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## Are jellyfish increasing in response to ocean acidification?

*Abstract*—Ocean acidification may negatively affect calcifying plankton, opening ecological space for non-calcifying species. Recently, a study of climate-forcing of jellyfish reported the first analysis suggesting that there were more jellyfish (generally considered a noncalcifying group) when conditions were more acidic (lower pH) from one area within the North Sea. We examine this suggestion for a number of areas in the North Sea and beyond in the Northeast Atlantic using coelenterate records from the Continuous Plankton Recorder and pH data from the International Council for the Exploration of the Sea for the period 1946–2003. We could find no significant relationships between jellyfish abundance and acidic conditions in any of the regions investigated. We conclude that the role of pH in structuring zooplankton communities in the North Sea and further afield at present is tenuous.

Elevated atmospheric carbon dioxide levels are altering the carbonate balance in the ocean, releasing more hydrogen ions into the water and lowering power of hydrogen (pH). There has been a drop of 0.1 pH units since the Industrial Revolution, representing a 30% increase in hydrogen ions (Raven et al. 2005). Such acidification of the ocean may make calcification more difficult for calcareous organisms, and tends to dissolve structures already formed. Experimental evidence suggests planktonic organisms with calcified shells, plates, or scales that could be negatively affected include coccolithophores (Riebesell et al. 2000) and mollusks (Orr et al. 2005), as well as echinoderms, foraminiferans, and some crustaceans (Raven et al. 2005). In the recent IPCC (Intergovernmental Panel on Climate Change) report, however, there was no empirical evidence reported for the effect of acidification on marine biological systems (Rosenzweig et al. 2007).

In a recent article by Attrill et al. (2007), one of their findings was the first example of an organism, they presumed was noncalcareous, benefiting from ocean acidification. Specifically they found a negative relationship between jellyfish abundance and ocean pH in the western

central North Sea over the period 1971–1995 (i.e., lower pH resulted in more jellyfish), but did not include analyses for any of their other five areas of interest. At face value this appears to suggest that we may now be observing a change in ecosystem state in the North Sea in response to ocean acidification. Although these authors accept that there is no known direct mechanism of ocean acidification benefiting jellyfish, they argue that jellyfish may take advantage of the vacant niches made available by the negative effects of acidification on calcifying plankton (*see also* Hays et al. 2005). We must remember, however, that more acidic conditions could also actually negatively affect jellyfish, since most scyphozoan medusae and some hydrozoan medusae such as *Aequorea victoria* possess statoliths. Currently it is not known whether statoliths are affected by reduced pH or whether they are sufficiently protected so they can continue functioning in equilibrium reception.

We feel that the issue of the response of jellyfish to pH is extremely important because at the recent International Zooplankton Production Symposium (Hiroshima, Japan, 28 May–01 Jun 07) the work by Attrill et al. (2007) was highlighted as the only evidence where ocean acidification has already affected (here benefiting) a marine organism. Whether jellyfish might benefit from ocean acidification is a question of considerable ecological and economic significance. In some systems, jellyfish can replace fish as the dominant higher trophic-level (Lynam et al. 2006) and the ecosystem may not easily revert back to one dominated by fish because jellyfish can suppress fish through their voracious predation on fish eggs and larvae (Purcell and Arai 2001). Jellyfish are sometimes regarded as trophic dead-ends, because they have few obligate predators, and those they do have (sunfish and some turtles) are relatively rare. Jellyfish blooms also have serious consequences for humans: they can cause loss of tourist revenue through forcing of beach closures; they can block the cooling-intake systems of coastal power-plants and force temporary shut-downs in electricity generation; they clog and burst fishing nets and contaminate fish catches; they can make pelagic

Table 1. Information on jellyfish samples from the CPR and pH data (top 50 m) from the ICES database within each of our seven regions (*see* Fig. 1).  $r$  is the correlation between jellyfish and pH, and  $n'$  is the number of effective data points after adjusting for temporal autocorrelation following the procedure of Pypers and Peterman (1998).

Box	R	$n'$	Jellyfish			pH	
			No. of CPR samples	No. of samples with coelenterate tissue	No. of years	No. of measurements	No. of years of data
1	-0.50	10	9281	783	37	6388	16
2	-0.36	20	38,152	6915	56	4933	26
3	-0.14	13	18,913	2982	48	6244	25
4	0.03	18	17,363	2690	57	3949	19
5	-0.35	17	29,837	4007	58	5657	17
6	-0.14	15	17,701	2238	57	5950	39
7	0.19	29	20,090	3109	47	3084	30

fish assessments difficult by interfering with acoustic signaling; and they can negatively affect commercial fish recruitment (Purcell and Arai 2001).

To subject the relationship between jellyfish abundance and pH identified by Attrill et al. (2007) to more extensive testing, we perform a new comparative analysis of this relationship over a broader spatial scale encompassing the North Sea and much of the North Atlantic. We could find no general negative relationship between jellyfish abundance and acidity in the region or in any of the specific regions tested. Here, we do not address other relationships described in Attrill et al. (2007) between jellyfish abundance and the North Atlantic Oscillation and inflow into the North Sea.

## Methods

We have extracted pH data from the ICES (International Council for the Exploration of the Sea) CTD (conductivity, temperature, depth) and bottle database <http://www.ices.dk/ocean/> for the period 1946–2003 for seven boxes in the North Atlantic (Table 1; Fig. 1). The number and box boundaries were chosen to have >3000 pH samples each, and to simultaneously maximize the number of Continuous Plankton Recorder (CPR) data (*see* Richardson et al. [2006] for more information on the CPR survey). We used pH data from the top 50 m of the water column only, because this is both typical of the mixed-layer depth and the CPR is a near-surface sampler. This gave a total of

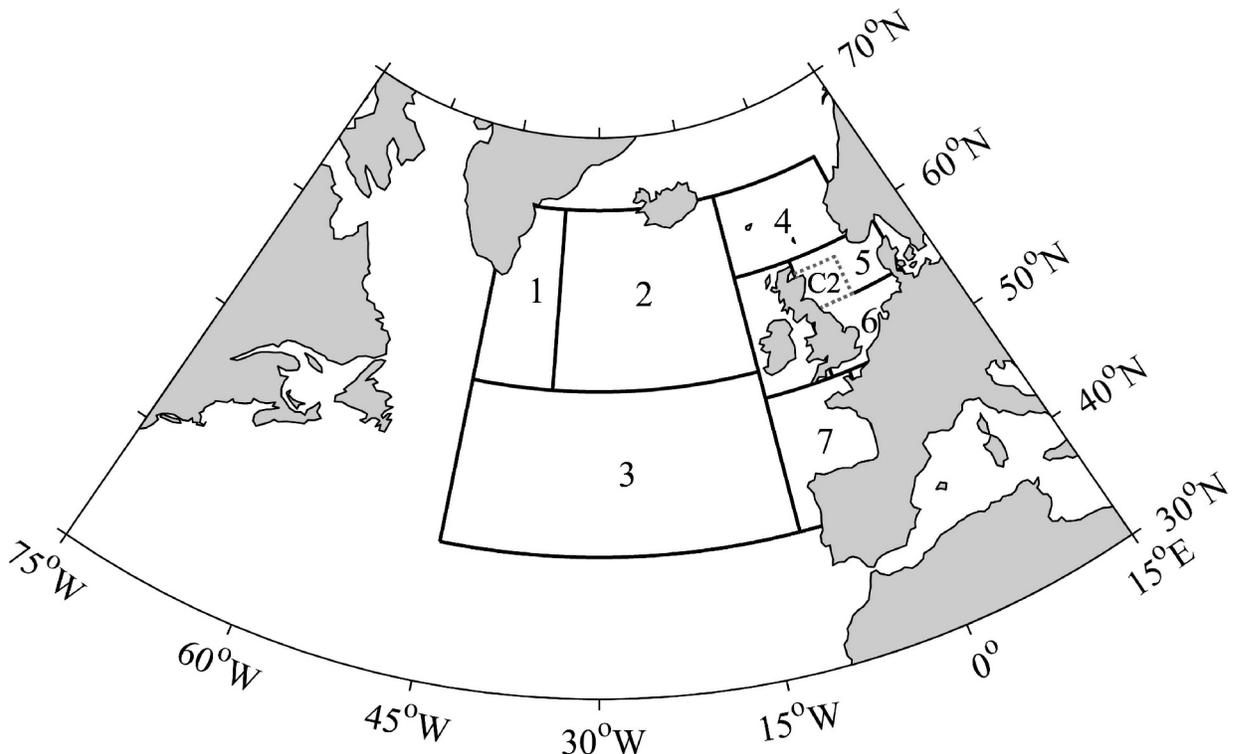


Fig. 1. The seven North Atlantic boxes we used in our analysis. Their number and boundaries were chosen so that each box had >3000 pH samples and also had suitable CPR coverage. Also shown is Box C2 (dotted line) that Attrill et al. (2007) used in their analysis.

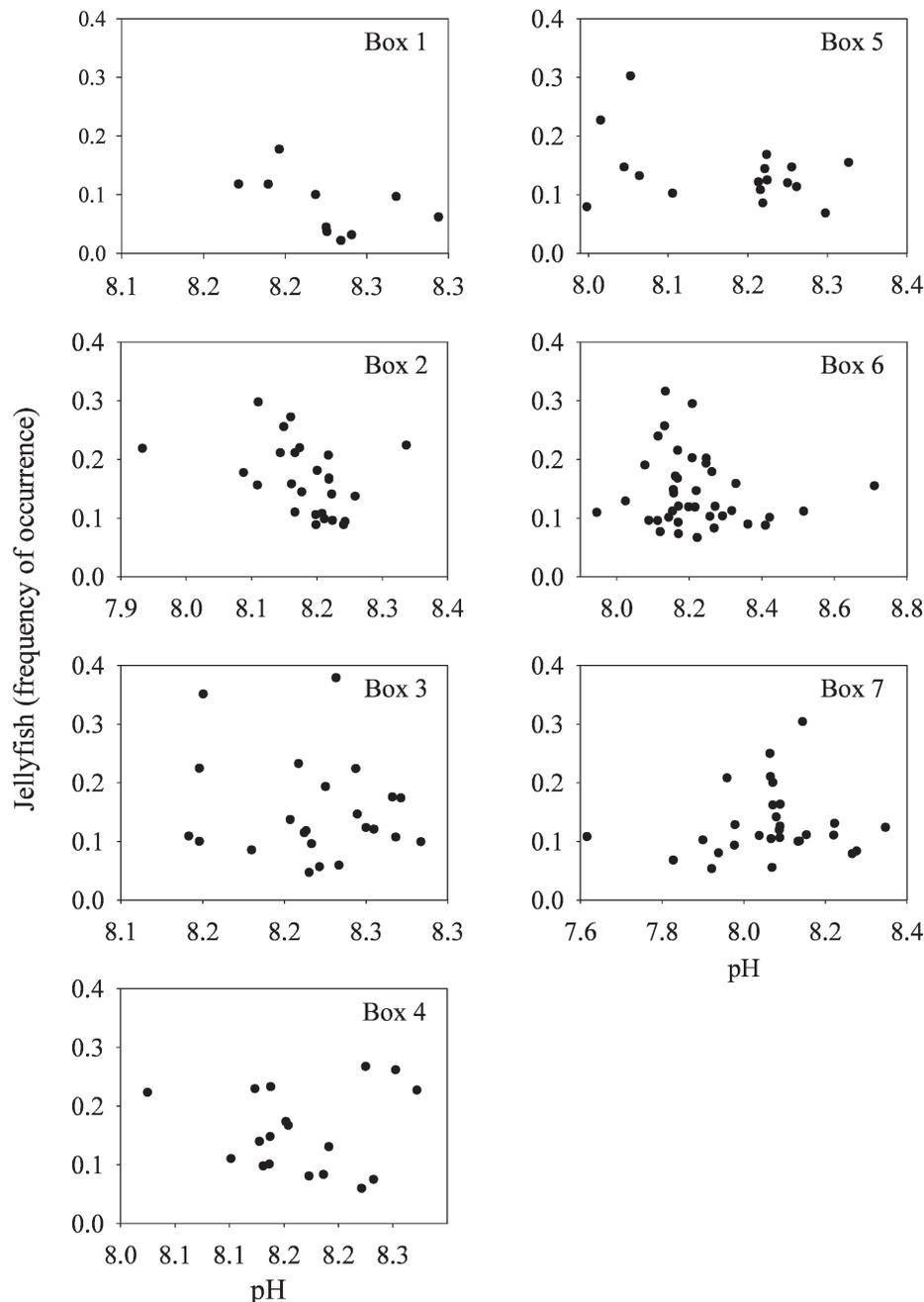


Fig. 2. Relationships between jellyfish and pH for the seven boxes in the North Atlantic (see Table 1 for details of the relationships).

36,205 pH measurements. This compares with a total of 8879 samples from Attrill et al. (2007) from one region.

In our comparison of jellyfish and pH, the coelenterate (jellyfish) data from the CPR were extracted for the same boxes as those used for pH. In calculating annual jellyfish abundances for each of our seven boxes, we have used the frequency of occurrence of coelenterate tissue on CPR samples as used by Attrill et al. (2007). Coelenterate tissue is often identified on CPR silks by the presence of nematocysts, but they are not always visible so often coelenterates are identified solely by the presence of their tissue.

The exact identity of CPR jellyfish tissue is unknown because fragile gelatinous organisms are not well-preserved in CPR samples (Richardson et al. 2006). Attrill et al. (2007) conclude that the CPR predominantly captures scyphozoans because the late-seasonal peak of CPR coelenterate tissue is similar in timing to that of *Aglantha digitale* in the western central North Sea (Nicholas and Frid 1999). However, Attrill et al. (2007) erroneously attributed *Aglantha digitale* to the Scyphomedusae, when it is in fact a small (~40-mm high) holoplanktic hydromedusa (sub-class Trachymedusae, Family Rhopalonematidae). Based on the extensive observations of Russell (1939, 1953) and Kramp

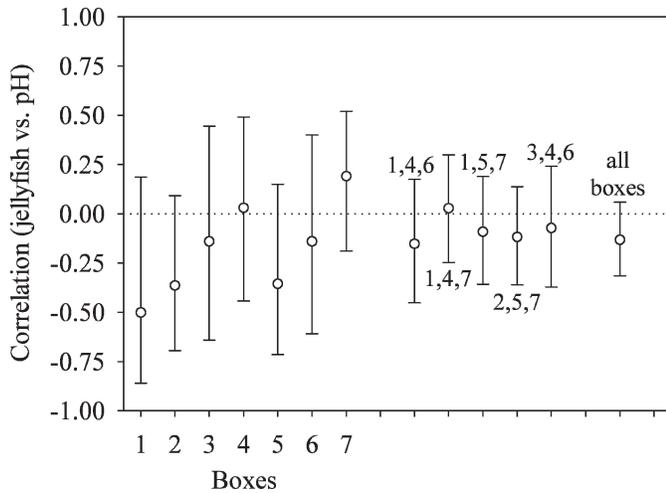


Fig. 3. A meta-analysis of the relationship between jellyfish and pH. Circles and bars represent correlation coefficients and 95% confidence limits, respectively. Correlations shown are for each individual box, for each of the five combinations of three noncontiguous boxes that account for spatial autocorrelation, and the overall meta-analytic correlation for all seven boxes. Confidence limits that overlap with the zero-correlation reference line imply there is no significant relationship between coelenterate abundance and pH.

(1959) regarding the distribution of cnidarians, Gibbons and Richardson (in press) argue that it is more likely that CPR records from the open ocean are dominated by holoplanktic Hydrozoa (Siphonophorae, Narcomedusae, and Trachymedusae), whilst those from coastal waters probably include meroplanktic Hydrozoa (primarily Leptomedusae and Anthomedusae). Definitive proof will only be provided by molecular analysis of CPR coelenterate tissue; such techniques have already been applied successfully to identify echinoderm larvae from the CPR silks (Kirby and Lindley 2005). We have, thus, used the same jellyfish data (i.e., coelenterate tissue) as Attrill et al. (2007) used, but think that it is more likely to be of hydrozoan than scyphozoan origin, although its exact identity does not affect our analyses.

In each of our seven boxes (Fig. 1), we then correlated jellyfish abundance with pH. To identify whether the relationship between jellyfish and pH is generic across our study area, we combined individual correlation coefficients over our seven regions using the meta-analytical method of Worm and Myers (2003). Fixed-effects meta-analytic

models (which assume effect sizes are the same for all correlation coefficients) were appropriate for our analysis. When conducting analyses over the spatial and temporal scales used here, there are two main areas of potential bias: spatial and temporal autocorrelation. Ignoring these inflates the Type I error rate of hypothesis tests, resulting in more significant results. We applied two procedures to ameliorate these effects.

An implicit assumption of a meta-analytic approach applied spatially is that each region is independent. Because our seven regions are contiguous, spatial autocorrelation might be significant because of interactions among jellyfish populations inhabiting adjacent regions. To err on the side of caution, we not only report results from the meta-analysis of all regions, but also results from a meta-analysis on a subset of our regions that are not contiguous and are, thus, likely to have very little spatial autocorrelation (Worm and Myers 2003). This reduced meta-analysis was conducted on all separate combinations of three noncontiguous regions (i.e., regions 1, 4, 6; 1, 4, 7; 1, 5, 7; 2, 5, 7; and 3, 4, 6); three is the greatest number of noncontiguous regions given our box configuration.

Time-series data also present the problem of temporal autocorrelation. One approach to dealing with this issue is to remove the autocorrelation beforehand by fitting a theoretical model and analyzing residuals. Such methods generally increase Type II error rates (probability of failing to detect a real effect) and, hence, reduce statistical power in situations where low-frequency (slowly changing) processes are important sources of covariation in time series (Pyper and Peterman 1998). Because we are interested in retaining this low-frequency variation, we used the approach of adjusting our Pearson correlation test procedure by reducing the effective number of degrees of freedom (Pyper and Peterman 1998). Specifically we used the modified Chelton Method to adjust the degrees of freedom (and, thus, the significance level) of the test procedure and the correlation coefficients remain unchanged.

## Results and discussion

Relationships between jellyfish and pH for the seven regions are shown in Fig. 2, and show that there is variability in both the magnitude and sign of the associations. Many of the time series have substantial temporal autocorrelation so that the effective number of independent data points for each region is sometimes

Table 2. Fixed-effect meta-analysis reporting the weighted mean correlation coefficients  $\bar{r}$ , variance  $v$ , and degrees of freedom  $df$ .

Correlation	df	$Q^*$	$p$	$v$	$\bar{r}$	$Z^\dagger$	$p$
1, 4, 6	2	1.70	0.43	0.0286	-0.15	-0.91	0.36
1, 4, 7	2	3.21	0.20	0.0205	0.03	0.20	0.84
1, 5, 7	2	4.82	0.09	0.0209	-0.09	-0.64	0.53
2, 5, 7	2	4.65	0.10	0.0173	-0.12	-0.91	0.37
3, 4, 6	2	0.27	0.87	0.0265	-0.07	-0.45	0.66
all 7 boxes	6	6.38	0.38	0.0097	-0.13	-1.35	0.18

\* The  $Q$ -statistic tests for heterogeneity of effect sizes.

† The  $Z$ -statistic tests whether  $\bar{r}$  is significantly different from zero.

relatively small (Table 1). Considering this temporal autocorrelation, none of the seven individual correlations between jellyfish abundance and pH were significant, with their 95% confidence intervals all crossing the zero reference line (Fig. 3). For the seven North Atlantic boxes, the overall correlation between jellyfish abundance and pH was also not significant ( $r = -0.13$ ,  $Z = -1.35$ ,  $p = 0.18$ ; Fig. 3; Table 2). Similarly, removing spatial autocorrelation and assessing all five combinations of three boxes, no correlations were significant ( $r$  varied  $-0.13$  and  $0.03$ ; Fig. 3; Table 2). We could thus find little support for the conclusion that more acidic conditions led to greater numbers of jellyfish in the North Sea or more widely in the North Atlantic. Of course, even though there does not appear to be a significant negative relationship between jellyfish abundance and pH currently, it is still possible that with the removal of some data points as outliers or more extensive sampling in the future, individual relationships or even the overall meta-analytic correlations may become significantly negative. However, with the data that are currently available and using a more extensive dataset over a larger spatial area than Attrill et al. (2007), we have to conclude that acidification is not a major influence on jellyfish populations in the region at the scale of our analysis.

From their results from a subarea of the North Sea, Attrill et al. (2007) suggested jellyfish might benefit from a reduction in pH. Although we feel there is no large-scale relationship between jellyfish and pH, this does not mean, necessarily, that there are no smaller local-scale relationships, because we know that relationships between jellyfish and climate can vary considerably across the North Sea (Lynam et al. 2005). Here our focus is on whether there is a general relationship between jellyfish and pH over large scales; assessing many finer-scale local relationships always has an associated risk of increasing the likelihood of spurious correlations.

There is also little evidence that calcifying organisms have declined to create ecological space for jellyfish. Presumably such changes would be marked and precede clear changes in jellyfish. Although laboratory studies have shown acidic conditions reduce formation ofoliths in coccolithophores (Riebesell et al. 2000) and shells in pteropods and have detrimental effects on other zooplankton (Raven et al. 2005), no observed declines in the abundance of calcifiers with lowering pH have yet been reported. In fact, much of the community in the North Sea is dominated by copepods, a noncalcifier, and these have been declining in abundance over the last 50 yr (Edwards et al. 2006). Further, important calcifiers are not major predators or competitors of jellyfish. In addition, community-level changes should manifest first in the Southern Ocean before the North Atlantic because these waters are likely to drop in pH faster than elsewhere and calcifiers such as pteropods are important in this system (Orr et al. 2005). There has been a long-term decline in crustacean zooplankton (krill) in the Southern Ocean with an increase in gelatinous grazers (salps), but there is strong evidence that this change is linked to sea-ice extent and duration and, thus, ocean warming (Atkinson et al. 2004).

Long-term data on echinoderm larvae from the North Sea provide additional compelling evidence to suggest that pH is

not currently an important factor regulating plankton community structure in the region. Larvae of sea urchins form skeletal parts comprising magnesium-bearing calcite, which is 30 times more soluble than calcite without magnesium (Raven et al. 2005). Lower ocean pH should drastically inhibit the formation of these soluble calcite precursors, which are essential for echinoderm shell construction. Echinoderm larvae from the CPR in the North Sea are dominated by the sea urchin *Echinocardium cordatum* and they have exhibited a 10-fold increase in recent times. This increase is linked predominantly to warming (Kirby et al. 2007), and there is no observable negative effect of pH. There is much evidence to link recent changes in composition, abundance, and phenology of North Sea plankton communities to warmer sea temperatures and not pH (Beaugrand et al. 2002; Edwards and Richardson 2004).

A suite of human effects are thought to promote jellyfish, and are more plausible than indirect changes in ocean acidification. These include global warming (Purcell 2005; Lynam et al. 2006), over-fishing (Lynam et al. 2006), eutrophication (Arai 2001), pollution (Parsons and Lalli 2002), alien translocations (Purcell et al. 2001), and habitat modification (Parsons and Lalli 2002). Clearly, there is an urgent need for investigating the effect of acidification on calcareous and other members of the plankton community in the laboratory, and to conduct large-scale manipulative in situ experiments. Field observations such as those here and by Attrill et al. (2007) will continue to provide testable ideas for laboratory work and to provide a baseline for actual changes in the wild. In conclusion, however, we caution against accepting the findings of Attrill et al. (2007) that lower pH benefits jellyfish in the North Sea.

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## References

- ARAI, M. N. 2001. Pelagic coelenterates and eutrophication: A review. *Hydrobiologia* **451**: 69–87.
- ATKINSON, A., V. SIEGEL, E. PAKHOMOV, AND P. ROTHERY. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**: 100–103.
- 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., P. C. REID, F. IBANEZ, J. A. LINDLEY, AND M. EDWARDS. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**: 1692–1694.
- EDWARDS, M., D. G. JOHNS, P. LICANDRO, A. W. G. JOHN, AND D. P. STEVENS. 2006. Ecological status report: Results from the CPR survey 2004/2005. Sir Alister Hardy Foundation for Ocean Science Technical Report 3. ISSN 1744-0750.
- , AND A. J. RICHARDSON. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**: 881–884.
- GIBBONS, M. J., AND A. J. RICHARDSON. In press. Patterns of pelagic cnidarian abundance in the North Atlantic. *Hydrobiologia*.
- HAYS, G. C., A. J. RICHARDSON, AND C. ROBINSON. 2005. Climate change and plankton. *Trends Ecol. Evol.* **20**: 337–344.
- KIRBY, R. R., G. BEAUGRAND, J. A. LINDLEY, A. J. RICHARDSON, M. EDWARDS, AND P. C. REID. 2007. Climate effects and benthic–pelagic coupling in the North Sea. *Mar. Ecol. Progr. Ser.* **330**: 31–38.
- , AND J. A. LINDLEY. 2005. Molecular analysis of continuous plankton recorder samples, and examination of echinoderm larvae in the North Sea. *J. Mar. Biol. Assoc. U. K.* **85**: 451–459.
- KRAMP, P. L. 1959. The hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Rep.* **46**: 1–283.
- LYNAM, C. P., S. J. HAY, AND A. S. BRIERLEY. 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. UK* **85**: 435–450.
- , M. J. GIBBONS, B. E. AXELSEN, C. A. J. SPARKS, J. COETZEE, B. G. HEYWOOD, AND A. S. BRIERLEY. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.* **16**: 492–493.
- 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. UK* **79**: 979–992.
- ORR, J. C., AND OTHERS. 2005. Anthropogenic ocean acidification over the twenty first century and its impact on calcifying organisms. *Nature* **437**: 681–686.
- PARSONS, T. R., AND C. M. LALLI. 2002. Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La Mer* **40**: 111–121.
- PURCELL, J. E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: A review. *J. Mar. Biol. Assoc. UK* **85**: 461–476.
- , AND M. N. ARAI. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. *Hydrobiologia* **451**: 27–44.
- , T. A. SHIGANOVA, M. B. DECKER, AND E. D. HOUDE. 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiologia* **451**: 145–176.
- PYPER, B. J., AND R. M. PETERMAN. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**: 2127–2140.
- RAVEN, J., AND OTHERS. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. London: Royal Society Special Report. The Clyvedon Press.
- RICHARDSON, A. J., A. W. WALNE, A. W. G. JOHN, T. D. JONAS, J. A. LINDLEY, D. W. SIMS, AND M. WITT. 2006. Using continuous plankton recorder data. *Progr. Oceanogr.* **68**: 27–74.
- RIEBESELL, U., I. ZONDERVAN, B. ROST, P. D. TORTELL, R. E. ZEEBE, AND F. M. M. MOREL. 2000. Reduced calcification of marine plankton in response to increased atmospheric CO<sub>2</sub>. *Nature* **407**: 364–367.
- ROSENZWEIG, C., AND OTHERS. 2007. Assessment of observed changes and responses in natural and managed systems, p. 79–131. In M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden and C. E. Hanson [eds.], *Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge Univ. Press.
- RUSSELL, F. S. 1938. The Plymouth offshore medusa fauna. *J. Mar. Biol. Assoc. UK* **22**: 411–439.
- . 1939. Hydrographical and biological conditions in the North Sea as indicated by planktonic organisms. *J. du Conseil* **14**: 171–192.
- . 1953. *The medusae of the British Isles*. Cambridge Univ. Press, Cambridge.
- WORM, B., AND R. A. MYERS. 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**: 162–173.

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