COMMENT

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Reconsidering evidence for potential climate-related increases in jellyfish

Attrill et al. (2007) in their paper "Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea" present data showing the occurrence of nematocysts in continuous plankton recorder (CPR) samples collected over more than 40 yr. They suggest that, contrary to previous work examining a shorter period (Lynam et al. 2004), cnidarian nematocysts "most likely to be from scyphozoans" have increased, especially since the mid-1980s. However, several problems with their analyses make it difficult to evaluate their conclusions.

Jellyfish—It is only marginally informative to talk about dynamics of generic "jellyfish" populations. According to the definition of Mills (2001), jellyfish include scyphomedusae, hydromedusae, siphonophores, and ctenophores. As she points out, there is evidence that the abundances of these animals have been changing recently, with some increasing and others decreasing. All cnidarians could potentially contribute to a nematocyst index, but Attrill et al. (2007) assert that because siphonophores are separately enumerated, they do not contribute to the counts. Siphonophore parts are difficult to count even under the best of conditions, and there would be little chance of obtaining accurate counts from CPR samples. Even if they could be accurately quantified, the authors do not explain why their numerous tentacles would not contribute to the nematocyst index. Small siphonophores are abundant and diverse in the region studied (Kirkpatrick and Pugh 1984), and Greve (1994) documented a large and anomalous occurrence of small calycophoran siphonophores in the southern North Sea at roughly the same time that the CPR data show their greatest increase. Without evidence to the contrary, it is not possible to discount the contribution of siphonophore nematocysts, nor is it clear why this widespread group should be singled out for exclusion.

Within the two remaining cnidarian groups, there are many hundreds of hydromedusae and scyphomedusae that can occur seasonally across the study region in the North Sea. Attrill et al. (2007) offer no taxonomic sampling to accompany their data, but they hypothesize that the dominant cnidarian species shift seasonally between *Obelia* spp. (coastal Leptomedusae) and *Aglantha*, which they misclassify as a scyphomedusa. Taxonomic distinctions are important because if there is an increase in gelatinous taxa, their differing life histories will suggest probable causes of the change. Initially, it is important to establish whether the more abundant taxa are typically oceanic, shelf-associated, or estuarine. *Aglantha digitale* is a small hydrozoan trachymedusa with a holoplanktonic life history. In contrast, large shallow-dwelling scyphomedusae common to the area (e.g., Russell 1970) release ephyrae (young medusae) seasonally (e.g., Barz and Hirche 2007) from polyps attached to coastal benthos. Thus *A. digitale*, which was quantified during the 1990s in this region (Nicholas and Frid 1999), would likely increase with an influx of Arctic water (Raskoff et al. 2005), whereas the benthic polyps of scyphomedusae would bloom subject to localized coastal influence. A variety of additional taxon-specific factors and adaptations have been suggested to explain fluctuations of scyphomedusae (e.g., Brodeur et al. 1999; Thuesen et al. 2005), cubomedusae (Hartwick 1991), hydromedusae (Nicholas and Frid 1999), and even hydroids (Madin et al. 1996; Bollens et al. 2001).

Given the lack of detail in the methods of the Attrill et al. (2007) manuscript, it is not possible for a reader to evaluate effectiveness of the CPR for sampling different types of planktonic cnidarians. One has to consult other literature, for example, to learn that the apparatus opening is only 1.61 cm^2. It would appear that, other than fragments of oral arms, only the smallest individuals of true scyphomedusae, along with small hydromedusae and siphonophores, could potentially be sampled by the CPR. This distinction undermines the validity of comparing CPR data with the data on large scyphomedusae obtained in the trawls of Lynam et al. (2004). By considering the variety of ways that nematocysts captured by the CPR relate to actual jellyfish abundance, one might be able to distinguish true community or ecosystem shifts such as a change in abundance of a particular dominant cnidarian; an increase or intrusion of a new species; a change in size from big scyphozoans to smaller hydrozoans (medusae or siphonophores); or a change in depth distributions, with deeper taxa moving up to CPR range.

Regression analyses—In the nematocyst data, there are two outliers that lie more than 2.5 standard deviations from the mean (Fig. 1, points x, y). There are a few approaches to treating suspected outliers in a data set. One way is to examine the overall distribution of the data and exclude outlying points on the grounds that they are nonrepresentative, improperly obtained, or anomalous. Another way is to remove points that do not fit a hypothesized trend. This second method begins with the assumption of a correlation and, with the obvious risks of biasing the result, removes points that do not fit that relationship. In either case, Grubbs' test is a simple way of quantifying where a point lies relative to the standard deviation of the distribution or the hypothesized regression.

Attrill et al. (2007) test correlations of their nematocyst index for six regions against three (and for one region

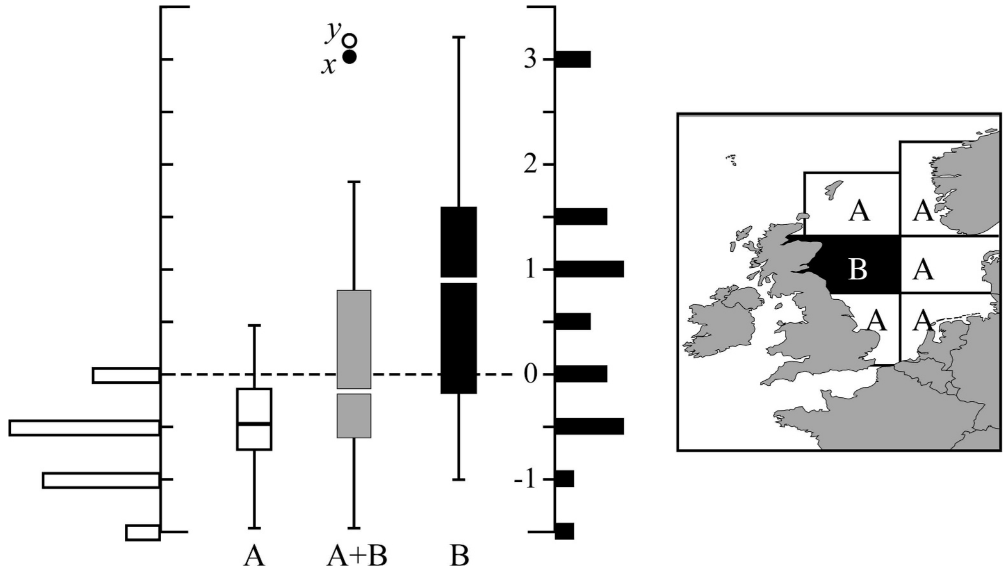

Fig. 1. Distribution of nematocyst data used by Attrill et al. (2007) in different analyses. *y*-axis is the normalized nematocyst index. Distribution A: Data from the five regions of low nematocyst counts (A on map), which were excluded from the pH regression but included in all other analyses. White-filled histogram at left also shows distribution of these data. Distribution B: Data from the one region (box B on map, data subset B) containing the nematocyst indices that were used in the pH regression. Data values, which include points *x* and *y* of A+B, also shown in black-filled histograms along right axis. Combined distribution of data (A+B, at middle) showing outliers that were either excluded (point *x*) or included (point *y*) in NAO and inflow regressions.

against four) environmental indices. Among these they find a moderate ($r = 0.33$) correlation with the North Atlantic Oscillation (NAO) in two of six regions (Attrill et al. 2007: table 1) and in the overall data set (Attrill et al. 2007: fig. 2A). In two of their regressions, they remove one outlier (point *x* in Fig. 1) while retaining an outlier (point *y* in Fig. 1) that is even more remote relative to the mean nematocyst distribution. As expected, the effect of this selective removal from the NAO analysis is to increase the r^2 value from 0.3 to 0.4. Point *x* is retained in a third regression (*see* below) where it strengthens the relationship between the nematocyst index and pH. The reader is left to consider the justification for removing outliers when they do not fit the correlations that are being tested. If they are truly anomalous, it would seem judicious to exclude both from the entire analysis.

Both outliers in the nematocyst index lie in region C2 (Fig. 1, region B), off the east coast of the United Kingdom, which is the only area selected for further analysis against pH (Attrill et al. 2007: fig. 2c). This region also includes nearly all the top values of the combined nematocyst index (Fig. 1, data subset B). The uppermost 13 values in the data set and 16 of the top 18 are from region C2, whereas 14 of the 17 lowest values are from outside C2, in the other five regions that were not used in the pH analysis (Fig. 1, data subset and region A). Region C2 also excludes the most recent data where nematocyst indices reach anomalously low values. Every one of the values ($n = 22$) excluded from pH analysis lies below the mean of the values that were included ($n = 20$) (Fig. 1, subset A vs. B). Attrill et al. (2007) mention the choice of years as constrained by data availability, but justification for the choice of this region as the sole locale for pH comparison is not presented in the methods—perhaps the pH data were only available for this area, or C2 was sampled more in recent times. In any case, the data used for pH analysis are not representative of the region as a whole. Within this selected data subset, the authors found a moderate relationship ($p = 0.042$; $r^2 = 0.21$) in the detrended pH data, and, despite the weak support, postulate a link between ocean acidification and the occurrence of jellies for "the first time."

Attrill et al. (2007) mention a positive correlation between nematocysts and a chlorophyll proxy in five of the six regions, and lack of correlation between salinity and oceanographic parameters. However, these data are not among the 22 results presented in their table 1, and it appears that these tests were not factored into the Bonferroni corrections that were applied to the other comparisons. Considering that the analysis of NAO vs. nematocysts across the whole region is not significant except in the detrended data, the selective exclusion of outliers and reduction of multiple comparisons could have a substantial effect on the significance of correlations.

Projections of a "gelatinous future"—Attrill et al. (2007) project their nematocyst counts over time to predict a "near-linear increase." This approach differs from the way that nearly identical changes in plankton populations have been described in other studies. For example, Beaugrand (2004) describes steplike changes in temperate copepods and flatfish recruits in the North Sea. He uses these examples as illustrative of a general shift between "alternate stable dynamic regimes." These taxa both increase near the same time that the nematocyst index undergoes a step increase. Greene and Pershing (2007) describe increases in phytoplankton and small copepods using two offset means, with the discontinuity coming in 1990. These analyses are more in line with the dynamics of the underlying data.

To take the observation of a steplike event and project it out to the future seems comparable with witnessing a tide rise 2 m over a day and predicting a 60-m tide by the end of the month. Even so, the model said to show a "more gelatinous future" (Attrill et al. 2007) only reaches a nematocyst index of 1.0 after 60 yr. This prediction seems less dire given that values three times higher are already represented in the data set analyzed. The mean of the values used in the pH regression actually exceeds the end point that the model predicts after 50 yr.

Broader implications—Baseline data sets of plankton abundance and distribution are important for detecting ecosystem change, yet such data sets, especially for gelatinous organisms, are rare. From this perspective, and for certain organisms, a time series like the CPR data is of great value and cannot be recreated or replaced. However, considering the strength of the analyses presented, the conclusions drawn by Attrill et al. (2007) appear to be overstated. Despite finding no significant relationship between sea-surface temperature and jellyfish, either in individual regions or in the combined data set, they describe their conclusions for the popular press in these terms: "…all climate projections expect the North Sea to become warmer, so jellyfish will become more and more common in our waters" (press release, also quoted in Sample 2007). Furthermore, despite finding a very weak relationship between ocean pH and the nematocyst index in a nonrepresentative subset of the data, they make general assertions about ocean acidification that a casual reader will not likely challenge. Broad statements about global warming and climate change are likely to garner a great deal of attention, and thus should be held to a relatively high standard of analytical rigor.

Scientific discourse should be conducted objectively, but there is a risk to challenging assertions of climate-related change: skeptics can point to this as evidence that the research community is divided, or that such changes are not occurring. However, because research of this kind can have lasting policy implications, it is important not to attribute all perceived ecological change to "global warming" or "ocean acidification" without reasonable evidence from an appropriately broad data set. Exclusive focus on these intimidating issues, which are not under the control of any single government, draws attention away from other potential causes of ecosystem change such as eutrophication, overfishing, and species introduction (Purcell 2005), which *can* be locally regulated. Anthropogenic shifts in the gelatinous community of the North Sea have already been documented (Boersma et al. 2007). The fact that all of the highest nematocyst counts occurred in one region off the coast of Scotland, adjacent to the Firth of Forth, supports the idea that local factors (that could in turn be affected by climate change) should not be discounted.

A conservative interpretation of the CPR data set is that the regime shift reported by others has modified the community structure of North Sea planktonic cnidarians to an extent that merits further detailed study. Such a conclusion preserves the intended warning of Attrill et al. (2007) about the consequences of global change and bolsters the case for long-term studies of gelatinous plankton, while not going beyond the strength of the evidence at hand.

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