend was unsubstantiated by effect-size analysis that showed no difference in the proportion of increasing vs. decreasing jellyfish populations over all time periods examined. Rather, the strongest nonrandom trend indicated jellyfish populations undergo larger, worldwide oscillations with an approximate 20-y periodicity, including a rising phase during the 1990s that contributed to the perception of a global increase in jellyfish abundance. Sustained monitoring is required over the next decade to elucidate with statistical confidence whether the weak increasing linear trend in jellyfish after 1970 is an actual shift in the baseline or part of an oscillation. Irrespective of the nature of increase, given the potential damage posed by jellyfish blooms to fisheries, tourism, and other human industries, our findings foretell recurrent phases of rise and fall in jellyfish populations that society should be prepared to face.

decadal cycles | synchrony

Concern about the deterioration of the world's oceans is supported by several lines of evidence (1–4), including decline of key ecosystems (5–7), depletion of fish stocks (8), the global expansion of hypoxia (9), eutrophication (10), ocean acidification (11), and increasing incidence of jellyfish blooms (1). Most of these changes have been documented by global assessments. In contrast, the perception that jellyfish blooms are increasing globally is largely based on reports of increases in a few disparate regions (12) [e.g., Bering Sea, the Sea of Japan, the Benguela Current, and the Black Sea (13–16)], and on an analysis of media reports and perceptions of scientific experts and fishers (17). An alternative hypothesis, that recent increases in jellyfish may be part of long-term cycles in jellyfish populations (18–20), has not been examined globally. Hence, the question of whether jellyfish populations are rising globally awaits a rigorous analysis (12). Here, we synthesized all available long-term time series of annual jellyfish abundances (Fig. 1 and Table S1) to test the null hypothesis

that jellyfish population sizes and the occurrence of blooms have not significantly increased in the world's oceans. We conclude that although there has been a weak but significant overall increase in jellyfish since the 1970s, the perceived global increase in jellyfish over the past decade coincided with the most recent rising phase of a pattern of decadal oscillations in jellyfish populations that have occurred for at least a century.

We gathered all available published and unpublished long-term time-series on jellyfish abundance across the oceans (Table S1). For simplicity, the term “jellyfish” is used synonymously with gelatinous zooplankton, and includes medusae, ctenophores, and pelagic tunicates. The datasets encompassed multiple metrics of abundance across different sampling frequencies (Table S1); therefore, each dataset was standardized to an annual mean of 0 and SD of 1 to create a jellyfish index, allowing comparisons among diverse metrics (21). Because previous long-term studies of jellyfish abundance have indicated decadal-scale variability (18–20), we only included observational series exceeding a decade.

Thirty-seven datasets were obtained including observations between 1790 and 2011, representing 1,140 observation-years of jellyfish abundance, with a mean and median length of 31 and 23 y, respectively (Fig. 1). Data between 1790 and 1874 were excluded from analyses because only five datapoints were collected during that period. Twenty-eight datasets (76%) used abundance or biomass units with most other datasets based on indices, including presence/absence and relative abundance data. In addition, most datasets were from the northern hemisphere (87%), in particular the Atlantic Ocean (17%) and the Mediterranean

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¹To whom correspondence should be addressed. E-mail: rcondon@disl.org.

²Present address: Department of Biology, Monash University, Clayton 3178, VIC, Australia.

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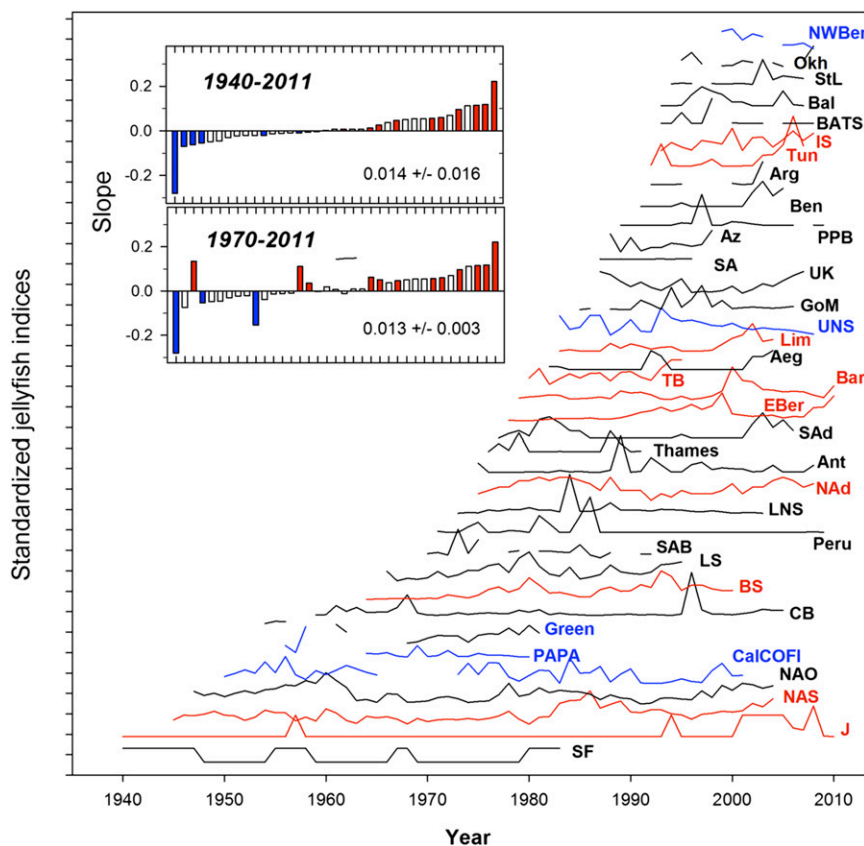


Fig. 2. Individual time-series of standardized jellyfish abundance from 1940 to 2011. Line colors show significant increase (red), decrease (blue), and no significant change (black) in jellyfish abundance over time (t test, $P < 0.05$). (Inset) The slopes of linear regressions for individual time series calculated over time periods of 1940–2011 and 1970–2011. Colored bars signify negative (blue) and positive (red) slopes; open bars show no significant deviation from 0 (t test, $P < 0.05$). Abbreviations of regions included in analysis and regression statistics are in Tables S1 and S2. Fig. S1 shows the three presence/absence datasets commencing before 1940.

The strongest nonrandom effect was that jellyfish indices showed significant oscillations from 1940 to 2011 with a periodicity of ~ 20 y in both linear and logistic mixed models (i.e., nonlinear component in mixed models, $P < 0.01$, $n = 1,007$) (Table S2), implying that residuals were not randomly distributed across the standardized mean of zero (Runs test; $P = 0.001$ and $P = 0.02$ for standardized and logistic data, respectively; $n = 71$). These oscillations involved three minima (1951, 1971, and 1993) and three maxima (1957, 1985, and 2004) (Fig. 3), with the rates of change in standardized jellyfish indices during consecutive rise and fall periods being an order-of-magnitude greater than the significant linear increase from 1970 (increase periods: 0.12 ± 0.08 SD yr^{-1} ; decrease periods: 0.10 ± 0.03 SD yr^{-1}). A recent decline in jellyfish indices also hinted at the possible onset of a negative phase after the maximum in 2004 (Fig. 3 *A* and *B*).

The probability of occurrence of extreme abundances (i.e., >90 th percentile) over time also exhibits approximately decadal oscillations, with periods when the probability of encountering extreme events was above and below the 10% expected by chance (Runs test; $P = 0.001$; $n = 71$) (Fig. 3C). Only 1 of 37 regions examined (Sea of Japan) exhibited a significant increase in blooms over time (Table S4). All of these patterns remained when pelagic tunicates and ctenophores were excluded from the analysis, suggesting that data on medusae could explain these global oscillations for at least the past century and the small linear increase from 1970 (Fig. S2).

Overall, most of the variance (85%) in standardized jellyfish abundance indices represented stochastic variability that could not be explained by either the oscillation or weak linear trend. Whereas a robust apportioning of the variance between oscillations and the

linear trend from 1970 to 2011 is not possible because of analytical limitations imposed by the nature of the data (see above), results showed that the oscillation signal is much stronger than the linear trend. Although the 20-y oscillation is present across all time windows, the linear trend was only significant since 1970. Provided a significant oscillation was present with a period of about 20 y, examination of trends at increasingly narrower windows of time carries increasing risk of aliasing the signal. In particular, the weak linear trend detected in the analysis over the past four decades may be an artifact because of the analysis including two or fewer cycles. Indeed, the trend seems to be determined by a relatively shallow minimum in 1993. Whereas this finding could signal at a recent change in baseline, a robust conclusion regarding the baseline must wait until a new minimum is reached in the future, confirming or refuting the apparent increase in baseline.

The complete analyses presented here (i.e., the mixed-model and effect-size analyses combined) do not provide a sufficient basis to reject the overall null hypothesis that jellyfish populations have not significantly increased globally (Fig. 3), with medusae providing the strongest indication of a possible increase. Nevertheless, despite our analysis being the most comprehensive yet conducted, it may be prone to type II errors because of the small number ($n = 37$) of locations where long-term time series of jellyfish abundance were available, their nonrandom spread, and the variable time windows covered by the different time series (Fig. 1). Moreover, a sizeable fraction (27%) of locations experienced increases, but 16% of the datasets also decreased, with the magnitude of change in locations with increases being similar to those supporting decreases. Increasing the precision of the analysis may be possible by use of a larger sample set. Many marine monitoring

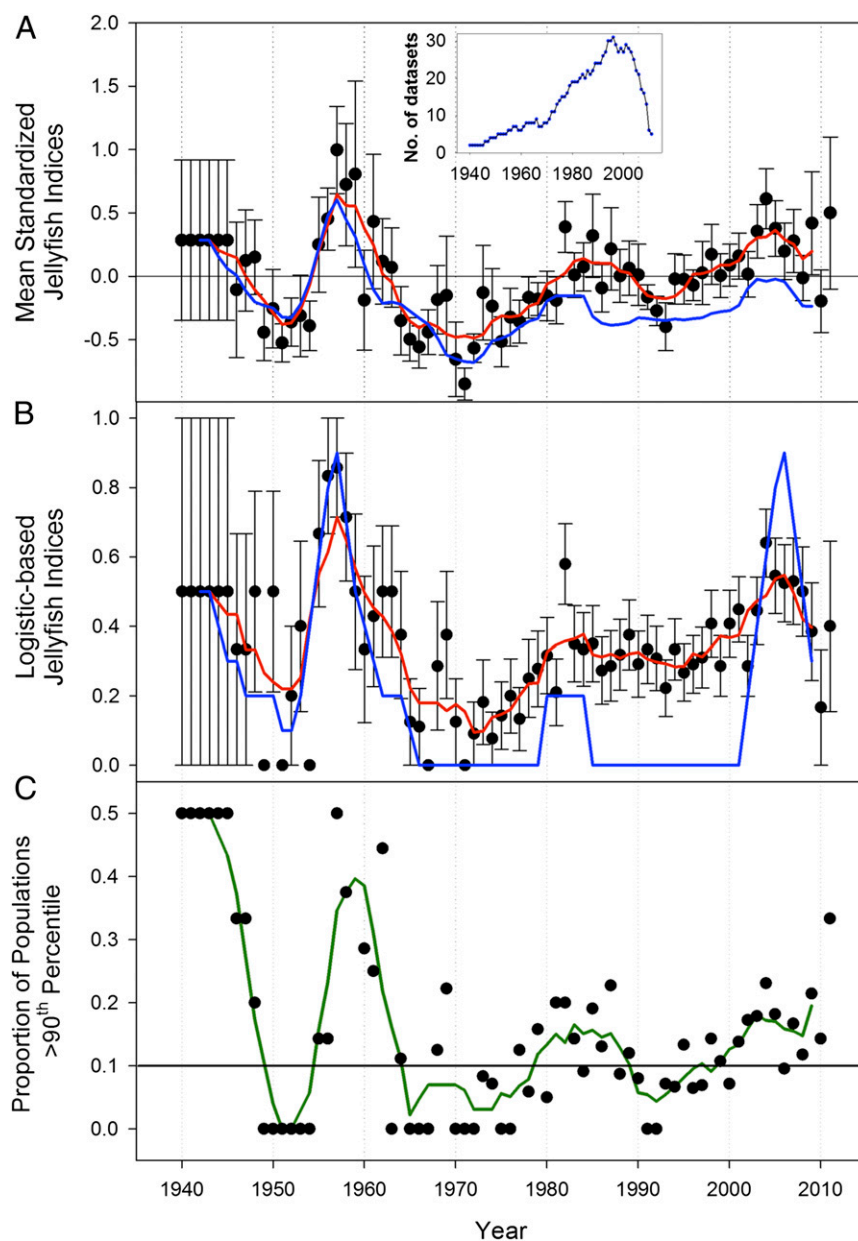


Fig. 3. Global oscillations of jellyfish. (A) Mean standardized and (B) mean logistic (binary) jellyfish indices, and (C) the probability of encountering maximum abundances of jellyfish for the global dataset between 1940 and 2011. Maximum abundance is defined as years when abundance exceeded the 90th percentile within each time series. The solid lines show a 5-y running average for annual mean (red and green) and median (blue) values. The 2 y occurring after 1940 and before 2011 are excluded from the running mean and median calculations because of incomplete data to calculate 5-y running means. *Inset* in A indicates the number of locations sampled over time. Error bars are ± 1 SE.

programs collect samples or data on jellyfish abundance, but do not analyze or report them, as those data are often a byproduct of fisheries programs. Indeed, some of the datasets included here were from fisheries sampling programs where long-term data on jellyfish abundance had not been previously reported (e.g., Peruvian upwelling). Increasing the sample size may increase the power of our time-series analysis, but both a strong linear trend and net increase in effect size should have been detected if present, as it includes all of the case studies suggesting a possible global rise (Table S1). Rather, our analyses yielded no detectable difference in the effect size (median test) (Table S3), suggesting the small but significant linear increase from 1970 was not driven by a net difference in the proportion of increasing vs. decreasing jellyfish populations.

Decadal Oscillations in Global Jellyfish. Although a weak, monotonic trend was present in our global analysis over the past 40 y, jellyfish abundance showed strong decadal oscillations over the entire time-series that explained 15% of the variance in the linear trends (Figs. 2 and 3). In particular, at least two periods of increased likelihood of encountering jellyfish blooms emerged from our results (1971–1985 and 1993–2004). The first period did not lead to scientific claims of increasing jellyfish blooms, but the second one did (17), prompting a number of papers published over the past decade that address the apparent increases in jellyfish blooms (3, 23–25). Despite a weak but significant increase in jellyfish from 1970, we suggest that the rise between 1971 and 1985 may not have led to widespread awareness because of limited research on jellyfish populations then [$\sim 2\%$ of the annual

publication rate during the past decade (12)], less awareness of global-scale problems, and a lower capacity (e.g., no internet-based data sharing) to examine ecological processes at the global scale. However, evidence of concern during earlier rising phases exists, including the Jellyfish Control Act passed by the US Congress in 1966 and two workshops on jellyfish blooms in the Mediterranean Sea (26).

The perception of a global rise in jellyfish, possibly prompted by more jellyfish blooms in the 1990s, may therefore be best interpreted as part of an oscillation (Fig. 3). For example, the expansion of gelatinous organisms in the Black Sea, involving extensive blooms of *Mnemiopsis leidyi*, collapsed in the late 1990s (16) (Fig. 2). The rise in jellyfish in the Bering Sea, initially interpreted as a consequence of climate change (27), subsequently returned to low or moderate levels (19) (Fig. 2), although recent reports indicate another rise of jellyfish in this region (28). Our analyses show that some coastal zones are experiencing enhanced blooms of medusae, such as the Sea of Japan, North Atlantic shelf regions, Barents Sea, Limfjorden (Denmark), and parts of the Mediterranean Sea, although jellyfish populations in these regions also exhibit decadal oscillations (Fig. 2). These blooms may be enhanced because local drivers may act synergistically with global drivers during a rising phase.

Despite all our efforts, some regions of the oceans were underrepresented in our dataset, including the tropics, open ocean gyres, and the Southern Hemisphere. Whether the patterns reported here apply to those regions is, therefore, an open question. Although the mixed models are weighted for heterogeneous sample sizes, the robustness of our results also varies over time because of changes in the number of observational programs. The number of datasets available increased to a maximum in 1996, but decreased in recent years probably because the results have not yet been reported (Fig. 2). However, our study provides compelling evidence for the power of long-term observational programs; neither modeling nor experimental research could have identified the decadal oscillations in jellyfish abundance emerging from this analysis.

Drivers of Jellyfish Blooms. Our study identified two patterns in jellyfish populations: (i) a weak but significant overall increase in jellyfish since 1970, and (ii) a strong recurrent pattern of oscillations that has persisted for over a century. The slight overall increase since the 1970s is correlated with global changes, including increased human activity along the coastline that could facilitate or amplify increases in jellyfish. These global changes include warming temperatures (24, 25), which enhance production, feeding, and growth rates of jellyfish (29), overfishing of competitors of jellyfish (30), an increased supply of planktonic food for jellyfish associated with eutrophication of coastal waters (31), and the spread of hypoxia, to which jellyfish exhibit greater tolerance than most other metazoans (25, 32). The proliferation of artificial structures associated with human activities has also been argued to promote blooms of meroplanktonic medusae by increasing suitable hard substrate for their benthic polyps (33).

The realization that jellyfish populations have been pulsing globally at decadal scales should lead to a broadening of the search for the drivers of change, from regional-scale (e.g., hypoxia) to global drivers (e.g., climatic oscillations). Jellyfish populations are regulated by bottom-up processes (25); therefore, the drivers responsible for the global oscillations probably involve increased productivity at time scales reflected by jellyfish oscillations. Such fluctuations may be forced by environmental oscillations, including coupled ocean-atmosphere oscillations (34, 35), solar activity (36), lunar nodal cycles (37, 38), and biotic interactions in food webs (39). Whereas planktonic medusae live for only months, benthic polyps of cnidarian jellyfish can be perennial (40), so that long-term oscillations can be generated by intrinsic life cycle and population processes as well (18, 33, 41). Understanding the drivers of jellyfish fluctuations will allow the

development of reliable early-warning indicators of phase-shifts and is fundamentally important to improve future management of jellyfish blooms.

Although there is, overall, no significant increase in jellyfish abundance over the observational period (1874–2011), the data signal a significant but weak increase since 1970. This trend involves an apparent increase in the baseline, reflected in a shallow global minimum in 1993 (Fig. 3), the last minimum in global jellyfish oscillations. Because jellyfish blooms show long (~20 y) oscillation cycles, a change in oscillatory behavior, such as an increasing baseline, requires >40 y to be evaluated with confidence. Hence, observation of the forthcoming global minima in these oscillations is essential to either confirm or reject the recent (after 1970) increase in baseline suggested by the available data. Whatever the nature of the recent increase—a shift in baseline or fluctuations in the long-term oscillations—indications that there was a significant, albeit weak, increase from 1970 to 2011 superimposed on a larger rising phase of the long-term oscillation between 1993 and 2004, support the perception that a global rise in jellyfish blooms occurred in the late 1990s and early 2000s (1, 3, 17). The impacts of rises in jellyfish abundance are enhanced by increasing exposure derived from the increased interaction between humans and the coastal ocean (33). Although our analyses do not currently allow forecasts, the dynamics uncovered here foretell future phases of global rise in jellyfish for which society should be prepared.

Methods

Compilation and Formatting of Datasets. Datasets were converted to an annual average and each dataset was standardized to an annual mean of 0 and a SD of 1 to create a jellyfish index (*J*) using Eq. 1:

$$J = \frac{(RD - \bar{X})}{SD}, \quad [1]$$

where *RD* is the raw datapoint for each year of the dataset, and \bar{X} and *SD* are the mean and SD of individual datasets, respectively. Presence/absence data were converted to 1 and 0 for presence and absence of jellyfish, respectively. In cases where published data on jellyfish abundances could not be obtained from the text or tables, we used Graph Click 3.0 software to extract data from figures. Biomass units were used to concatenate data for multiple gelatinous groups within a particular location, using published empirical equations to convert raw data. We concatenated data sources to produce a longer time-series at Chesapeake Bay using linear regressions to estimate consistency for the overlapping period and using the fitted linear-regression analysis to concatenate the datasets. There was no significant difference between the biometric type used in our analysis (i.e., biomass, abundance and indices) (Table S1) over time (two-way ANOVA, \log_{10} transformed data, $F = 1.1$, $df = 1,089$, $P = 0.36$). Statistical analyses were performed using SAS v9.2 and JMP v9.0.2 software.

Statistical Analysis. LMM and GLMM (logit link) were used to assess patterns (linear and nonlinear) in the standardized abundance data and the binary data, respectively, over three consecutive time periods—1874–1939, 1940–1969, and 1970–2011—as well as an overall time frame from 1874 to 2011. The year 1874 represents the earliest date of continuous, empirical records on jellyfish populations (presence/absence data), 1940 indicates the earliest long-term record with quantitative data, and 1970 reflects the start of accelerated research into the functional biology of jellyfish, which includes the period 1990–2011 that led to the perception that jellyfish numbers were increasing. LMMs are an extension of linear models in which random effects can be added to the linear predictor and their associated error structure can be explicitly defined. Furthermore, within these models, the residual error can be defined in a variance-covariance structure if a temporal autocorrelation error structure is present in the data. The incorporations of these random effects and their associated variance-covariance structures generate a rich class of correlated data models that would be difficult to specify directly in standard linear models (42). For GLMM, standardized data were converted to binary form by scoring individual standardized values falling above and below 0 within each dataset as 0 (positive jellyfish indices) and 1 (negative jellyfish indices), respectively, because the logistic analyses estimates the probability of a difference in the data from 1 (compared with 0 and the *y*-intercept with linear regressions).

Supporting Information

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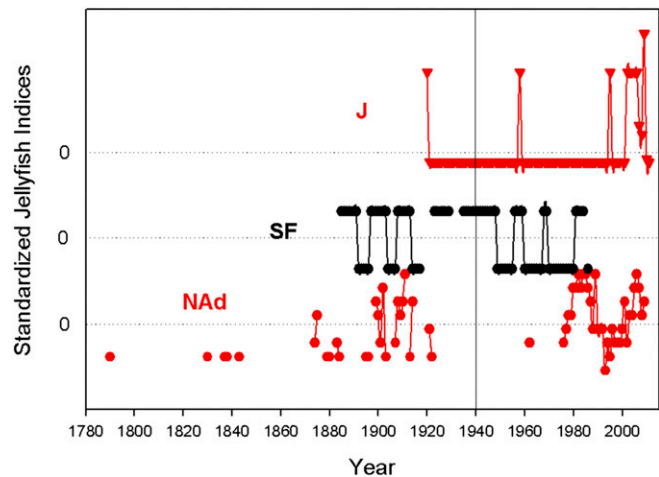


Fig. S1. Standardized time-series 1874–2011 for datasets that commenced before 1940. Abbreviations as denoted in Table S1: North Adriatic Sea/Gulf of Trieste (NAd), Sea of Japan (J), and South of France (SF). Line colors show significant increase (red) and no significant change (black) in jellyfish abundance over time (t test; $P < 0.05$). Vertical line shows beginning of global analysis in 1940 (Fig. 2).

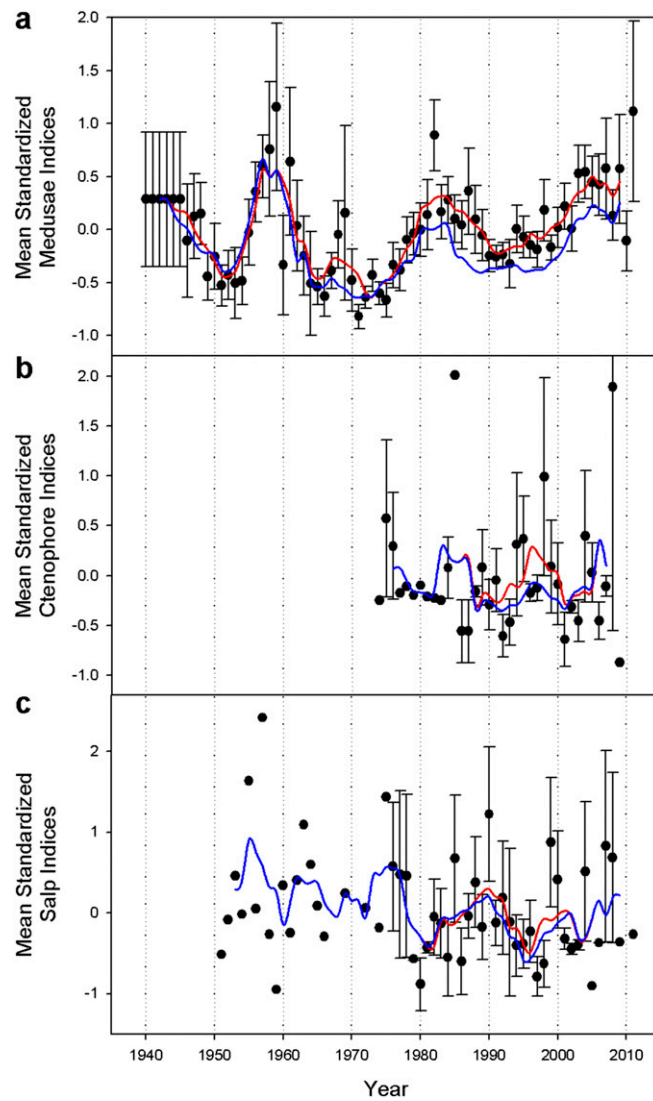


Fig. S2. Mean annual standardized jellyfish abundance. (A) Medusae, (B) ctenophores, and (C) pelagic tunicates only (Table S1). The solid lines show a 5-y running average for annual mean (red) and median (blue) values. The 2 y occurring after 1940 and before 2011 are excluded from the running mean and median calculations because of incomplete data. Error bars are ± 1 SE.

Other Supporting Information Files

[Table S1 \(DOCX\)](#)

[Table S2 \(DOCX\)](#)

[Table S3 \(DOCX\)](#)

[Table S4 \(DOCX\)](#)

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