

LETTER

Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming

Hal Whitehead,* Brian McGill and Boris Worm

Department of Biology,
Dalhousie University, 1355
Oxford St, Halifax, NS, Canada
B3H 4J1

*Correspondence: E-mail:
hwhitehe@dal.ca

Abstract

Understanding the effects of natural environmental variation on biodiversity can help predict response to future anthropogenic change. Here we analyse a large, long-term data set of sightings of deep-water cetaceans from the Atlantic, Pacific and Indian Oceans. Seasonal and geographic changes in the diversity of these genera are well predicted by a convex function of sea-surface temperature peaking at *c.* 21 °C. Thus, diversity is highest at intermediate latitudes – an emerging general pattern for the pelagic ocean. When applied to a range of Intergovernmental Panel on Climate Change global change scenarios, the predicted response is a decline of cetacean diversity across the tropics and increases at higher latitudes. This suggests that deep-water oceanic communities that dominate > 60% of the planet's surface may reorganize in response to ocean warming, with low-latitude losses of diversity and resilience.

Keywords

Biodiversity, cetacean, climate change, dolphin, marine mammal, pelagic ocean, sea temperature, whale.

Ecology Letters (2008) 11: 1198–1207

INTRODUCTION

A pressing challenge to ecological science is the prediction of climate change impacts on the world's complex pattern of biodiversity. Most studies to date have focused on terrestrial biota (Pounds *et al.* 1999; Thomas *et al.* 2004; Parmesan 2006); however, there is growing concern about rapid and sometimes surprising changes that have been observed in coastal marine (Hoegh-Guldberg *et al.* 2007) and continental shelf assemblages (Beaugrand *et al.* 2002; Perry *et al.* 2005). Relatively little is known about the open oceans, which comprise most of our biosphere. Yet there are indications that oceanic top predators such as tuna and billfish can react sensitively to changes in climate and may redistribute quickly following El Niño perturbations (for example, Sund *et al.* 1981; Lehodey *et al.* 1997). Individual species' responses to temperature yield a pattern of biodiversity that changes dynamically with climatic fluctuations (Worm *et al.* 2005; Boyce *et al.* 2008). How general these responses are is currently unclear, and their implications for global warming have not yet been explored. It is important to note that biodiversity is not only seen as an important response variable in the context of global change, but also as an insurance against the effects of perturbations including global warming (Petchey *et al.* 1999; Loreau *et al.*

2001; Folke *et al.* 2004). Observations and experiments in both aquatic and terrestrial ecosystems have indicated that eroding biodiversity, both at the genetic and species level, can make ecosystems less resilient, and more vulnerable to climate change and other perturbations (Tilman & Downing 1994; Loreau *et al.* 2001; Reusch *et al.* 2005; Worm *et al.* 2006). Little is known about deep-water pelagic systems and, in particular, deep-water cetaceans. Research on the controls and correlates of diversity can help us to understand and predict how biodiversity will be affected by anthropogenic or natural changes to the environment (Gitay *et al.* 2002).

Here we examine empirical measures of the biodiversity of deep-water cetaceans for the first time (order Cetacea; whales and dolphins), using scientific surveys in three oceans and both hemispheres at a wide range of latitudes and sea temperatures. Relatively little is known of this species-rich group of cosmopolitan predators that range over most of the ocean surface and intermediate waters, foraging down to several 1000 m depth. Although vulnerable to fisheries by-catch, noise and chemical pollution (Reeves *et al.* 2003), the deep-water cetaceans are particularly mobile, wide-ranging and face few barriers, so they might be expected to readily adapt to systematic changes in ocean climate by changing their spatiotemporal distribution. Thus, when considering the effects of climate change, they are

perhaps an indicator group that could signal changes in ocean temperature. From a conservation perspective, they may be considered a 'least concern' group of organisms, those least likely to be affected severely by global warming (Gitay *et al.* 2002).

In this paper, we highlight the effects of variation in ocean temperature on deep-water cetacean diversity using long-term cetacean surveys in three oceans. Our data set spans 26 years and includes 1930 deep-water cetacean sightings (Fig. 1). We use, as a measure of diversity, the number of genera encountered in a fixed number of sightings. This measure approximates the ecological richness of the assemblage independent of overall animal density. The geographical and seasonal richness of genera sighted is well predicted by a convex function of sea-surface temperature (SST). This allows us to examine the potential consequences of ocean warming on large-scale patterns of diversity for these species.

Investigations of the potential effects of climate change on biodiversity often use a 'bottom-up' approach in which niches of individual taxa are estimated and then overlaid to map diversity variability in space and with changing environments (e.g. Jetz & Rahbek 2002; Thuiller *et al.* 2005). In contrast, our macroecological 'top-down' approach analyses measures of empirically observed diversity (as in Rutherford *et al.* 1999; Worm *et al.* 2005). While niche-climate modelling is valuable and the approaches are to some extent complementary, the top-down method has the advantages that the measure of diversity is much more direct, and that it can be employed when there is little information on the niches of individual taxa, as with the

pelagic cetaceans. Furthermore, in our case, we compare diversity measures with simultaneously collected environmental measures, rather than the less direct time-averaged records or interpolations for spatial cells.

METHODS

Field data

Primary data originated from field studies directed at two species of deep-water whale, sperm whales (*Physeter macrocephalus*) and northern bottlenose whales (*Hyperoodon ampullatus*) between 1985 and 2007 in the Atlantic and Pacific Oceans, using the auxiliary sailing vessels *Elendil* (10 m; 1985–1990) and *Balaena* (12 m; 1991–2007). Much of the data originated from the Galápagos Islands, Ecuador (2° N–2° S, 88°–94° W) and the Gully, Canada (43°40'–44°20' N, 58°40'–59°30' W). We also present data from the northern Indian Ocean from *Elendil* (1981–1984 from Alling 1986) for comparison in Fig. 2b. However, in the Indian Ocean data, baleen whale sightings are not available and the time-of-day is not given by Alling (1986), so some duplicate sightings may be included. Thus these data are not fully comparable with those from the Atlantic and Pacific, and were not used in model fitting. HW was the principal scientist aboard the research vessel for more than 50% of the field work. Most other crew were professional cetologists or graduate students studying cetaceans.

While in transit, searching for primary study species, and tracking them, we recorded all sightings of cetaceans

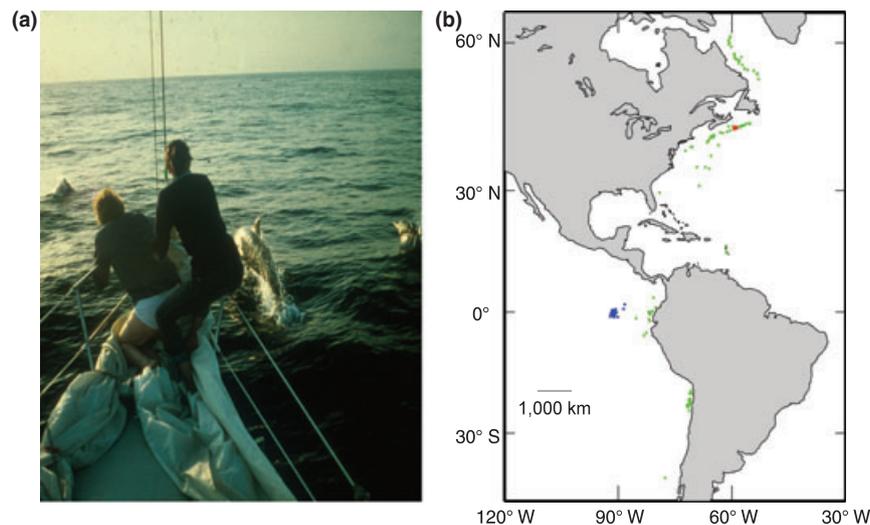


Figure 1 Deep-water cetacean sightings. (a) Cetologists identifying deep-water whales and dolphins from *Elendil*, one of the two research vessels used in this study (Ph. courtesy A. Alling). (b) Locations (mean latitudes and longitudes) of blocks of five consecutive sightings used in the analysis for the Atlantic and Pacific Oceans. Blocks in the Gully offshore canyon (Canada) are in red, those off the Galápagos Islands (Ecuador) in blue, and all others in green. The location of one block in the western Pacific (at 1°9.6' S 157°18.9' W) is not shown. For Indian Ocean sightings, see Supporting information Fig. S1.

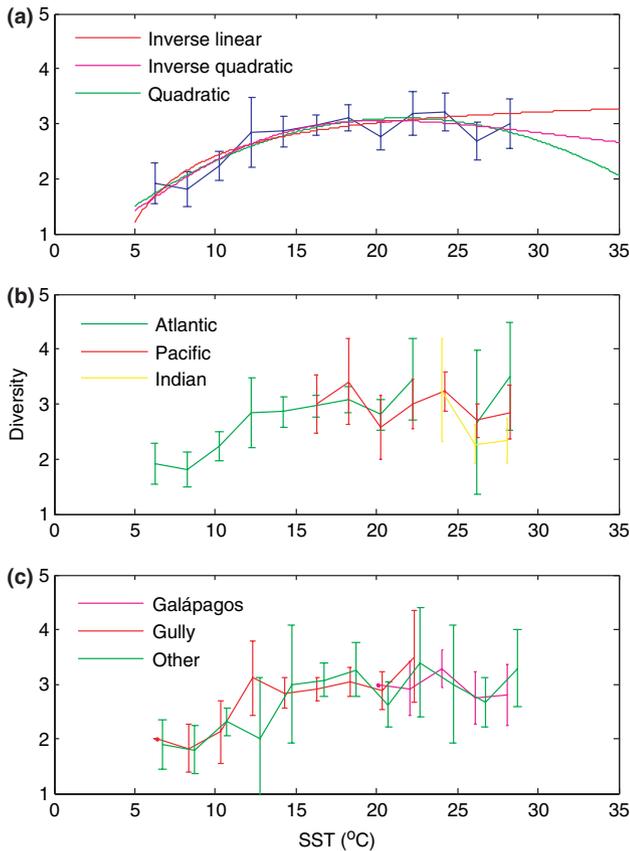


Figure 2 Temperature effects on diversity. Mean genus richness (number of genera observed in five consecutive sightings \pm 95% CI) of deep-water cetaceans in relation to observed sea-surface temperatures, (a) overall, with regression curves from the best-fitting models; (b) for data from Atlantic, Pacific and Indian oceans; (c) for data from the intensely sampled Gully, and off the Galápagos Islands, and other areas (see Fig. 1).

together with the date, time first sighted, identification to highest taxonomic level that could be ascertained with certainty and location (using SatNav 1981–1991; GPS 1992–2007). The crew usually recorded SSTs every 3 h.

We concatenated sightings of the same species made within 1 h, and omitted all sightings of the primary study genera (*Physeter* and *Hyperoodon*, as they were actively sought out), as well as sightings without identification to genus, and those in waters < 200 m depth [as determined using the ETOPO2 (2-min resolution) database; http://www.gfdl.noaa.gov/products/vis/data/datasets/etopo2_topography.html]. We chose genus as the taxonomic level for this study, as there are considerable uncertainties in cetacean taxonomy below the genus level (e.g. within *Stenella* where the generally agreed species taxonomy changed over the course of the field work; Perrin *et al.* 1987), distinguishing species within some genera is difficult in the field (e.g. for *Mesoplodon*, Reeves *et al.* 2002) and a substantial proportion of our

sightings were identified to the genus but not the species (particularly for *Balaenoptera* and *Mesoplodon*). While some cetacean genera are not clearly defined (e.g. *Tursiops*, Rice 1998), problems are fewer than at the species level. Records of *Hyperoodon* from the tropical Indian Ocean were replaced by *Indopacetus*, following recent taxonomic clarification (Dalebout *et al.* 2003).

For most sightings, we estimated the SST from the 06:00-h (local time) record of that day (to minimize the effects of solar warming). However, in areas of rapidly changing SST, such as the Gulf Stream, or if there was no 06:00-h SST record, we used the closest 3-h SST record to the sighting. If no SST was recorded on the day of the sighting, but the vessel was in an area of stable SSTs, then we used the 06:00-h SST 1 day prior or 1 day later. We noted SST for a sighting as missing if there was no SST record within 1 day, or within 3 h in areas of rapidly changing SST.

Analysis

We divided the sighting record into blocks of b sightings such that, among the sightings in each block, there were differences of no more than 30 days, 1000 km or 4 °C SST. Sightings were sequentially omitted from the analysis until a block of b consecutive sightings was found satisfying these conditions. We carried out all the analyses with $b = 3, 5, 8$ and 12.

Our measure of biodiversity, genus richness (y), was the number of different cetacean genera in each block of sightings and could range from 1 to b . We fitted general linear models to the values of y . We assumed that y was normally distributed about a function of SST, depth (logged), absolute latitude, ocean (categorical: Atlantic or Pacific) or area (categorical: Galápagos, Gully or elsewhere), as well as polynomial functions and combinations of these (Table 1). To check for robustness, we also used generalized linear models with binomial error, which produced very similar results (apart from one reversal, the ordering of the support for the different models was the same as that shown in Table 1, and Δ AICs (Akaike Information Criteria) for the different methods differed by < 0.6 for all models with Δ AIC < 10).

An alternative model form is the inverse polynomial (Nelder 1966). Inverse polynomials allow discrimination between the situations when diversity approaches an asymptote with an increasing independent variable, such as SST, and when there is a decline beyond an optimal SST. This decline can be small, in contrast with a standard quadratic function in which the decline above the SST level of maximum diversity has to be symmetric with the increase beneath it. So, we fit the following two inverse polynomial models with normal error terms:

Table 1 Fits of general linear models to data on genus richness of deep-water cetaceans: log-likelihood, number of parameters (K), AIC, Δ AIC (difference between the AIC of the model in question and that of the best-fitting model), AIC weight and deviance explained by each model as a per cent of the deviance of the null model

Model	log(L)	K	AIC	Δ AIC	AIC weight	Deviance reduction (%)
Null (constant)	30.69	2	-57.37	57.56	0.00	0.0
SST (linear)	49.94	3	-93.87	21.06	0.00	10.3
SST, SST ² (quadratic)	61.47	4	-114.93	0.00	0.21	15.9
SST, SST ² , SST ³ (cubic)	62.20	5	-114.40	0.53	0.16	16.2
lat	35.13	3	-64.26	50.67	0.00	2.5
lat, lat ²	42.35	4	-76.69	38.24	0.00	6.3
lat, lat ² , lat ³	49.18	5	-88.37	26.56	0.00	9.9
SST, SST ² , lat	61.47	5	-112.94	2.00	0.08	15.9
SST, SST ² , lat, lat ²	62.35	6	-112.69	2.24	0.07	16.3
SST, SST ² , lat, lat ² , lat ³	62.90	7	-111.80	3.13	0.04	16.6
Ocean	32.64	3	-59.28	55.65	0.00	1.1
SST, SST ² , ocean	61.54	5	-113.09	1.84	0.08	15.9
Area	33.22	4	-58.45	56.48	0.00	1.4
SST, SST ² , area	61.53	6	-111.05	3.89	0.03	15.9
Depth	33.79	3	-61.58	53.35	0.00	1.7
SST, SST ² , depth	61.52	5	-113.04	1.90	0.08	15.9
SST, SST ² , depth, depth ²	61.57	6	-111.14	3.79	0.03	15.9
(SST - a)/[b + c (SST - a)] (inverse linear)	59.29	4	-110.57	4.36	0.02	14.8
(SST - a)/[b + c (SST - a) + d (SST - a) ²] (inverse quadratic)	62.44	5	-114.87	0.06	0.20	16.3

SST, sea-surface temperature; AIC, Akaike Information Criterion.

Factors included were SST, latitude ('lat'), ocean (categorical: Atlantic or Pacific), area (Galápagos, Gully or elsewhere) and the logarithm of water depth ('depth').

$$y = 1 + \frac{\text{SST} - a}{b + c(\text{SST} - a)}, \quad (1)$$

which approaches an asymptote of $y = 1 + 1/c$ as SST increases, and

$$y = 1 + \frac{\text{SST} - a}{b + c(\text{SST} - a) + d(\text{SST} - a)^2}, \quad (2)$$

which peaks when $\text{SST} = a + \sqrt{(b/d)}$. If the model of eqn 2 fits better than that from eqn 1, then this indicates a decline in diversity at high SST.

Minimal AIC indicated the preferred model, while support for other models was suggested by Δ AIC, the difference between their AIC and that of the preferred model (Burnham & Anderson 2002).

Effects of ocean warming

To examine the potential effects of projected ocean warming on deep-water cetacean biodiversity, we used empirically determined relationships between genus diversity and SST and applied them to predicted SST fields from a

range of global circulation models. The model data (in http://www.ipcc-data.org/sres/ccsr_download.html) are from five Intergovernmental Panel on Climate Change (IPCC) SRES scenarios (A1a, A1F, A2a, B1a, B2a) produced by three models (CCSR/NIES; CGCM2; CSIRO-Mk2), although not all scenarios were examined by all the models. We used eqns 3 and 4 together with monthly predictions of SST in cells of $c. 3\text{--}6^\circ$ latitude and longitude (cell sizes vary among the IPCC models) in the years 2020, 2060 and 2080 respectively, together with observations in 1980, to estimate genus diversity in each cell and each month in each period, and then averaged over months for each cell. We present estimated changes in diversity between 1980 and future periods as percentages of the mean, over months for each cell, of the diversity in 1980.

RESULTS

Our filtering procedures yielded 356 observational blocks of five consecutive sightings identified to genus level ($b = 5$) in the Atlantic and Pacific Oceans (Fig. 1b), and an additional 30 blocks in the Indian Ocean (Supporting information

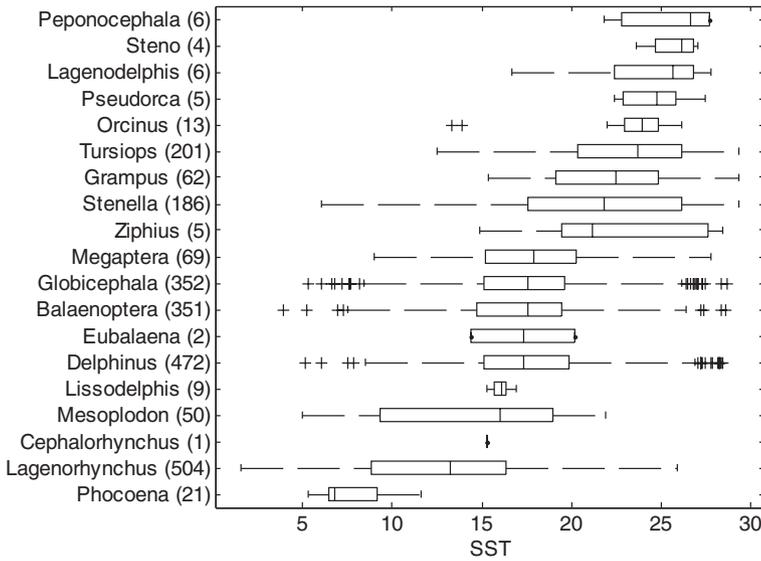


Figure 3 Distribution of individual genera with temperature. Boxplot showing sea-surface temperature (SST) range of sightings for all observed deep-water cetacean genera in Atlantic and Pacific Oceans together with the number of sightings. Each box has lines at the lower quartile, median and upper quartile values. Whiskers extend to the most extreme values within 1.5 times the interquartile range from the box. Values beyond this are shown by '+'.
 Peponocephala (6)
 Steno (4)
 Lagenodelphis (6)
 Pseudorca (5)
 Orcinus (13)
 Tursiops (201)
 Grampus (62)
 Stenella (186)
 Ziphius (5)
 Megaptera (69)
 Globicephala (352)
 Balaenoptera (351)
 Eubalaena (2)
 Delphinus (472)
 Lissodelphis (9)
 Mesoplodon (50)
 Cephalorhynchus (1)
 Lagenorhynchus (504)
 Phocoena (21)

Fig. S1). Substantial numbers of sightings were logged in the Gully, a submarine canyon off Nova Scotia, Canada (177 blocks), and near the Galápagos Islands, Ecuador (45 blocks) (Fig. 1b).

Of the models fit to the data, that representing a quadratic polynomial on SST fit the best (Table 1). Any model without SST and SST² had ΔAIC > 20, indicating very poor support. The inclusion of latitude as a factor in addition to SST and SST² made virtually no difference. The best-supported model was:

$$\text{No. of genera} = 0.395 + 0.250 \cdot \text{SST} - 0.00579 \cdot \text{SST}^2. \quad (3)$$

The convex relationship between genus richness and SST is shown in Fig. 2a, together with the results of fitting inverse polynomial models (eqns 1 and 2). This convex relationship with SST seems to be very well conserved when contrasting data from the Atlantic and Pacific oceans (Fig. 2b), or between the Gully, Galápagos and other areas (Fig. 2c). Diversity appears somewhat depressed in the Indian Ocean (Fig. 2b) but this may be partially due to limitations of the Indian Ocean data set (see Methods). Importantly, as SST varied seasonally or interannually in the intensely sampled Gully or off the Galápagos, genus richness always followed the same general trend (Fig. 2c). In particular, genus richness in the Gully increased rapidly as SST increased over the summer months (Fig. 2c).

The inverse quadratic in SST fit almost as well (ΔAIC = 0.06) as the quadratic (eqn 3):

$$\text{No. of genera} = 1 + \frac{\text{SST} - 2.78}{5.50 - 0.136(\text{SST} - 2.78) + 0.0176(\text{SST} - 2.78)^2}. \quad (4)$$

The first-order inverse polynomial described in eqn 1 fit the data substantially worse with ΔAIC = 4.36 (Table 1). This strongly supports a decline in diversity at higher SSTs, in contrast with the alternative of an asymptotic increase in diversity with SST. The inverse quadratic, quadratic and cubic fit very similarly within the range of the data but differ somewhat in the projected magnitude of the decline in diversity above 30 °C, where we have no data (Fig. 2a). Currently, such high temperatures are largely confined to the western Pacific ‘warm pool’. The cubic model projected increasing diversity above 33 °C, which is probably biologically unrealistic.

Thus, a convex function of SST well described both the temporal and spatial variation in deep-water cetacean biodiversity in both the Atlantic and Pacific oceans (Fig. 2). The estimated temperatures for peak diversity were 21.6 °C (quadratic), 20.5 °C (inverse quadratic) or 21.3 °C (AIC-weighted mean of all models including SST). The temperature ranges of the observations of the cetacean genera also suggested such a relationship, with the greatest number of genera found in water temperatures between *c.* 17 and 26 °C (Fig. 3).

Neither changing the number of sightings per block, nor making the blocks more compact in terms of SST, time or distance, nor increasing the minimum water depth, changed the results substantially (Supporting information Table S1). In all but one case, the quadratic or inverse quadratic function of SST was the model chosen based on AIC criteria, although sometimes functions that also included latitude were well supported.

Thus the available data on the distribution of deep-water cetacean diversity over space and time were generally well predicted by one environmental variable, SST, with very similar functional responses across oceanographically diverse regions. As this is an output of global circulation models, we

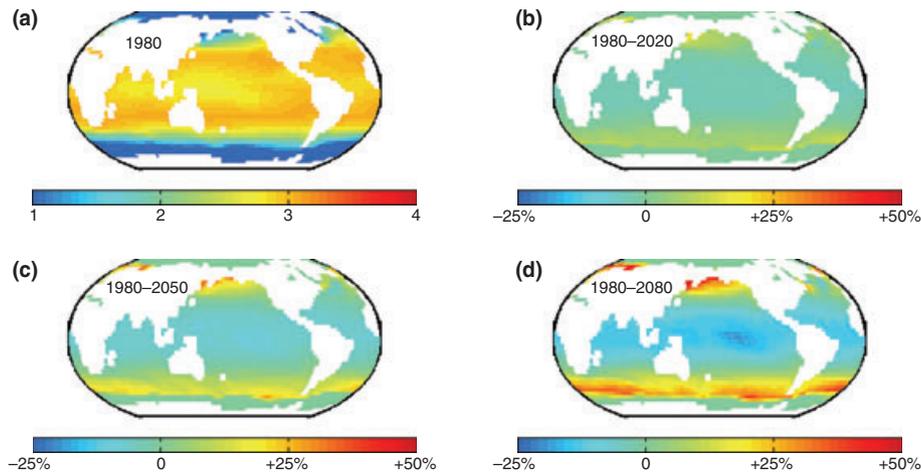


Figure 4 Projected response of diversity to ocean warming. Maps of mean genus richness of deep-water cetaceans in (a) the baseline year of 1980, and relative changes in diversity between (b) 1980 and 2020, (c) 1980 and 2050 and (d) 1980 and 2080 are shown. These were predicted using eqn 3 and mean monthly sea-surface temperatures from the CGCM1 model using scenario A2a (which projects moderate warming; results using all models are shown in Supporting information Figs S2–23). Changes are expressed as per cents of the mean (overall ocean areas < 65° latitude) diversity in 1980 minus 1 (as the minimum diversity is 1.0).

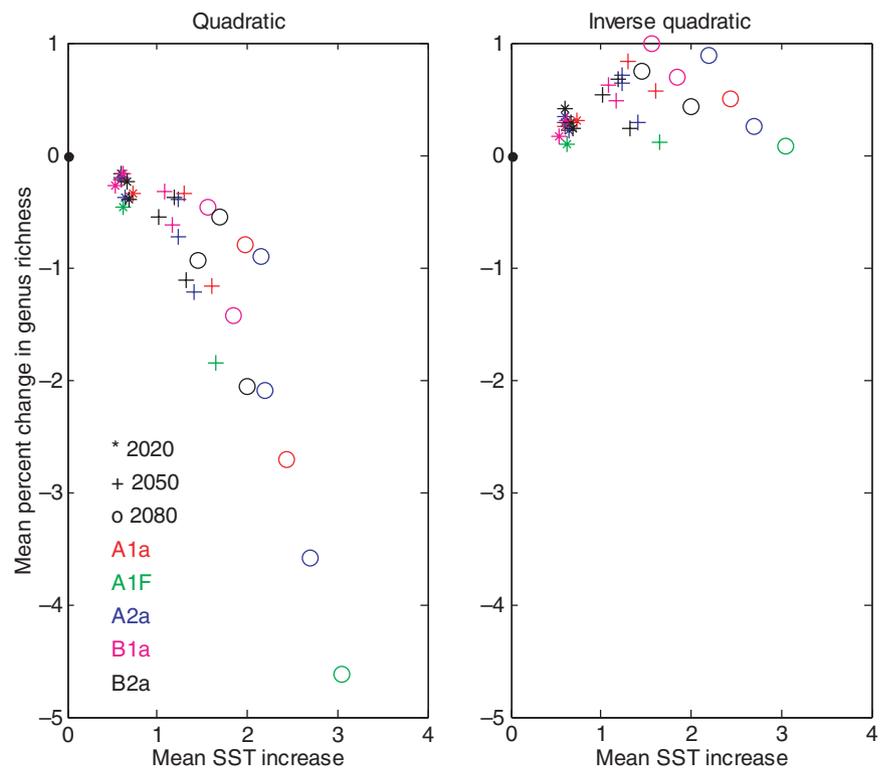


Figure 5 Changes in mean global diversity of deep-water cetaceans from climate-change scenarios. Mean per cent change in predicted generic richness plotted against mean increase in sea-surface temperature (SST, °C), with both measures averaged over months of the year and the surface of the ocean (< 65° latitude, to avoid the effects of changes in ice extent) between 1980 and 2020, 2050 or 2080 for different climate change models and scenarios, using the quadratic model of generic diversity on SST (left) and the inverse quadratic (right).

can produce scenarios exploring the effects of ocean warming on deep-water cetacean diversity. Figure 4a shows a global mapping of deep-water cetacean genus diversity, which was calculated by applying eqn 3 to mean monthly SSTs, and then averaging over the 12 months of the year.

For the baseline 1980 data set deep-water cetacean diversity was predicted to be highest at latitudes of *c.* 30°,

falling towards the equator, and more precipitously towards the poles (Fig. 4a). With global warming, the bands of maximal diversity are predicted to move polewards. The warming tropical oceans may lose some of their diversity, while substantially increased genus richness is predicted at latitudes of *c.* 50–70° in both hemispheres. Predicted changes using the moderate A2a scenario are shown in

Fig. 4b–d; those for other IPCC scenarios are displayed in Supporting information Fig. S2–23. The tropics constitute a larger proportion of the ocean than the regions where richness should rise. However, the magnitude of predicted declines in tropical biodiversity above 30 °C (outside the range of our empirical data) is influenced by the model used (Fig. 2a). With the best-fitting quadratic model (eqn 3), there is a predicted decrease in global mean genus diversity as waters warm, with a *c.* 1–2% decline in average genus diversity for each 1 °C increase in mean SST, and also a mean decline in genus richness over latitudes < 65° of between 2% and 7% from 1980 to 2080. However, using the inverse quadratic model (eqn 4), overall biodiversity is projected to remain nearly constant as the tropical decline is balanced by increased diversity at higher latitudes (Fig. 5).

DISCUSSION

This paper presents a first attempt to quantify macroecological patterns of cetacean diversity in response to temperature changes. Our data on the diversity of deep-water cetaceans were best predicted by convex functions of SST. The observed decline in diversity at higher SSTs was confirmed by the considerably better fit of the second-order inverse polynomial compared with the first, and is independently corroborated by the decline in diversity at high SSTs in the Indian Ocean data, which were not used in the modelling (Fig. 2b). We realize that this is a simplification, as biodiversity is generally maintained by a complex set of ecological processes, including the direct effects of physical variables, and indirect relationships mediated for example by changing prey distributions, competition and other factors. In the pelagic ocean, however, SST has emerged a particularly powerful determinant and predictor of large-scale patterns of biodiversity. For instance, among a number of tested variables, SST was by far the best predictor for the diversity of foraminiferan zooplankton as well as tuna and billfish (Rutherford *et al.* 1999; Worm *et al.* 2005). As in our analysis, these studies reported a convex function of SST with peaks at ~24 °C, when compared to ~21 °C for cetaceans. This difference in peak position may reflect generally greater adaptation of marine mammals to colder climates compared with plankton and fish. The general shape of the curve and the latitudinal patterns, however, are similar, and point towards a more general difference between marine pelagic and terrestrial diversity gradients, which almost uniformly peak around the equator (Hillebrand 2004). This may have potential implications for the effects of global warming.

With the observed unimodal patterns in diversity, as oceans warm, pelagic diversity is predicted to decline in the tropics and increase at high latitudes (Fig. 4). We expect that this will be a general trend among groups of pelagic

organisms, as many have similar relationships between SST and diversity (Rutherford *et al.* 1999; Worm *et al.* 2005). However, the lower temperature of the peak in marine mammal diversity may make tropical marine mammal diversity particularly susceptible to a decline with ocean warming, as these waters become an increasingly unsuitable habitat for some genera. Marine mammals, characterized by wide and adaptive movements (Stevick *et al.* 2002), will quickly desert unsuitable waters. Such changes might, however, pass unnoticed as very limited baseline information has been available in these waters.

As temperatures warm above 30 °C, however, it is unclear from our data how steep will be the drop in cetacean biodiversity. The quadratic model suggests an overall global decline in diversity with global warming, whereas with the inverse quadratic, the tropical decline is roughly balanced by increases in biodiversity at higher latitudes. Increases in low latitude sea temperatures are correlated with decreased diversity over geological time (Mayhew *et al.* 2008). Thus, organisms of the pelagic realm, most of which is located at low latitudes, will be affected. In particular, the tropical oceans will become less diverse with increasing global temperature (Mayhew *et al.* 2008). Our results suggest that, like tropical coral reefs (Hoegh-Guldberg *et al.* 2007), tropical pelagic oceans may decline in diversity over the next century. Baseline data such as presented here will likely prove important in anticipating, tracking and understanding these profound ecological changes as they unfold.

A number of important caveats apply to our analysis. There are some potential correlates of biodiversity that we were unable to incorporate into our models, of which productivity is perhaps the most obvious. During surveys in the South Pacific in 1992–1993, we measured the transparency of the water column with a Secchi disk at noon most days. Secchi depth is a very good inverse correlate of phytoplankton productivity in the open ocean (Lewis *et al.* 1988). There was a trend towards a negative correlation between Secchi depth and diversity in these data ($r = -0.553$, $P = 0.062$, $n = 12$, using $b = 3$ to increase the sample size), suggesting that productivity may play a role. Conversely, in the Gully, productivity peaks at *c.* 12–16 °C, decreasing substantially at warmer temperatures (Kepkay *et al.* 2002), which is in disagreement with the diversity pattern in Fig. 2c. Thus productivity does not seem to be a general predictor of deep-water cetacean biodiversity, which again is similar for other pelagic taxa (Rutherford *et al.* 1999; Worm *et al.* 2005). A related issue is that, in our construction of future scenarios, we ignore all potential changes other than the temperatures predicted by the climate change models. Other systematic developments, such as acidification (Orr *et al.* 2005), changes in currents, upwelling, nutrient flux into the photic zone, prey abundance and food-web structure, may profoundly affect the

pelagic ocean and its biodiversity in ways that are poorly understood for pelagic cetaceans.

Furthermore, we caution that diversity of deep-water cetaceans from sightings does not perfectly reflect the diversity of their biomass. Variations among genera in group size, body size, sightability and identifiability were not incorporated, and the observational target genera *Physeter* and *Hyperoodon* were omitted from the analysis because they were actively sought and tracked. However, these factors are not obviously biased by SST, latitude or ocean, and thus we believe that our measure of genus diversity is a reasonable proxy for the ecological diversity for this group of animals. Neither *Physeter* nor *Hyperoodon* has a distribution well correlated in space or time with that of other genera (e.g. Hooker *et al.* 1999), and our samples cover a wide range of areas with widely different density and taxonomic composition of deep-water cetaceans. For example, in Fig. 2c, genus richness was not noticeably different in the Gully (a hotspot with very high cetacean density) compared with Galapagos (moderately low cetacean density), or elsewhere (generally low cetacean density).

We also emphasize that producing global maps of deep-water cetacean diversity (Fig. 4) required extrapolating beyond the spatial and thermal limits of our field data (Fig. 1b), which makes predictions for undersampled regions and very warm temperatures uncertain. However, deep-water cetacean diversity responses to SST changes were very similar (Fig. 2b) in two of the most oceanographically contrasting areas on Earth, the northwest Atlantic (dominated by the warm Gulf Stream) and southeast Pacific (dominated by the cool Humboldt Current). Also, the genera listed in Fig. 3 are very wide-ranging and, with two exceptions involving a total of 10 sightings (< 0.5% of data), present in all ocean basins. Geographically, uncertainty is probably highest in the very warm waters of the western tropical Pacific, from where we have only one data point, and there is no sampled region with similarly high temperatures. However, we believe that the broad-scale geographic patterns shown in Fig. 4 are generally representative, and could be verified by further observations.

We also need to consider some potential biases. First, it has been found that there is generally considerable skewness in the distributions of the different taxonomic units in biodiversity analyses, which are thus disproportionately influenced by a few widespread organisms (Jetz & Rahbek 2002). However, this bias may not exist in our case as pelagic marine mammal genera all have very wide distributions. Using range maps from Reeves *et al.* (2002), the 19 genera in our study (listed in Fig. 3) have a skewness in their areas of distributions of -0.02 (i.e. virtually no skew) when compared to 1.99 for the land birds studied by Jetz & Rahbek (2002). Second, spatial or temporal autocorrelation

can lead to over-fitting of species richness models (Diniz-Filho *et al.* 2003). There was a moderate autocorrelation in the residuals of our data after fitting the quadratic ($r = 0.13$, $P = 0.02$) and inverse quadratic ($r = 0.12$, $P = 0.02$) models. To investigate whether this affected the model fitting, we reran the analyses, introducing minimum time intervals between the final sighting of one block and the first sighting of the next block. With a minimum of 1 day between the sightings in successive blocks, the number of acceptable blocks was reduced to 252 (from 356) and the autocorrelation in the residuals was essentially removed ($r = 0.04$, $P = 0.50$ for quadratic model; $r = 0.04$, $P = 0.49$ for inverse quadratic model). With this reduced data set, the quadratic model was still best supported, with the inverse quadratic its runner-up ($\Delta AIC = 1.44$). Thus the moderate autocorrelation in the data set has not led to over-fitting.

In conclusion we note that deep-water cetaceans display predictable patterns of diversity that resemble those of other pelagic organisms with very different life histories and evolutionary origins. Patterns of diversity in the open ocean seem to be predictably influenced by variation in ocean temperature; this includes seasonal, interannual and latitudinal variation. Further ocean warming may lead to a successive reorganization of biodiversity with predicted losses at the equator and gains at high latitudes (Fig. 4). Together with recent concerns about climate-related threats to tropical reefs, this suggests that tropical marine regions may become more compromised in terms of diversity loss than other regions. This is possibly quite different from what is expected on land, where effects of warming are strongest at high latitudes (Walther *et al.* 2002) and are predicted to occur mainly for specialized species with restricted ranges and limited dispersal (Thomas *et al.* 2004, 2006). Similarly, concerns about the effects of global warming on whales and dolphins so far have focused on a few species with restricted ranges and specialized habitat requirements, mainly the polar, inshore and riverine species (Würsig *et al.* 2002; Learmonth *et al.* 2006; Simmonds & Isaac 2007). The challenges to these species posed by global warming can quite easily be envisaged and may be dire, but our analysis suggests that the effects of ocean warming on cetaceans and other pelagic creatures may be more widespread and general.

ACKNOWLEDGEMENTS

The authors wish to thank those who helped collect the field data, and the organizations that funded the research, particularly the Natural Sciences and Engineering Research Council of Canada, the National Geographic Society, the Whale and Dolphin Conservation Society, the World Wildlife Fund Canada and Environment Canada Endangered Species Research Fund, the Canadian Federation of

Humane Societies, the Canadian Whale Institute, Fisheries and Oceans Canada and World Wildlife Fund Netherlands. B.W. acknowledges support by the Sloan Foundation (Census of Marine Life; Future of Marine Animal Populations Program). Thanks to A. Aguayo and his colleagues at the Chilean Antarctic Institute, A. Alling, S. Gero, D. Herfst, S. Hooker and T. Wimmer for compiling databases. C. Minto suggested the use of the inverse polynomial functions. B.W. Brook, S. Iverson, K. Kaschner, J. MacPherson, D. Tittensor, S. Wong and referees provided helpful comments on manuscripts.

REFERENCES

- Alling, A. (1986). Records of odontocetes in the northern Indian Ocean (1981–82) and off the coast of Sri Lanka (1982–84). *J. Bombay Nat. Hist. Soc.*, 83, 376–394.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A. & Edwards, M. (2002). Reorganization of North Atlantic marine copepod diversity and climate. *Science*, 296, 1692–1694.
- Boyce, D.G., Tittensor, D.P. & Worm, B. (2008). Effects of temperature on global patterns of tuna and billfish richness. *Mar. Ecol. Prog. Ser.*, 355, 267–276.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Dalebout, M.L., Ross, G.J.B., Baker, C.S., Anderson, R.C., Best, P.B., Cockcroft, V.G. *et al.* (2003). Appearance, distribution, and genetic distinctiveness of Longman's beaked whale, *Indopacetus pacificus*. *Mar. Mamm. Sci.*, 19, 421–461.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003). Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol. Biogeogr.*, 12, 53–64.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. *et al.* (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.*, 35, 557–581.
- Gitay, H., Suárez, A., Watson, R.T. & Dokken, D.J. (2002). *Climate Change and Biodiversity*. Intergovernmental Panel on Climate Change Technical Paper V, Geneva, Switzerland, pp. 1–86.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E. *et al.* (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, 318, 1737–1742.
- Hooker, S.K., Whitehead, H. & Gowans, S. (1999). Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conserv. Biol.*, 13, 592–602.
- Jetz, W. & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1458–1511.
- Kepkay, P.E., Harrison, W.G., Bugden, J.B.C. & Porter, C.J. (2002). Seasonal plankton production in the Gully ecosystem. In: *Advances in Understanding the Gully ecosystem: A Summary of Research Projects Conducted at the Bedford Institute of Oceanography (1999–2001)* (eds Gordon, D.C. & Fenton, D.G.). Department of Fisheries and Oceans, Dartmouth, NS, Canada, pp. 65–72.
- Learmonth, J.A., MacLeod, C.D., Santos, M.B., Pierce, G.J., Crick, H.Q.P. & Robinson, R.A. (2006). Potential effects of climate change on marine mammals. *Oceanogr. Mar. Biol. Ann. Rev.*, 44, 431–464.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A. & Picaut, J. (1997). El Niño Southern Oscillation and tuna in the western Pacific. *Nature*, 389, 715–718.
- Lewis, M.R., Kuring, N. & Yentsch, C. (1988). Global patterns of ocean transparency: implications for the new production of the open ocean. *J. Geophys. Res. Oceans*, 93, 6847.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- Mayhew, P.J., Jenkins, G.B. & Benton, T.G. (2008). A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. *Proc. R. Soc. Lond., B, Biol. Sci.*, 275, 47–53.
- Nelder, J.A. (1966). Inverse polynomials, a useful group of multi-factor response functions. *Biometrics*, 22, 128–141.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A. *et al.* (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437, 681–686.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637–669.
- Perrin, W.F., Mitchell, E.D., Mead, J.G., Caldwell, D.K., Caldwell, M.C., Van Bree, P.J.H. *et al.* (1987). Revision of the spotted dolphins, *Stenella* spp. *Mar. Mamm. Sci.*, 3, 99–170.
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308, 1912–1915.
- Petchey, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N. *et al.* (1999). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 437, 161–167.
- Reeves, R.R., Stewart, B.S., Clapham, P.J. & Powell, J.A. (2002). *Guide to Marine Mammals of the World*. Alfred A. Knopf, New York.
- Reeves, R.R., Smith, B.D., Crespo, E.A. & Notarbartolo di Sciara, G. (2003). *Dolphins, Whales and Porpoises: 2002–2010 Conservation Action Plan for the World's Cetaceans*. IUCN/SSC Cetacean Specialist Group. IUCN, Gland, Switzerland.
- Reusch, T.B.H., Ehlers, A., Hämmerli, A. & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl Acad. Sci. U.S.A.*, 102, 2826–2831.
- Rice, D.W. (1998). *Marine Mammals of the World: Systematics and Distribution*. The Society for Marine Mammalogy, Lawrence, KS.
- Rutherford, S., D'Hondt, S. & Prell, W. (1999). Environmental controls on the geographic distribution of zooplankton diversity. *Nature*, 400, 749–753.
- Simmonds, M.P. & Isaac, S.J. (2007). The impacts of climate change on marine mammals: early signs of significant problems. *Oryx*, 41, 19–26.

- Stevick, P.T., McConnell, B.J. & Hammond, P.S. (2002). Patterns of movement. In: *Marine Mammal Biology: An Evolutionary Approach* (ed. Hoelzel, A.R.). Blackwell, Oxford, UK, pp. 185–216.
- Sund, P.N., Blackburn, M. & Williams, F. (1981). Tunas and their environment in the Pacific Ocean: a review. *Oceanogr. Mar. Biol. Ann. Rev.*, 19, 443–512.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Thomas, C.D., Franco, A.M.A. & Hilla, J.K. (2006). Range retractions and extinction in the face of climate warming. *Trends Ecol. Evol.*, 21, 415–416.
- Thuiller, W., Lavelle, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proc. Natl Acad. Sci. U.S.A.*, 102, 8245–8250.
- Tilman, D. & Downing, J.A. (1994). Biodiversity and stability of grasslands. *Nature*, 367, 363–365.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. (2005). Global patterns of predator diversity in the open oceans. *Science*, 309, 1365–1369.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. *et al.* (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, 787–790.
- Würsig, B., Reeves, R.R. & Ortega-Ortiz, J.G. (2002). Global climate change and marine mammals. In: *Marine Mammals – Biology*

and Conservation (eds Evans, P.G.H. & Raga, J.A.). Kluwer Academic/Plenum, New York, pp. 589–608.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1 contains the following

- **Figure S1** Locations of blocks of sightings in Indian Ocean.
- **Figure S2–S23** Changes in deep-water cetacean biodiversity with various climate change scenarios.
- **Table S1** Robustness of results using general linear model.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, Wilfred Thuiller

Manuscript received 16 June 2008

Manuscript accepted 6 July 2008