Limnol. Oceanogr., 53(6), 2008, 2763–2766

Reply to Haddock, S.H.D. Reconsidering evidence for potential climate-related increases in jellyfish

Introduction and errata

Following the publication of our paper (Attrill et al. 2007), we became quickly aware of a couple of errors. We have subsequently been collaborating with Dr. Chris Lynam (Lynam et al. 2004, 2005) to bring together our two datasets, explore the common patterns within our data, and attempt to provide a consensus on how climate is affecting gelatinous plankton in the North Sea. During this reanalysis, two errors within the data were discovered, one involving a transcription error of a column of residuals during de-trended analysis, the other a major data entry error deep in the Continuous Plankton Recorder (CPR) database for sector B2.

Here we present a revised version of table 1 from Attrill et al. (2007) to incorporate corrections to these transcription and data entry errors. These corrections alter some of the results in our original data table, mainly to increase and strengthen the number of significant relations we found (e.g., for sector B2 and whole sea area); all previous main results remain robustly significant. Following discussions with Dr. Lynam, two clarifications of statements made in Attrill et al. (2007) are also required. Page 482, Results, last line of first column: "*There were no...robust, consistent relations between jellyfish frequency and any environmental variables for B and D… contrary to the findings of previous shorter time series (Lynam et al. 2005)*." The Lynam et al. (2004, 2005) papers presented no data for the D sector and found no link in the B sector, contrary to our revised results. Page 482, Discussion, paragraph 1, last sentence: "*… positive association … North of Scotland (Lynam et al. 2005) … does not appear to be maintained*." Our paper did not report on any data that covered Lynam et al.'s (2005) North of Scotland area so the statement is not directly supported, although their positive relation North of Scotland, when considered in conjunction with inflow, may agree with the C2 and B2 results of Attrill et al. (2007).

Overall considerations

We wish to clarify an interpretation by Purcell et al. (2007) that our paper was reporting changes in jellyfish abundance. Haddock (2008) also inferred this (e.g., comments such as "highest counts" and "most abundant taxa"). The methods in our original paper attempted to make it clear that we were not presenting data on changes in jellyfish abundance, but on the more conservative measure: frequency of occurrence (although unfortunately we used the word "abundance" occasionally in discussion) in samples taken by the CPR. We were interested in whether or not a sample showed evidence of encountering a pelagic cnidarian. We make no comment about blooms, but how frequently cnidarians appear in the CPR record and how this has changed over time, potentially in response to climatic and oceanographic variables.

"Jellyfish" section in Haddock comment

Addressing Haddock's (2008) *Jellyfish* section, the first submission of our paper was ataxonomic because we were interested in the overall occurrence of pelagic gelatinous predators and we felt it was difficult, if not impossible using morphology alone, to separate samples into major cnidarian groups. Following review, we were requested to provide discussion on the main taxonomic groups or species we thought were to be found on CPR silks. All evidence suggested the most common species is likely to be *Aglantha digitale* (Williams and Conway 1981; Nicolas and Frid 1999; Hosia and Båmstedt 2007), but we unfortunately erroneously classified this species as a scyphozoan. The species is indeed a hydrozoan trachymedusa, so we suspect that the CPR is mainly sampling small hydrozoan medusae. We feel this actually makes the significant positive correlations with Lynam et al.'s (2004) scyphozoan data we reported (Attrill et al. 2007) even more interesting, contrary to the comments of Haddock (2008), as potentially two very different groups (Scyphozoa, Hydrozoa) are responding in similar ways. Our main interest, however, was to look at the overall level of occurrence of North Sea pelagic cnidarians, which we demonstrated was related to changes in climate variability and Atlantic inflow (Attrill et al. 2007). The mechanisms, or "causes" as discussed by Haddock (2008), beneath this would be interesting to explore but are beyond our study.

Quantitative published data on siphonophores in the North Sea are relatively scarce. Exceptional single-year blooms of siphonophores occasionally have been reported in shallow, southern coastal (and eutrophicated) areas (Greve 1994); such abundances had not appeared before and did not do so again during Greve's (1994) survey. Williams and Conway (1981) reported that siphonophores are found deeper than hydromedusae, below the sample depth of the CPR, while Hosia and Båmstedt (2007) commonly found them only in deep, oceanic fjords. This general lack of information on siphonophores could be due to different factors, including the inability of traditional nets to quantitatively collect these very fragile organisms and the scarce taxonomic expertise available for the identification of such complex colonial jellyfish. Nematocysts from any siphonophores can possibly be included in the nematocyst index, but where nectophores are identifiable, this group has been enumerated separately in the CPR analysis, similar to other methodologies used to enumerate siphonophores (Hosia and Båmstedt 2007). We have compiled these siphonophore records within the CPR database: these show an interesting increasing pattern over time (Fig. 1). In summary, we stress that our primary interest was in long-term change in overall cnidarian frequency and the relation between this measure and environmental variables, including climate. Proportional changes in taxonomic groups resulting from environmental

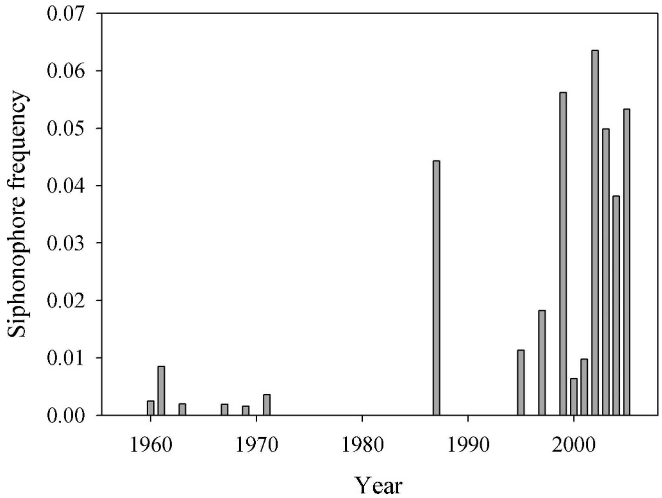

Fig. 1. Frequency of siphonophores recorded in the CPR database for the whole North Sea region 1958–2006. Data expressed as percentage of samples containing siphonophores, identified by the presence of a nectophore on the silk.

variation, as suggested by Haddock (2008), could possibly be one factor (among several) explaining our trends, but do not affect or diminish the general patterns we present, namely the strong relation between jellyfish occurrence, climatic variation, and inflow.

Statistical analyses

Haddock (2008) makes several comments on our regression analysis. Our analyses were as robust as in most such papers, including: full consideration and testing of residuals' structure, autocorrelation assessment, de-trending, and suitably adjusted probability levels. We concentrated the presentation of our results a priori on CPR region C2 because that most closely fits the North Sea area presented by Lynam et al. (2004) where they demonstrated their negative relation between jellyfish and the North Atlantic Oscillation Index (NAOI; east of Scotland site). Lynam et al. (2004; fig. 2) presented other similar, and stronger, trends from west of Denmark, but this area did not coincide so closely with any CPR region, so we focused on C2 because this was the best spatial match between datasets. Further relations for other northeast Atlantic regions were presented in Lynam et al. (2005). Our revised analysis following data-error corrections increases the number of significant results for other regions, most of which have strong significance levels (Table 1). It is interesting to note that where our (Attrill et al. 2007) positive relation is strongest (C2), Lynam et al.'s (2004, 2005) relation is weakest (east of Scotland), but where their negative relation is strongest (west of Denmark) ours is weakest (C1). Haddock (2008) focused extensively on the question of outlier removal; similar to Lynam et al. (2004), we had removed one point from the main analysis. Our figure (Attrill et al. 2007; fig. 2) clearly shows this one point is remarkably different from all other 42 points in terms of the relation between jellyfish and NAOI and, in particular, jellyfish and inflow. This point is therefore an outlier in terms of the residuals of the relations and, thus, we used Grubb's test in good faith to see if we were justified in removing it (rather than doing it without test). Considering its incongruous nature, we feel we were justified in removing this one point; keeping the point in does not affect the significance of either relation (e.g., jellyfish-NAOI: $r^2 = 0.296$, $p = 0.00016$). Inclusion, of course, affects the r^2 value but, like most such analyses, we were attempting to model the general trend over >40 yr and explain the main variation. What is actually interesting here is why this year (1987) is such an outlier. All we can do is speculate, but it is most likely due to the behavior of the NAOI and, particularly, inflow at that time, which we have shown to have the closest relation with jellyfish frequency. The year before the outlier (1986) had the highest modeled inflow value in the time series up to this point (1.424), which was followed in 1987 by a flip to the lowest recorded value (1.089), probably associated with the general regime shift that was occurring at the time (Reid et al. 2001; Beaugrand 2004). Following 1987, the inflow built up again to high values, this time correlated with increases in jellyfish frequency. We feel that the most likely explanation is that this year was anomalous in terms of inflow, rather than jellyfish frequency, being a single low-inflow year in a period of otherwise high inflow. It may be that this dramatic, and fast, change was not reflected in jellyfish frequency, other changes in NAOI and inflow being a bit more gradual and lasting longer, thus allowing a response of jellyfish to be apparent. A single anomalous, low-inflow year my not have been enough to trigger such a change.

pH analysis

A further Haddock (2008) comment to address here is that we included this point in our pH analysis, inferring that this allowed the trend to be significant. We pulled out data from an International Council for the Exploration of the Sea (ICES) database equivalent to sector C2, following our focus on this area in response to Lynam et al. (2004), just to see if this parameter explained any of the variation in jellyfish abundance. Unfortunately, suitable pH data were only available for limited years and we used all of these, including 1987. The point was not an outlier in this analysis in terms of residuals from the relation, but for completeness and consistency we have removed the point and redone the pH analysis for $n = 19$. Contrary to the suggestion of Haddock (2008), removal of this point actually strengthens the relation (Table 1; previous values: $r = -0.546$, $p = 0.013$; de-trended, $r = -0.460$, $p = 0.042$). We stress that we presented this as an interesting additional finding that is the first to significantly demonstrate a relation between pH and some measure of jellyfish populations, not demonstrating "a link between ocean acidification and jellies for the first time" as Haddock (2008) states. We attempted to put this result in the context of current debate, but have no information on mechanisms. We did not attempt further regional analyses of pH due to our focus on C2 (unfortunately in hindsight), so it is entirely possible, as Haddock (2008) suggests, that this is an

Table 1. Results are from bivariate correlation analyses (Pearson's) between mean annual jellyfish frequency in each North Sea sector (e.g., B1 = mean annual frequency for sector B1) and North Atlantic Oscillation Index (NAOI), Atlantic Inflow Index, and Sea Surface Temperature (SST, annual mean for each sector). All $n = 42$. One separate analysis is presented on existing ICES data for mean annual pH and C2 jellyfish frequency ($n = 19$), with original outlier removed (see text). All significant results are in bold; those in italics are not significant following Bonferroni adjustment for multiple tests. For all significant results, de-trended analysis was also undertaken by correlating the residuals from variable–year regressions.

Pair of variables	Pearson's correlation *r*	Pearson's correlation *p*	De-trended correlation analysis *r*	De-trended correlation analysis *p*
B1 vs. NAOI	0.247	0.115		
B1 vs. inflow	0.315	***0.042***	0.148	0.348
B1 vs. SST	0.083	0.602		
B2 vs. NAOI	0.529	**<0.001**	0.282	0.070
B2 vs. inflow	0.545	**<0.001**	0.401	**0.009**
B2 vs. SST	0.191	0.226		
C1 vs. NAOI	0.412	**0.007**	0.273	0.081
C1 vs. inflow	0.501	**0.001**	0.411	**0.007**
C1 vs. SST	0.211	0.180		
C2 vs. NAOI	0.637	**<0.001**	0.484	**0.001**
C2 vs. inflow	0.711	**<0.001**	0.636	**<0.001**
C2 vs. SST	0.213	0.180		
C2 vs. pH	−0.585	**0.009**	−0.510	**0.026**
D1 vs. NAOI	0.016	0.920		
D1 vs. inflow	0.321	***0.038***	0.383	**0.012**
D1 vs. SST	−0.018	0.911		
D2 vs. NAOI	0.226	0.150		
D2 vs. inflow	0.283	0.069		
D2 vs. SST	0.160	0.311		
Whole sea vs. NAOI	0.556	**<0.001**	0.372	**0.015**
Whole sea vs. inflow	0.645	**<0.001**	0.550	**<0.001**
Whole sea vs. SST	−0.061	0.703		

anomalous region and that no wider relationship between pH and jellyfish exists. Further analysis of this wider relationship between pH and CPR nematocyst occurrence may shed more light on the consistency of this relation evident in C2, but we have neither collected these pH data nor undertaken these analyses.

Future trends

Finally, Haddock (2008) questions the validity of our projection analysis, where we couple our regression analysis with models for future behavior of the North Atlantic Oscillation (NAO). Again here we have been very conservative, interested in direction as much as extent and attempting to achieve a consensus trend by concentrating on the central tendency of models. Over a 40-yr period we found a significant relation between NAOI and jellyfish frequency, which captures the dramatic changes occurring during the late-1980s regime shift that Haddock (2008) mentions. We are very familiar with this phenomenon, being part of the team that has described it (Edwards et al. 2002; Reid et al. 2003; McQuatters-Gollop et al. 2007); it seems likely that the event was triggered by major oceanographic change (including inflow) in response to an extremely positive NAO (Beaugrand and Reid 2003; Reid et al. 2003). Because the regime shift was intimately linked to NAO behavior, and our results demonstrate a relation between NAO and jellyfish occurrence over 40 yr, we feel confident that our trend has captured some of the largest variations in the NAO, including stepwise regime shifts, and yet remained robust. Therefore, using this relation to predict possible direction of trends into the future when the NAO is modeled to move more strongly positive is very reasonable; we are looking at the central tendency around which there is likely to be extensive variation, but all indications suggest a move towards increased jellyfish occurrence if our 40-yr trend continues. From our data this jellyfish trend is modeled around changes in hydromedusae, but because the CPR data and Lynam et al.'s (2004) scyphomedusa data are significantly correlated, it is possible that such patterns may hold for jellyfish as a whole.

Martin J. Attrill[1]
Marine Biology & Ecology Research Centre
Marine Institute
University of Plymouth
Drake Circus, Plymouth PL4 8AA, UK

Martin Edwards
Marine Biology & Ecology Research Centre
Marine Institute
University of Plymouth
Drake Circus
Plymouth PL4 8AA
UK; Sir Alister Hardy Foundation for Ocean Science (SAHFOS), The Laboratory
Citadel Hill, Plymouth PL1 2PB, UK

References

Attrill, M. J., J. Wright, and M. Edwards. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol. Oceanogr. **52:** 480–485.

Beaugrand, G. 2004. The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progr. Oceanogr. **60:** 245–262.

———, and P. C. Reid. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Glob. Change Biol. **9:** 801–817.

Edwards, M., G. Beaugrand, P. C. Reid, A. A. Rowden, and M. B. Jones. 2002. Ocean climate anomalies and the ecology of the North Sea Mar. Ecol. Prog. Ser. **239:** 1–10.

Greve, W. 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. ICES J. Mar. Sci. **51:** 355–358.

Haddock, S. H. D. 2008. Reconsidering evidence for potential climate-related increases in jellyfish. Limnol. Oceanogr **53:** 2759–2762.

[1] Corresponding author (mattrill@plymouth.ac.uk).

Hosia, A., and U. Båmstedt. 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. Mar. Ecol. Prog. Ser. **351:** 113–127.

Lynam, C. P., S. J. Hay, and A. S. Brierley. 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol. Oceanogr. **49:** 637–643.

———, ———, and ———. 2005. Jellyfish abundance and climatic variation: Contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J. Mar. Biol. Assoc. U.K. **85:** 435–450.

McQuatters-Gollop, A., D. E. Raitsos, M. Edwards, Y. Pradhan, L. D. Mee, S. J. Lavender, and M. J. Attrill. 2007. A long-term chlorophyll dataset reveals regime shift in North Sea phytoplankton biomass unconnected to increasing nutrient levels. Limnol. Oceanogr. **52:** 635–648.

Nicholas, K. R., and C. L. J. Frid. 1999. Occurrence of hydromedusae in plankton off Northumberland (western central North Sea) and the role of planktonic predators. J. Mar. Biol. Assoc. U.K. **79:** 979–992.

Purcell, J. E., S. Uye, and W. T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. Mar. Ecol. Prog. Ser. **350:** 153–174.

Reid, P. C., M. F. De Borges, and E. Svendsen. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fish. Res. **50:** 163–171.

———, M. Edwards, G. Beaugrand, M. Skogen, and D. Stevens. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish. Oceanogr. **12:** 260–269.

Williams, R., and D. V. P. Conway. 1981. Vertical distribution and seasonal abundance of *Aglantha digitale* (O. F. Muller) (Coelenterata: Trachymedusae) and other planktonic coelenterates from the northeast Atlantic Ocean. J. Plankton Res. **3:** 633–643.

Acknowledgments

We thank Chris Lynam for his help in spotting some of the errors in the original de-trended data analysis, confirming results of reanalysis published here, and providing useful comments on the text of this response. These corrections have strengthened the results of our study. Thanks also to Priscilla Licandro (SAHFOS gelatinous plankton analyst and taxonomist) for advice on CPR sampling of jellyfish material and comments on the text. Jade Wright was a coauthor on our original paper as the research assistant aiding extraction of data; she has since left the field and so was not included in this reply.

Received: 9 March 2008
Accepted: 9 July 2008
Amended: 14 July 2008