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Emerging *Vibrio* risk at high latitudes in response to ocean warming

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There is increasing concern regarding the role of climate change in driving bacterial waterborne infectious diseases. Here we illustrate associations between environmental changes observed in the Baltic area and the recent emergence of *Vibrio* infections and also forecast future scenarios of the risk of infections in correspondence with predicted warming trends. Using multidecadal long-term sea surface temperature data sets we found that the Baltic Sea is warming at an unprecedented rate. Sea surface temperature trends (1982–2010) indicate a warming pattern of 0.063–0.078 °C yr^{-1} (6.3–7.8 °C per century; refs 1,2), with recent peak temperatures unequalled in the history of instrumented measurements for this region. These warming patterns have coincided with the unexpected emergence of *Vibrio* infections in northern Europe, many clustered around the Baltic Sea area. The number and distribution of cases correspond closely with the temporal and spatial peaks in sea surface temperatures. This is among the first empirical evidence that anthropogenic climate change is driving the emergence of *Vibrio* disease in temperate regions through its impact on resident bacterial communities, implying that this process is reshaping the distribution of infectious diseases across global scales.

Recent evidence suggests that global average temperatures have risen by nearly 0.8 °C since the late nineteenth century and have risen by approximately 0.2 °C per decade over the past 25 years[3]. In addition to increasing temperatures, altering patterns of precipitation and runoff are expected that may drive a consequent reduction in the salinity of estuaries and coastal wetlands[4]. Many marine bacterial pathogens of relevance to human health, such as vibrios, grow preferentially in warm (>15 °C), low-salinity (<25 ppt NaCl) sea water[5]. The anticipated warming and reduced salinity of coastal regions located at high latitudes will provide new areas for the natural occurrence of pathogenic strains. Warming patterns have been related to the emergence of *Vibrio* outbreaks in temperate and cold regions, such as in Chile[6], Peru[7], Israel[8], the US Pacific northwest[9] and northwest Spain[5]. Despite the increasing number of reports showing the poleward spreading of *Vibrio* diseases, conclusive evidence linking the emergence of infections with climate change remains contentious. This situation is in part owing to the effects of warming being more pronounced at higher latitudes[3] and often in areas that lack detailed historical epidemiological data sets[5], meaning the emergence of cases is often interpreted as a sporadic event owing to exceptional conditions, rather than a response to long-term environmental change.

The Baltic Sea area provides a particularly interesting region to study emerging *Vibrio* disease. During the extremely warm summers of 1994, 2003 and 2006, a plethora of reports emerged documenting *Vibrio*-associated wound infections linked to recreational exposure in this area[10–14] and included numerous fatalities[12–14]. The Baltic Sea is warming rapidly[1,2] and represents one of the largest low-salinity marine ecosystems on Earth. Low sea surface salinity (<NaCl 25 ppt) is a major risk factor contributing to *Vibrio* prevalence and associated clinical risk in marine systems[5,15]. Furthermore, more than 30 million people live within 50 km of the Baltic Sea and this, coupled to an increasingly susceptible population in Europe, may substantially increase clinical risk[5]. All these factors suggest the population neighbouring the Baltic Sea is at particular risk from pathogenic vibrios, particularly in light of future projections regarding increasing sea surface temperature (SST) and freshening salinity conditions[3,16].

We examined associations between epidemiological data on the emergence and dynamics of *Vibrio* disease in the Baltic and long-term SST records and recent satellite-derived fields (see Methods). The analysis of the different SST data sets corroborated a significant warming trend evident across the Baltic Sea area, especially during the summer (Fig. 1a and Supplementary Fig. S1A,B). For the region between 54° N–60° N and 10° E–20° E, the increasing trend in annual SST from 1854 to 2010 was 0.51 °C per century (approximately 1 °C for summer months) and this rate increased for the 1900–2010 period to 0.77 °C (approximately 1.5 °C for summer). Significantly, the warming rate from 1980 to 2010 increased to approximately 5 °C (6 °C for summer months) per century, a sixfold increase from the 1854 to 2010 rate. Autoregressive integrated moving average (ARIMA) models also showed a clear warming trend in the region, higher than 1 °C per century (Fig. 1a). These findings augment analysis[1] that indicated significant and unprecedented recent warming trends in the Baltic Sea region up to 2003 and demonstrate that this trend has continued recently. From recently analysed Hadley SST data sets, the post-1987 warming rate in the Baltic Sea exceeded 1.0 °C per decade, more than seven times the global rate, and the Baltic area experienced the fastest net SST warming trend (∼1.35 °C) of any large marine ecosystem between 1982 and 2007 (ref. 2). The recent warming trend identified here represents, to our knowledge, the fastest warming marine

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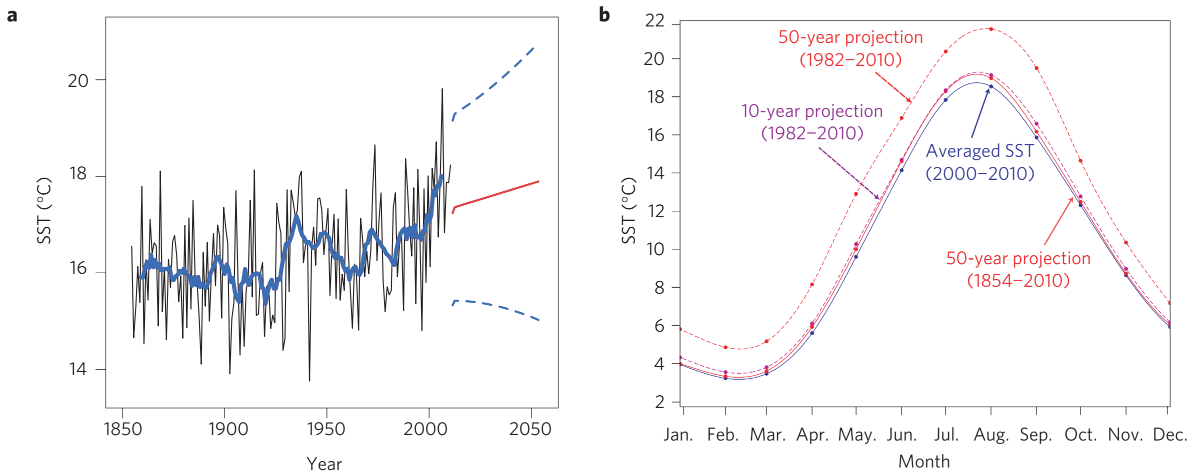

Figure 1 | Warming trends in the region limited by 54° N–60° N, 10° E–20° E in the Baltic Sea. a, Mean temperatures for July (black line) between 1854 and 2010, ten year running mean (blue line) and projection of temperatures according to the ARIMA model using the SST series for the whole year (red line) and 95% confidence intervals (dashed blue lines). **b**, Average monthly SST for the 2000–2010 period (blue solid line) and 10- and 50-year linear projections obtained from SST monthly fields between 1982 and 2010 (purple and red dashed lines, respectively) and 50-year projection using the 1854–2010 interval (red solid line).

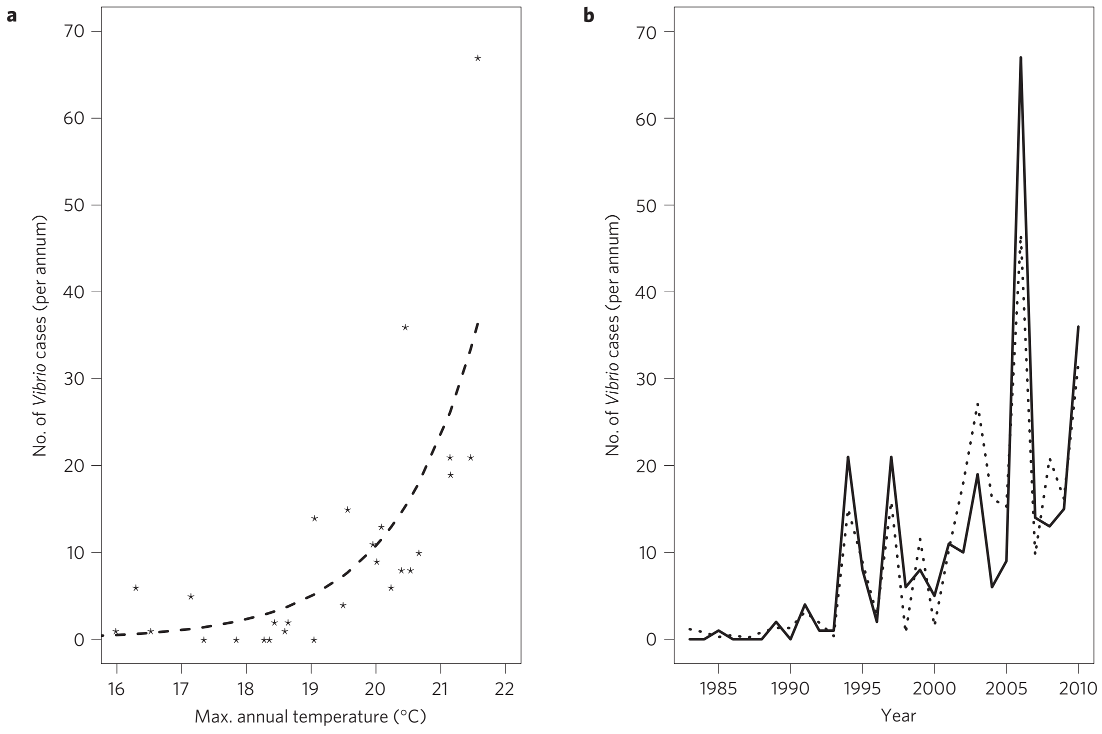

Figure 2 | *Vibrio* cases and SST. a, The relationship between *Vibrio* infections reported around the Baltic Sea area and maximum annual SST. Stars show observed data, dashed line shows GLM model predictions (based on the influence of SST alone). **b**, Time series of Baltic Sea *Vibrio* cases. Solid line shows observed cases and dotted line shows GLM model predictions based on the influence of maximum SST and time.

ecosystem examined so far anywhere on Earth. The strong SST increase was most pronounced in summer months, with notable intensity when the time series is truncated to span the most recent years (Supplementary Fig. S1B). Assuming the observed SST trends continue, 50-year forwards projection based on the whole 1854–2010 SST data set anticipates a similar warming and seasonal pattern of SST to that predicted for the next ten years using the 1982–2010 series (Fig. 1b). These results also show a widening SST summer season, especially important when the strongest warming scenario is considered, where the expected average SST temperature reaches values above 18 °C during most of the summer (Fig. 1b).

The number of *Vibrio* cases occurring each year in the Baltic Sea region was highly aggregated and followed a negative binomial distribution (mean $= 10$, shape parameter—$k = 0.541$, Supplementary Fig. S2), with low numbers observed in most years. Based on this distribution less than 38 cases would be expected in 95% of years and the probability of observing 67 cases as in 2006 would be only 0.83% if it is assumed that conditions remained constant. However, generalized linear models (GLMs) demonstrated that a large amount of the observed variability can be explained by the maximum annual SST and time (Supplementary Table S1). These models suggest that each year *Vibrio* cases increase

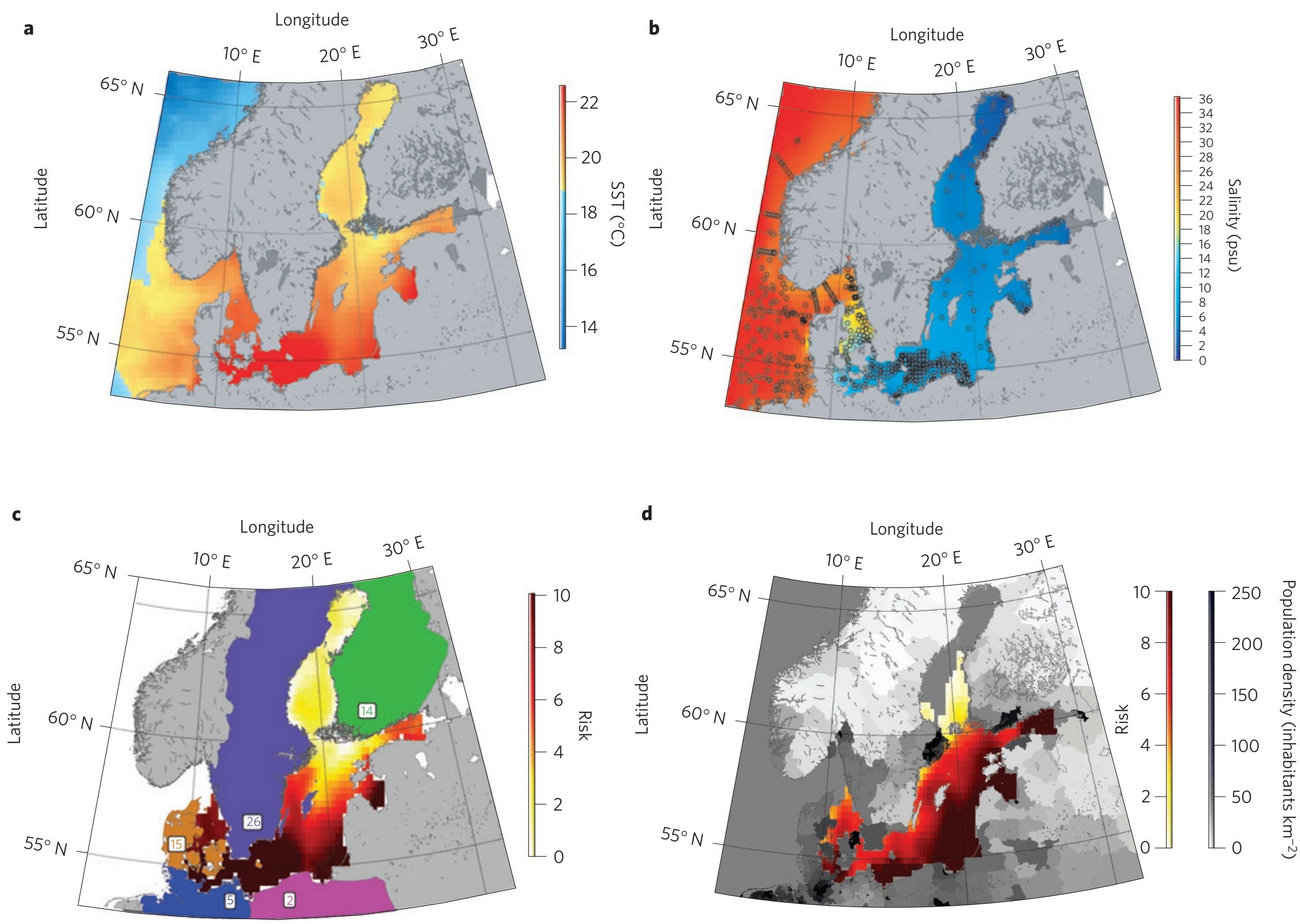

Figure 3 | SST temperature and salinity for the summer of 2006 and estimation of the risk of infection. a, Maximum SST in the Baltic area for the summer of 2006. **b**, Sea surface salinity obtained from *in situ* measurements for the same period calculated using a surface tension algorithm to grid the irregularly spaced measurements (circles). **c**, Risk model map during summer 2006 and number of cases in countries reporting infections. **d**, Projection of the risk of infection in 2050 using as baseline the maximum SST summer field for 2010 and applying the projections of temperature estimated by the ARIMA model, with the grey scale inland indicating the population density (Nomenclature of Territorial Units for Statistics 3). The SST field shown on the map has a spatial resolution of 0.25°. The ARIMA model was applied on area-averaged long-term ERSST data (originally at 2° × 2° spatial resolution) and HadISST (to confirm and compare results using independent data sets). The projection of temperatures from the ARIMA model were applied on higher resolution SST fields that better delineate regional differences and provide more detail on coastal regions.

1.09 times and, additionally, for every 1 °C increase in the maximum annual SST, the number of observed cases increases by 1.93 times. Maximum annual SST showed a very strong association with the number of *Vibrio* cases reported (Fig. 2a) and there are several biologically plausible explanations that may suggest a causal link. High temperatures increase bacterial replication and environmental studies in the Baltic area show that *Vibrio vulnificus* abundance peaks at seawater temperatures >19 °C (ref. 17). Recent studies[18,19] also suggest that regulation of pathogenic competence of some *Vibrio* species is temperature mediated. Furthermore, warm temperatures are likely to be associated with increases in leisure activities such as bathing, further increasing risk. Although maximum SST was a significant predictor *of Vibrio* cases alone, it underpredicted the number of cases in the later part of the time series. Time was a significant predictor of cases in its own right and although ARIMA models demonstrated a clear increasing trend in SST with time, there was only a moderate direct correlation between them (Spearman's rank $r = 0.56$, $P = 0.002$). After controlling for the confounding effects of SST on time in the GLMs, the increase in cases was still significant over time (no significant interaction effect was detected between time and SST) and retaining both variables led to much better model predictions than obtained with SST alone (Fig. 2b). Several time-correlated variables (other than temperature), on which we can only speculate, may explain this relationship. These may include: rising patient and general practitioner awareness increasing reporting, shifts in population density increasing exposure and changing demography in terms of population age structure and the prevalence of predisposing factors increasing susceptibility. Putting these data into context with the 2006 anomaly when 67 *Vibrio* infections were reported from around the Baltic region and western North Sea (Figs 2b, 3 and Supplementary Fig. S3 and Table S2) an obvious association with temperature is evident. The 2006 heatwave lasted approximately one month (26 June 2006–30 July 2006), with seasonal SST peaking towards the end of July 2006 at 21.57 °C, ≥2.75 °C higher than the 1983–2005 average of 18.82 °C for the region (Supplementary Fig. S3). Differences in salinity between the Baltic and adjacent connected oceanic areas (18 versus 34 ppt— Fig. 3b) suggest that these observed high temperatures in the Baltic sea were not driven by the incursion of warm waters from these areas. The high SST remained for several weeks and extended over most of the Baltic Sea area (192,000 km^2—Supplementary Fig. S3). Where specific timings of *Vibrio* cases were available, these coincided with this warm weather anomaly. However, based on maximum SST alone, only 36 cases were predicted by the GLM (Fig. 2a). The inclusion of time as a predictor substantially improves this, predicting 47 cases (Fig. 2b), but also suggests additional unknown factors contributing to the high number of cases in this year.

Of the clinical cases reported so far in the Baltic Sea, the highest mortality rates have been associated with *V. vulnificus* infections (Supplementary Table S3). To analyse the potential of *V. vulnificus* presence (and potential risk) in this region, we constructed a risk model based on observed SST (>19 °C) and low-salinity water (<25 ppt NaCl; Supplementary Figs S3D, S4 and S5 and Animation S1). The latter allows delineation of the region of interest, with intermediate- or low-salinity regimes where higher concentrations of vibrios have been historically found[17,20], whereas SST acts as a predictor of risk, which is defined from the number of cases in relation to changes in SST according to the GLM model. This risk model was first validated using the cases reported and areas affected over the period of study (Fig. 3c) and subsequently projected forwards using various warming scenarios. The linking of *Vibrio* case reports and remote sensing data suggests that the recent emergence of *Vibrio* infections in the Baltic is probably driven by a general warming of SST in the region, coupled to significant climatic anomalies during summer months (for example July and August 1994, 2003 and 2006, Supplementary Fig. S1). Several recent environmental studies using molecular approaches have further demonstrated the role of increased temperature in driving *Vibrio* abundance in both the North Sea and Baltic Sea region[21–23]. We applied the risk model constructed for summer 2006 to obtain projections of the estimated risk of infection for 2050 using as baseline the maximum SST summer field for 2010 and applying the worst-case projections of temperature estimated by the ARIMA model (Fig. 3d). According to the model and the expected warming rate, projections anticipated an enlargement of areas of maximum risk of infection in the Baltic shifting northwards and affecting most of the high-populated coastal areas of the mid and southern Baltic Sea. A significant expansion of waters capable of sustaining large *Vibrio* populations in the Baltic is anticipated leading to an increase in the risk of *Vibrio* infections in the region. We must stress that these predictions are based on rapid warming trends recently experienced in the Baltic Sea area continuing to the middle of the twenty-first century. Lower forecasts for SST warming of the Baltic Sea are predicted using mechanistic process-orientated modelling[24,25]. These multimodel ensemble approaches could be particularly useful for risk prediction purposes over longer timescales than presented here.

Specific limitations to accurately link *Vibrio* infections in a temporal and spatial context alongside climatic conditions remain in Europe, caused by the lack of accurate, reliable and joined-up epidemiological data sets. Across much of Europe, the risk of *Vibrio* infections is considered to be low[5]. Differences in the quality and coverage of epidemiological data sets across the Baltic region must be considered, as should changes in reporting effort over time. Both factors may reduce the accuracy of the epidemiological data presented here, which by their very nature are fragmentary and probably represent an underestimation of clinical burden. With a changing demography in the populations surrounding the Baltic Sea, this study underlines the importance of improved understanding and associated epidemiology, particularly in light of recent rapid warming in northern Europe (Fig. 1a,b) as well as globally[3,26]. There is a need for a centralized and systematic method for case reporting between and within countries in Europe, such as the Cholera and Other *Vibrio* Illness Surveillance reporting system introduced by the Centers for Disease Control in the USA. Consistent with numerous other studies[5–7,27], our data suggest that near-real-time remote sensing data sets can be used as an early warning system to forecast the health risks of *Vibrio* disease. Focussing efforts on areas with high population density, for example St Petersburg, Stockholm and the southern Baltic coastline (Fig. 3), and expanding the risk analysis to other regions undergoing rapid warming such as the Pacific northwest, the Sea of Okhotsk and the East China Sea[26] may represent the most fruitful approach to predict areas where new *Vibrio* infections are likely to emerge. Key risk factors include sustained SST warming (for example, in the case of 1994, 2003 and 2006 peak SSTs in the Baltic Sea exceeding 19 °C for three weeks or more) and efforts should be made to inform at-risk groups to prevent them from recreational contact with unsafe coastal water during these periods. Future work should include assessing the effects of long-term climate change on pathogen growth and survival and determining routes of exposure as well as the role of host susceptibility in disease emergence.

Methods

Epidemiological data sets. Epidemiological data were obtained from a variety of sources. With the absence of detailed transnational surveillance data sets from all Baltic countries, information regarding the temporal and spatial incidence of *Vibrio* cases was obtained from peer-reviewed publications using generic search engines such as NCBI/PubMed and Web of Science. Additional case data were obtained from grey literature (for example, surveillance data from national communicable disease agencies and medical profession newsletters) and bulletins from EU laboratories and European surveillance websites (for example, EpiNorth, EuroSurveillance). Finally, researchers from different Baltic Sea research laboratories engaged in *Vibrio* research were contacted, to provide informal feedback on gathered cases data and to provide additional information on reported cases. Where available, information regarding the timing, geographical location and agent responsible was subsequently gathered. Cases that were not domestically acquired were removed and where suspected (for example, *Vibrio* cases reported during the winter) were subsequently omitted from the list (Supplementary Table S2). Data were adjusted, where applicable, to omit foreign-travel-acquired *Vibrio* infections where these were known.

Long-term SST and remote sensing data. To assess the influences of recent warming trends on the emergence and dynamics of *Vibrio* disease in the Baltic, we analysed epidemiological data alongside long-term SST records (Hadley Centre Sea Ice and Sea Surface Temperature (HadISST) data set and National Oceanic and Atmospheric Administration (NOAA) Extended Reconstructed Sea Surface Temperature (ERSST) data set v3b) as well as shorter-term data from NOAA's Optimum Interpolation v2 Daily SST Analysis data set that integrates satellite SST retrievals. Both the HadISST and ERSST data sets represent some of the longest and highest quality recorded and calibrated sea temperature series in the world, providing monthly fields since 1854 and 1870, respectively. ERSST v3b has been selected over v3, as it does not integrate satellite data, which introduced a residual cold bias, and therefore provides a satellite-independent data set that we use to confirm our results, especially those related to the strong summer warming trend detected in the Baltic Sea during the past three decades when remote sensing data became available.

Statistical analysis. Infection risks were estimated using GLM techniques where SST acts as main risk predictor. ARIMA modelling was applied to forecast the SST and these results were used to evaluate and forecast the risk. ARIMA models, based on autocorrelation analysis and used for statistical forecasting, include autoregressive, integration order and moving average terms. A forecast can then be assembled using combinations of the three terms[28]. Therefore, infection risk uses ARIMA modelling indirectly through SST future estimates. Long-term trends of SST data were evaluated using different approaches, including linear regression. ARIMA techniques were applied over the monthly non-stationary SST time series to identify and forecast trends. Finding the satisfactory ARIMA model usually involves four steps: first, tentative identification of the ARIMA model by examining the sample autocorrelation and sample partial autocorrelation functions; second, estimation of the model parameters; third, a diagnostic checking part where the adequacy of the model is evaluated; and fourth, when the model is finally accepted, use it to forecast the future values of the time series. Both analytical and brute force procedures were applied to select the best candidate models using as selection criteria the Akaike information criterion and the Bayesian information criterion. The input data fields were the monthly mean ERSST values within the region limited by 54°–60° N and 10°–20° E. Best results were obtained using an ARIMA model of order (1, 1, 2) and seasonal terms (1, 1, 1). Therefore and for the non-seasonal part, the order of the autoregressive and integrated parts are 1, whereas the higher order of the moving average term is 2. All the seasonal factors are 1.

As epidemiological data were in the form of counts and demonstrated clear over dispersion (assessed graphically and by comparing the residual deviance with residual degrees of freedom), GLMs assuming either a quasi-Poisson or negative binomial distribution and log link function were used. Graphical methods were used to assess model fit and ensure a linear relationship existed between predictor variables and link transformed outcome variable. Model fit was also assessed by comparing the difference between the null and residual deviance. Models were built using a forward stepwise process and only terms significant at $P \leq 0.05$ were retained. Analysis was conducted in *R* version 2.13.0 (ref. 29).

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Author contributions

C.B-A., J.A.T. and J.M-U. conceived the project. J.A.T. and J.M-U. designed experiments and C.B-A., J.A.T., J.M-U. and N.G.H.T. analysed the data. R.H. and A.S. provided valuable interpretations. C.B.A, J.A.T., N.G.H.T. and J.M-U. wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to C.B-A.

Competing financial interests

The authors declare no competing financial interests.

Corrigendum: Emerging *Vibrio* risk at high latitudes in response to ocean warming

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In the version of this Letter originally published, an outdated version of Figure panel 3d was displayed in Fig. 3, and so the population density and risk data shown was incorrect. Figure panel 3d has been replaced in the online version of this Letter.