

Recurrent jellyfish blooms are a consequence of global oscillations

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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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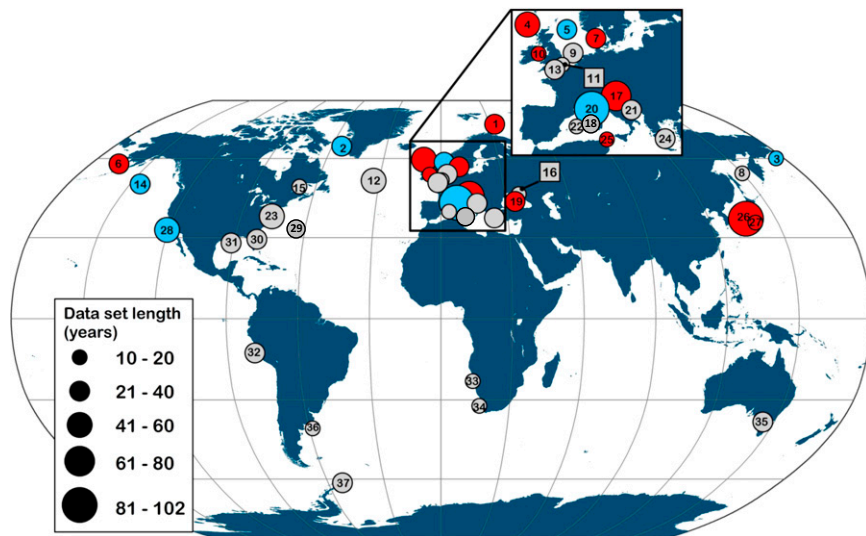


Fig. 1. Distribution of jellyfish time-series. Time-series of observations on jellyfish abundance >10 y in length from 1874 to 2011. The diameter of the symbols is proportional to the duration of the dataset, colors indicate trends (linear regressions, $P < 0.05$): significant decrease (blue), significant increase (red), or no trend (gray) in jellyfish abundance over time for the duration of the study. Numbers identify the datasets described in Table S1. Most datasets were from the northern hemisphere (87%), in particular the Atlantic Ocean (17%) and the Mediterranean region (17%), and comprised medusae (89%).

region (17%) (Fig. 1). Although our analysis does not represent a random sample of the ocean, it reflects all available time-series of jellyfish data in the global ocean, including all those used in the published literature to support the current perception of an increase in jellyfish. We are aware of a couple of additional existing datasets, but we were unable to access them. These missing datasets represent, to the best of our knowledge, less than 10% of the total datasets analyzed. Thus, this compilation provides the most comprehensive effort to assess changes in jellyfish abundance across the ocean.

The debate has focused on the rise of jellyfish blooms and their mean abundance (3, 13–16); thus, we examined both the distribution of the annual standardized abundance and maximal jellyfish values (i.e., blooms or data >90 th percentile for each location) over time using linear mixed model (LMM) and generalized linear mixed model (GLMM) analyses that incorporate random effects and nonlinear components and are adjusted for temporal autocorrelation (heterogeneous AR1 estimates). The fact that time-series start and end at different years imposes limitations on the analysis, as this results in differences in the sets of data available for analysis in any single year. We used three approaches to determine whether standardized jellyfish abundances have significantly increased over time. First, we determined whether there was a significant departure from the expected zero linear slope of standardized abundance over time (i.e., the baseline) by comparing between slopes of linear regressions from individual datasets over the time period 1874–2011, as well as three consecutive time periods: 1874–1939, 1940–1969, and 1970–2011. The second approach involved GLMM (logistic) analyses of binary data to test whether there was a change in the likelihood (odds) of observing a higher vs. lower proportion of jellyfish over time. Third, we computed effect sizes, as the $\ln[(Jp1/Jp2)/D]$, where $Jp1$ and $Jp2$ are the predicted jellyfish data for start and end years and D is the number of decades in the time series (see *Methods* for summary), allowing comparison of changes across datasets based on different metrics (22). Because effect sizes deviated from a normal distribution and no suitable transformation to normalize the data were found, we used a nonparametric median test to test whether populations showing significant increases or decreases over time differed in effect size. To reject the null hypothesis of no global increase in jellyfish, all three of these analyses combined should yield

significant results within each respective time period because the baseline increase would be substantiated by a net increase in the magnitude of change (22). Finally, we used a Runs test to examine the null hypothesis that the temporal distribution of annual jellyfish index values were not randomly distributed over time, with a significant result signifying that the jellyfish time-series data are organized into series of runs consisting of consecutive rise and fall periods.

Results and Discussion

Global Analysis of Jellyfish Abundance. The combined datasets spanning over a century from 1874 showed that the mean linear slope of standardized abundance did not deviate significantly from zero across this time span (1874–2011: mean \pm SE slope = 0.0014 ± 0.0016 yr $^{-1}$; $P = 0.37$; $n = 1,090$). Moreover, although the regression slopes of 46% of the individual time-series significantly deviated from the expected value of zero throughout the full duration of each study (one-sample t test; $P < 0.05$; $n = 10$) (Figs. 1 and 2, and Table S2), the odds of observing higher jellyfish indices did not change over time (GLMM: $P = 0.57$; $n = 1,090$) (Table S2) and the median test showed no difference in effect size between populations that significantly increased or decreased over time (Table S3). When shorter time windows were analyzed (1874–1939 and 1940–1969), similar nonsignificant trends in standardized mean slopes and magnitude of jellyfish changes were observed (Tables S2 and S3). In contrast, a weak but significant increase in jellyfish was detected using linear and logistic regression mixed models for the past four decades (1970–2011: mean \pm SE slope = 0.012 ± 0.004 SD yr $^{-1}$; $P = 0.004$; $n = 849$), although this increase was modest and corresponded to an average of 0.63 ± 0.28 SD per decade for the 11 of 37 regions (30%) that showed significant increases in jellyfish abundance over this time period. Furthermore, median tests showed that there was no significant difference between the effect sizes of increasing vs. decreasing jellyfish populations over the same period (Table S3). The same linear trends were observed over all time periods when region (e.g., Mediterranean Sea) and Longhurst provinces were also included as factors in the LMM (Tables S1 and S2). Trends among the datasets synthesized here were independent, as spatial autocorrelation was not significant ($P > 0.05$) in the mixed-model analysis of trends in global jellyfish indices.

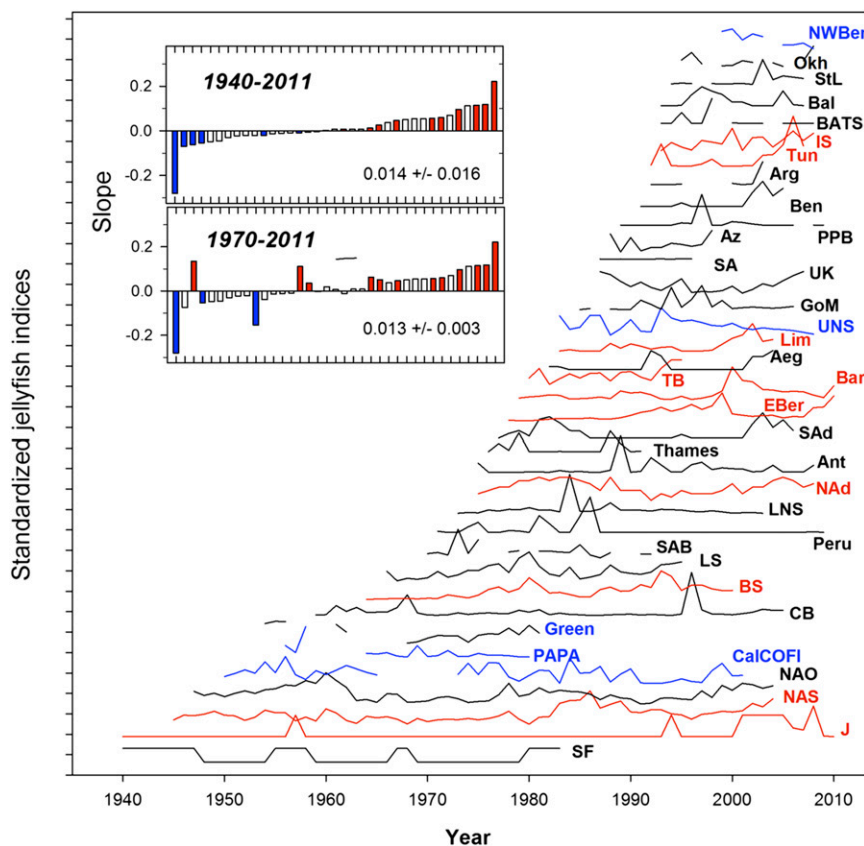


Fig. 2. Individual time-series of standardized jellyfish abundance from 1940 to 2011. Line colors show significant increase (red), decrease (blue), and no significant change (black) in jellyfish abundance over time (t test, $P < 0.05$). (Inset) The slopes of linear regressions for individual time series 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

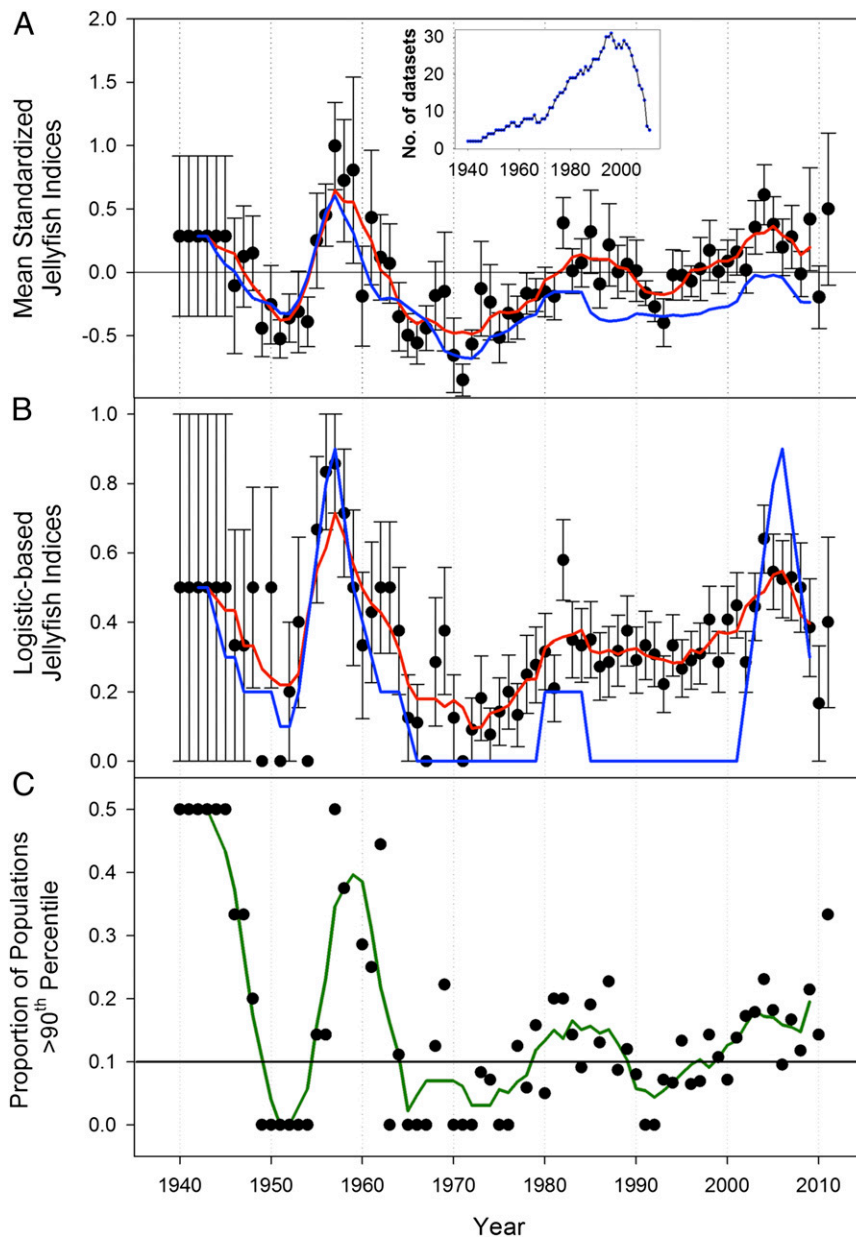


Fig. 3. Global oscillations of jellyfish. (A) Mean standardized and (B) mean logistic (binary) jellyfish indices, and (C) the probability of encountering maximum abundances of jellyfish for the global dataset between 1940 and 2011. Maximum abundance is defined as years when abundance exceeded the 90th 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).

A range of models, using various fixed and random effects, as well as autocorrelated error structures, were investigated for each time period. The “best” model was obtained by a comparison of various goodness-of-fit statistics for each model (e.g., Akaike and Bayesian information criterion). The “best” model varied for each respective time period analyzed but usually included a variance components structure for the random effects (linear and nonlinear effects), with the temporal effect having an explicit variance covariance structure modeling the autocorrelation errors [e.g., heterogeneous autoregressive (AR1)]. Preliminary analysis, using nonlinear regression, was used to estimate the function parameters for the nonlinear oscillations in the model for the various time periods (i.e., nonlinear terms listed in Table S2). These estimates were used to develop linear forms to represent the nonlinear components in the LMM and GLMM analysis. For example, if the model required a nonlinear component in the form $\beta_1 \sin\left(\frac{2\pi year}{\beta_3} + \beta_4\right)$ where $\beta_3 = 10$, then the equivalent linear form is

$$\left(\beta_1 \sin\frac{2\pi year}{10} + \beta_2 \cos\frac{2\pi year}{10}\right)$$

In addition, as standardization techniques removed the effect of magnitude of change existent in the raw data, we computed effect sizes allowing comparison of changes across datasets based on different biometrics (22). The effect size (ES) or magnitude-of-change were calculated for each dataset over the various time periods using Eq. 2:

$$ES = \ln\left(\frac{\left(\frac{J_p}{J_p 1}\right)}{D}\right), \quad [2]$$

where J_p is the actual predicted jellyfish population size as determined by linear regressions with random effects, where $J_p 1 > J_p 2$. $J_p 1$ is the predicted

end and start year value for regions with jellyfish increases and decreases, respectively, and vice versa for $J_p 2$. D is the number of decades in the time period examined where $D > 1$. Because effects sizes deviated from a normal distribution and no suitable transformation to normalize the data were found, we used a nonparametric median test to test whether populations showing significant increases or decreases over time differed in effect size.

Runs tests for randomness were used to examine the null hypothesis that trends in annual jellyfish indices in standardized and binary form were not randomly distributed over time. Annual mean standardized and binary (logistic) data were determined for each year and Runs tests performed on the combined data between 1940 and 2011. A significant result indicates the dataset exhibits nonrandomness. We also examined the trends of extreme events (i.e., blooms) as defined by values that exceeded the 90th percentile for each time-series to determine whether the frequency of blooms in sample regions had increased over the period 1940–2011. For these analyses, logistic regressions and Runs tests were performed on binary data; blooms (>90th percentile) were scored as 0 and all other data were scored as 1.

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