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Abstract

The redistribution of species with climate change is well-documented. Even so, it remains unknown what proportion of apparent shifts in species ranges reflect real change due to ecological processes, and which are simply artefacts of variable detectability. Here, we use simulations under scenarios of varying abundance-related occupancy and sampling effort to describe the null expectation of patterns in the magnitude and variability of range shifts. We compare simulated patterns to empirically derived assemblage range shift data from two regional-scale (100s km) field studies and find that even with a well-designed sampling regime, accurate estimation of range edges are difficult to obtain for many species. We illustrate that a time-to-extinction model can be applied to spatial distribution data to provide species-specific confidence limits for range edges. These simulation and modelling approaches are particularly valuable for studies of marine species, where observations are typically few and patchy. Attempts to estimate null expectations of assemblage-level range shifts in the marine environment, and assigning confidence in the values obtained for particular species, represent important steps in advancing our understanding of global change.

Introduction

Species are tracking environmental warming by moving towards the poles through range extensions at the poleward (high-latitude) boundary and range contractions at the equatorward (low-latitude) range boundary (Chen et al. 2011, Sunday et al. 2012, Pinsky et al. 2013, Poloczanska et al. 2013). Yet even in areas experiencing rapid temperature change, the magnitude of observed biological responses differs among species (Poloczanska et al. 2013). At least some of this variation maybe due to the magnitude and spatio-temporal distribution of sampling effort, which has the potential to generate inaccurate range shift estimates. This is a particular problem for species unlikely to be observed due to low population numbers, patchy occupancy patterns, or cryptic characteristics (Dorazio and Royle 2005, Shoo et al. 2006, Blanchard et al. 2008, Hassall and Thompson 2010, McCarthy et al. 2012). Thus when entire assemblages of species are systematically surveyed with the same effort, biases or error in observed range shifts can be expected due to the abundance and occupancy patterns of different species, and their biological traits.

Difficulties in measuring species' distribution patterns are well-known and have been acknowledged in a range shift context (reviewed in Tingley and Beissinger 2009). In particular, locating the middle of species' distribution ranges can be achieved with greater accuracy than for estimates of range edges, especially for rarer species (Shoo et al. 2006, Hassall and Thompson 2010, Pinsky et al. 2013). Yet range edges may be of particular interest because, for example, range extension into new regions and contraction from previously occupied areas will ultimately drive changes in novel species interactions. It is therefore important to understand what error exists in the estimation of range edges.

Species detectability, i.e., the probability a species will be observed by a sampling protocol when it is present, differs among species in marine environments. As range shift data often encompass entire assemblages, species detectability may influence our understanding of the true scale of range expansions and contractions occurring. This is a particular problem at the edge of species' geographical range limits, where population numbers typical tail off. Quantifying the extent of uncertainty associated with species range edges will therefore be of value.

However, in most cases, the power of a particular sampling method to detect each species present within a community is unknown. Biases due to variable species detectability have been acknowledged when interpreting observed range shift patterns, but are generally not accounted for using statistical methods (Tingley and Beissinger 2009, Tanadini and Schmidt 2011, Brown et al. 2011, Monk 2013). For instance, Hassall and Thompson (2010) have suggested a range edge statistic based on a gamma frequency distribution rather than the most extreme or averaged range edge values (e.g., mean of the 10 most extreme range records, as in Hickling et al. 2005, Thomas and Lennon 1999). Alternatively, in order to increase the probability that observed range edge shifts represent true distributional change, Jones et al. (2010) suggest considering only shifts that are greater than a threshold distance, set for example by the upper 95th percentile of the distances among survey sites. However, both of these examples assume that all species are equally likely to be detected if present (Dorazio and Glimskar 2006, Wintle et al. 2012). Indeed quantifying species detectability using distance sampling has recently been attempted for butterflies (Isaac et al. 2011), a model taxonomic group for understanding climate-driven range shifts (Parmesan et al. 1999, Sunday et al. 2012).

Evaluation of range shifts in the ocean, for pragmatic reasons, have generally ignored species detectability, indirectly assuming uniformly high detectability across species, despite the fact that detectability can vary markedly even among similar species (e.g., within reef fish assemblages, MacNeil et al. 2008). This is likely because approaches for quantifying species detectability are laborious and costly in comparison to terrestrial environments and may therefore not be not always be feasible, especially for regional-scale analyses.

In this paper, we first assert that the uncertainty in the range edges of marine species will result in biased estimates of species range shifts, in particular for species with low abundance or detectability. We use simulations (and provide R code for interested readers) to show how factors related to species detectability influence whether range shifts are observed and the variability of those estimates – even when observed change is modeled as zero. We also provide two examples that demonstrate evidence of detection-related biases as predicted by our simulations, and thus illustrate the utility of using simulations based on simple assumptions to understand underlying biases or error.

Second, we explore how occupancy information can inform uncertainty in range edge estimates. We apply a time-to-extinction model, an optimal linear estimator tool (Solow 2005), to spatial distribution data for species with geographic ranges that fall near the edge of Tasmania. Time-to-extinction models estimate the most likely date of extinction based on the timing of observations leading up to the last sighting and are commonly used in contexts related to palaeontology and conservation biology (e.g., Solow 2005). In the same way that the last sighting of an individual from a near-extinct species is unlikely to represent the very last individual of a population (except where the entire population is known), the most extreme location at which a species is observed is unlikely to represent its true range edge (except in cases such as where known habitat barriers exist). Exchanging space for time therefore estimates confidence in the tails of spatial distributions and we test the accuracy of this application using real data.

Materials and methods

Simulation of methodological artefacts

We simulated differing species abundances and levels of sampling effort to provide null expectations for the magnitude of variability in range edges that may be due to sampling error. While many factors influence whether a species will be observed in a given sample or survey, in the marine realm, species abundance is one of the more important determinants of both site occupancy and detectability (McCarthy et al. 2013). Rare or patchily distributed species will be observed in fewer samples and will have lower occupancy, while those with higher abundance and more uniform distributions will be observed more frequently with higher occupancy. Abundance is also a convenient descriptor, varies by orders of magnitude within and between species, and can be assessed as categories (i.e., rare versus common), often suitable to describe relative abundance differences between species.   Moreover, at higher sampling effort, the probability of detecting species with low abundance and occupancy is expected to increase.

As range edges were of interest here, we simulated the tails of the species abundance distributions. While one or more peaks in abundance can be expected across the range of a species (McGill and Collins 2003), the shape and number of peaks in the middle of a species range are irrelevant to the present analysis. We therefore simulated an abundance distribution with a single peak and long tails in which abundance was 1–2 orders of magnitude lower than the peaks (McGill and Collins 2003). We first generating a standard normal probability density function (though different distributions were tested and produced similar patterns) centred at 10 degrees latitude and tails that extended 7.5 degrees above and below this mean. To simulate species with differing abundance levels, we then inflated the height of this distribution by values between 1 and 500, depending on the scenarios described in Table 1. To simulate a shift in range, we displaced the entire distribution by 5 degrees of latitude (Fig. 1).

Estimates of species range edges are typically based on the last observed sightings, which depend both on species detectability and sampling effort. To relate the detectability of a species within a latitudinal band to its abundance (or prevalence) at that latitude, we assumed that there were 100 available habitat spaces at each band of latitude. We then took the abundance score from the normal distribution described above and divided it by 100 to get a measure of habitat occupancy. Where the number within a degree of latitude exceeded the 100 available habitat spaces, we set the occupancy to one (Fig 1). We simulated observations of the occurrence of species within their range by modelling survey data as a series of Bernoulli trials along the latitudinal gradient, with the probability of success equal to the occupancy score. We therefore only considered the influence of abundance on species' detected presence, ignoring the role of crypsis or habitat patchiness and our simulations are intended to characterize the variability in range edge estimates that can be attributed to abundance-related sampling error alone. However, any other process that would lead to a tailed distribution in the probability of observing a species as described above would result in similar patterns.

In each simulation, characterization of a species' distribution was then achieved by randomly sampling a number of positions along the latitudinal gradient (depending on total sampling effort, summarized in Table 1). The minimum range edge for each simulation was recorded as the most extreme latitude in which the species was observed and the observed range shift was recorded as the difference between the minimum latitudes detected in the 'historical' and 'recent' distributions (Fig. 1b).

Simulation scenarios

Based on the assumption that abundance and sampling effort influence species detectability, we test how variation in these two factors, in combination with sampling stochasticity, affect range shift estimates. We first varied mean abundance, while keeping sampling effort constant, and shifted the species distribution by 5° of latitude (scenario 1). Next, we kept abundance constant, and varied sampling effort across the species range, again shifting the distribution by 5 degrees (scenario 2). Finally, we simulated observations for a variety of species abundances with no underlying shift (scenario 3); this scenario describes the level of observed change that may be expected due simply to stochasticity in sampling. For all three scenarios, we simulated 1000 datasets at each level of abundance or sampling effort and recorded the observed range change (simulation parameters are summarized in Table 1).

Real data for comparison to simulated community scenarios

We analysed two datasets to determine if the kinds of patterns identified using scenarios 1, 2 and 3 are present at the community level in the marine environment.

We tested for a relationship between the two factors, sampling effort and species' abundances, with the magnitude and direction of measured range shift estimates in two published datasets using linear models.

The first dataset comprised 45 seaweed species from the southwestern Australian coastline (Wernberg *et al.* 2011). Latitudinal displacement was determined from ~1950 (historical) to ~2000 (recent) on the basis of opportunistic collections in herbaria where sampling effort was episodic and varied among species (Wernberg *et al.* 2011). As this dataset did not contain information on the abundance of the species included, we asked experts to score each species on a qualitative scale of 1 to 5 with respect to their expected relative abundance across the region (Table S1: pooled into low (1 to 3) and high (>3) categories for presentation). Based on simulations, we expected that if abundance and sample size are important drivers of observed range changes, we should see a positive relationship between these factors and observed range changes. We tested for influences of each of these factors on the extent of macroalgal range shifts with a generalized linear model.

The second data set was limited to Tasmania, comprised of range shift responses in shallow reef fishes. In this case sampling effort was even in 1994 and 2006, spanned from -43.58°S to -39.21°S (n = 108 sites), and followed a rigorous underwater visual census protocol in which local abundances were recorded for each species (Stuart-Smith *et al.* 2010). The relationship between the measured difference in the lowest latitude at which each species was recorded in the two sampling intervals and their mean abundance was determined for 66 fish species.

Confidence in range edges using prevalence data and a time-to-extinction model

Rivadeneira *et al.* (2009) used simulated data to evaluate time-to-extinction models under varying sampling scenarios. From these models we selected “RandS” because it provides conservative estimates and does not assume even distribution of sampling effort (Roberts and Solow 2003). Briefly, the RandS model uses an optimal linear endpoint estimate based on the spacing of the *k* last sightings on record. Thus, in the case of range edge, S_{ci} is upper bound of the confidence interval of the range edge, S_n is the location of the sighting (1994 range edge position for southwards shifts, 2006 range edge position for northwards shifts), H is the total number of sightings, and α is alpha (0.05).

$$S_{ci} = S_n + \frac{S_n - S_n - H + 1}{c(\alpha) - 1}$$

$$c(\alpha) = \left[\frac{-\log\left(\frac{\alpha}{2}\right)}{H}\right]^{-\nu}$$

$$\nu = \frac{1}{H - 1}\sum_{i=1}^{H-2} log \frac{S_n - S_n - H + 1}{S_n - S_i + 1}$$

This approach for estimating confidence in range edges is thus independent of distribution shape and considers only the shape of the tail of the range distribution, which generally matches a Weibull distribution (Roberts and Solow, 2003). Solow (2005) describes the temporal model in full, now available as an R package (Clements 2012).

Our distance-to-edge model replaces time in the RandS model with latitude to compare estimates of the range edge for different species, based on their pattern of occupancy within the study area. Occupancy was estimated with prevalence data (#

sites in which a species was observed within a latitudinal band), quantified for 28 species that occurred in both sampling years and were present in at least three of the 108 sites sampled in each year. To satisfy the assumption of discrete sampling effort, we binned the occupancy data by 0.1° of latitude. The reef fish dataset offers the unique benefit of having a known geographical range limit for shallow marine species at the southern end of Tasmania (the continental margin). Whether the range edge confidence estimate from our distance-to-edge model overlapped the southern edge of Tasmania, and the precision of this estimate, could therefore be visually assessed.

Results

Range shifts and sampling design

Due to the stochastic nature of the sampling, under scenarios 1 and 2 which simulated a range shift of 5° of latitude, range shifts remained undetected in some cases. As expected, our simulations demonstrated that the proportion of observed range edge shifts increased with abundance (sigmoidal relationship, Fig. 2a) and that variability in estimates was reduced with higher sampling effort (Fig. 2c). Under scenario 3, where the range edge of species did not change, we further illustrate that range shifts in less abundant species are identified, even when the simulations did not include a latitudinal displacement in the location of the range edge. This is because range shift estimates in rarer species in the simulated community were markedly more variable than for abundant species (Fig. 3a).

These same patterns were observed in field data, where other sources of variability could conceivably swamp any variability in the detection of range edges due to abundance. First, in macroalgae, range shifts were less evident in species with relatively low abundance throughout the region (Fig. 2b). However, the measured change in the equatorward range edge of species was not significantly related to abundance when five qualitative scores where included in a generalized linear model as a predictor (Table 2). Second, less variable estimates of range change were observed for macroalgal species with more sampling (i.e. museum records, Fig. 2d, Table 2). Third, in the dataset of reef fish abundance, variability in the magnitude and direction of range change spanned from 4 to -4° latitude for species which averaged less than 2-3 individuals per site across the region, while estimates for more abundant species converge on zero. This finding supports the hypothesis that assessments for less abundant species are inaccurate and that range shifts in both directions will be observed due to sampling variability alone (Fig. 3b).

Distance-to-edge model of confidence in range edges for Tasmania reef fish data

Confidence intervals assessed for range edge estimates in the reef fish data from 2006 and 1994 substantially overlapped for most fishes (Fig. 4a). There was thus little confidence in shifts in southern range limits of fishes during the study period, with the exception of three species. One species was observed shifting southwards (*Enoplosus armatus*) and the southern range edge shifted northwards for two species (*Atypichthys strigatus* and *Upeneichthys vlamingii*). The confidence intervals for the remaining 25 species overlapped in the two time intervals. For species with low prevalence (i.e., presence at 3 to 5 sites in each of the two years), the location of the modelled range edge fell further from the location of the last observed presence and the confidence limits were wider (Fig. 4b). With increasing prevalence (occurrence at >10 sites in 1996 and 2004) the range edge estimate fell closer to the last observed location with reasonable confidence, so that we could confirm that a northward range shift occurred in *Upeneichthys vlamingii* (Fig. 4c). Moreover, the model performed well for abundant species that occurred throughout Tasmania in predicting the range edge at a location close to the true geographic range limit with high confidence (Fig. 4d).

Discussion

While the issue of variability in detection among species is well-known in ecological studies (e.g., Tanadini *et al.* 2011), we here show how species detectability has the potential to confound our understanding of range shifts of marine species. Failure to account for non-detection leads to inaccurate and inconsistent conclusions of range shifts among species. We demonstrate the influence of abundance-related occupancy and varying sampling on accuracy in estimated range shifts using simple simulations. We further suggest that exchanging space for time in a time-to-extinction model to create a distance-to-edge model can estimate confidence in range edge locations when species distributional limits are of interest. Tools such as simulations and modeling confidence intervals will allow more realistic descriptions of range changes for individual species and entire communities, leading to better understanding of the environmental and ecological factors underpinning range-shift dynamics.

Simulations of range change provide a null expectation for species with different abundance for comparison to field data and subsequently assist in interpretation of patterns. As expected, the likelihood of observing and correctly estimating a range change is greater for more abundant species and with increasing sampling frequency in time and space (Shoo *et al.* 2006; Tanadini and Schmidt 2011).

While these sampling issues associated with detectability (not just related to abundance) are a well-known problem, the large spatial and temporal scale required to obtain accurate range edge locations presents particular challenges in marine systems (Monk 2012). Simulations indicate that even under a best-case scenario of high-resolution sampling, estimates of range-edge boundaries are highly variable for less abundant species, patterns that are also observed in regional-scale field data sets. This issue is likely to be more acute for marine than terrestrial systems, due to the sampling effort limitations imposed by logistics of collecting data underwater. Therefore, while solutions such as subsampling data to equalize sampling effort between time periods have been advised on the basis of terrestrial studies (Hill *et al.* 2002; Hassall and Thompson 2010), such solutions may be counter-productive for marine studies, where sample sizes can be much lower to start with and maximizing information is a key consideration. Moreover, subsampling techniques only exacerbate the fact that rarer species are going undetected or, if measured, are more likely to have inaccurate estimates of change in comparison to more abundant species. These results suggest that the available baseline data in marine systems is insufficient to estimate range movements of rare and inconspicuous species due to quality (e.g., museum collections: Przeslawski *et al.* 2012) or limited sampling resolution (e.g., spatial positioning of samples may not capture range changes), especially when sampling is focussed at the expected range edge.

The signatures of abundance-related occupancy and sampling effort (both of which influence species detectability) are therefore present in published data sets of marine range shifts, illustrating the importance of confidence estimates when quantifying range shifts. If we are to improve our ability to model and predict both current and future range extensions and contractions, variable detectability of species needs to be considered in analyses and monitoring efforts (Monk 2013). Unfortunately, approaches such as estimation of range statistics based on the gamma frequency distribution or the use of distance thresholds to provide a minimum cut-off for defining a level of change that constitutes a range shift (Jones *et al.* 2010) do not incorporate species detectability.

Here we show that simulations and a distance-to-edge model can be applied to identify real range shifts, approaches that can be used across both marine and terrestrial ecosystems. Our application to museum collection (macroalgae) and quantitative survey data (fishes) highlights that species with low detectability are unlikely to be observed in regional analyses of range change. For those species that are observed, range shifts estimates will be inaccurate, and issue that is of particular concern at low sample sizes.

To provide a solution for identified range shift data that is more likely to represent true distribution change, we assessed the performance of a time-to-extinction model (distinguished here as the distance-to-edge model) for species found near the southern edge of Tasmania. Doing so allowed us to assess the performance of the model where the true range edge was known. In species with higher occupancy (measured here as prevalence), the model estimated the range edge location with high precision. However, at lower occupancy, precision in the range edge position was also low, as expected. Thus we were able to assign a threshold – presence at less than 5 sites in each of the two years – for which confidence was considered too low. Moreover, the model indicated several range shifts for which the confidence intervals for the two sampled time periods did not overlap, and thus indicate a likely range change with >95% confidence. Overall, the range edge estimates between the two time periods were generally similar for most species, further supporting the original interpretation of stability in the range edges of reef fish communities for a 13 year period where warming was minimal (Stuart-Smith *et al.* 2010). We therefore suggest that further evaluation of different time-to-extinction models with data that have different sampling resolutions and spatial distribution patterns will be important. Including habitat variables (such as by using species distribution modelling approaches) in conjunction with range edge estimates based on spatial occupancy patterns has the potential to build more accurate estimates of where species are located. In addition, trait-based time-to-detection models, such as described by Garrard et al. (2012), may be applicable to a spatial setting.

Although confidence in the accuracy of range edge estimates is a step forward, the most fundamental issue is that baseline data are either lacking or were not collected at a spatial and temporal resolution designed for rarer species (Maxwell and Simon 2005). Statistical tools may help to account for the patchy nature of present and historical data and inherent variation in species detectability, such as hidden-Markov or Bayesian hierarchical models (Wintle *et al.* 2012). However, monitoring programs designed to detect future range shifts should be implemented now with the goal of detecting changes in species distributions for species with different detectability, in combination with robust quantitative approaches tailored for climate change ecology (Brown *et al.* 2011). Well-designed surveys will provide baseline data for comparison to the present, facilitating systematic assessments so that range change in rarer species are not going unnoticed and more accurate quantification of range edges for species with varying detectability.

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Tables

Table 1. Parameters tested in simulations of range shifts for species in a theoretical community. Sampling effort is the number of randomly allocated sites included from an array of 200 evenly spaced sites surrounding the true range edge. Abundance is the multiplier used to generate distributions of prevalence throughout the range.

Scenario	**Sampling effort**	**Abundance**	**Shift (degrees latitude)**
1. shifts detected: Fig. 2a	40	1 to 500	-5
2. range change: Fig. 2b	8 to 200	100	-5
3. range change: Fib. 3	40	1 to 500	0

Table 2. Model results for relationships between measured change in the latitudinal location of the range edge in macroalgae versus abundance and sample size. Negative values indicate a declining slope. In addition to the fixed effects of interest (abundance and sample size), we further included a covariate for change in sampling effort through time (as reported in Wernberg et al. 2011) which is known to influence range edge detection (Shoo et al. 2006).

	coefficient	**standard error**	**t-value**	**P-value**
intercept	-0.51	0.90	-0.57	0.57
abundance category	-0.40	0.26	-1.51	0.11
sample size	0.065	0.024	2.70	0.010
log(effort ratio)	-1.61	0.69	-2.35	0.024

Figures

Figure 1. Schematic diagram of a theoretical relationship between occupancy and latitude at two time periods (historical = hatched, present = filled) for a species under three abundance levels (high: purple, medium: yellow, low: green). A ‘peak-and-tail’ pattern is expected if range limits are set by environmental conditions (although this may include multiple peaks). More abundant species have higher occupancy because they are more likely to be both observed and present during sampling. The poleward (high latitude) and equatorward (low latitude) range boundaries are predicted to shift towards the poles (black arrow) with increasing climate warming. This leads to an extension at the poleward boundary and contraction at the equatorward boundary.

Figure 2. Relationship between abundance and sampling effort versus proportion of range shifts detected (a-b) and shift magnitude (latitudinal change; c-d) from simulations of a theoretical community and field data for macroalgae in southwest Australia (blue) (Wernberg *et al.* 2011). For all panels, range shift estimates are based on differences in minimum latitude a species was observed, or the equatorward range boundary. Details of simulations are reported in Table 1 (as scenarios 1 and 2 for plots a and c, respectively).

Figure 3. Changes in latitudinal range limit versus abundance in a simulated theoretical community (a, orange) and measured from field data on reef fishes (b, blue). The simulated range change was set to 0 degrees in latitude (scenario 3, Table 1); thus range shifts in (a) suggested in rarer species are artefacts of low

detectability (due to abundance-related occupancy). Abundance data on 66 reef fish species were collected from the same 108 sites in 1994 and 2006 (Stuart-Smith et al. 2010).

Figure 4. (a) Range edges (symbols) and 95% confidence intervals (bars) predicted using a distance-to-edge model for 28 fish species in 1994 and 2006. Species are ranked by increasing occupancy. While range shifts were detected (filled symbols), the majority of the 2006 range edge estimates fell clearly within the 95% confidence interval (CI) of the 1994 estimate. Letters indicate example species highlighted in panels b-d. The dotted line represents the latitude of the southern edge of Tasmania (which is the southern limit of shallow marine habitat on the continent and thus limits the range edges of species and allows for comparison to the model estimates). (b-d) Latitude (sites were binned into 0.1 degrees latitude) versus prevalence (# sites occupied per latitudinal band) for three species with the true range edge estimates and 95% CIs for 1994 and 2006 (offset to the right of each panel).

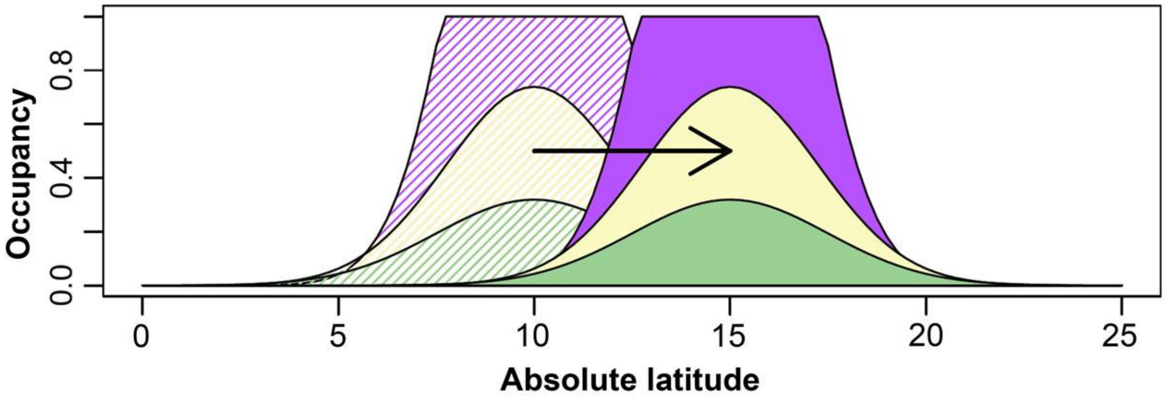

Figure 1

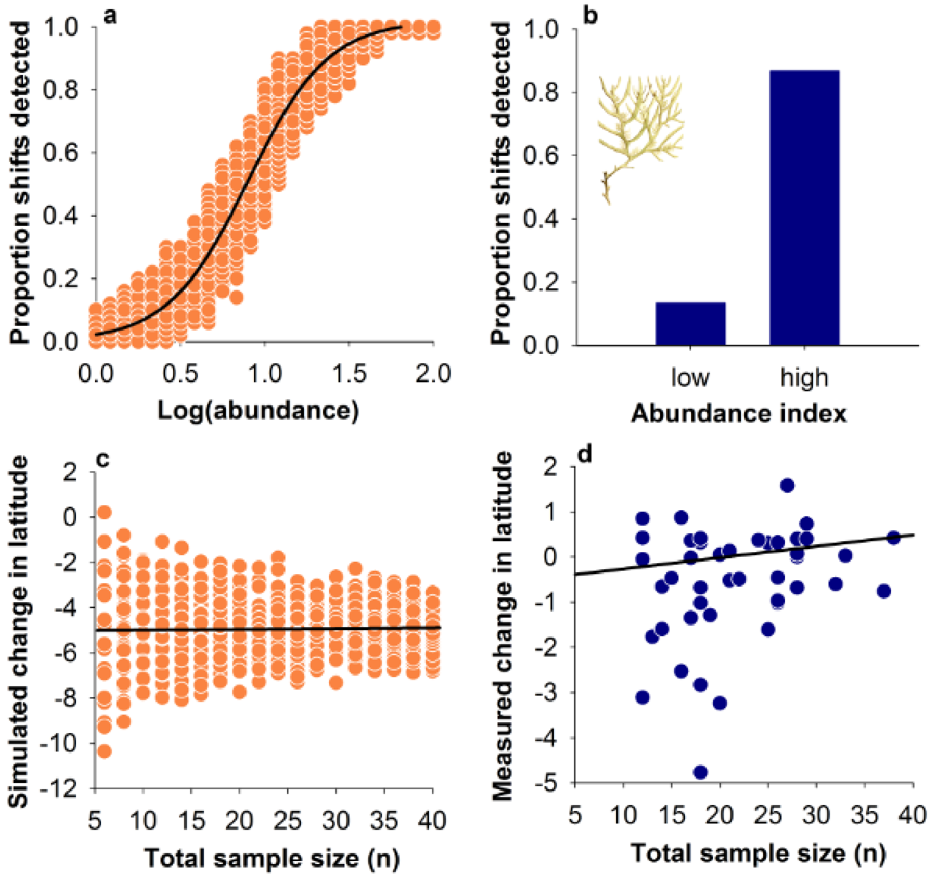
a
Proportion shifts detected
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.5
1.0
1.5
2.0
Log(abundance)
b
Proportion shifts detected
1.0
0.8
0.6
0.4
0.2
0.0
low
high
Abundance index
c
Simulated change in latitude
2
0
-2
-4
-6
-8
-10
-12
5
10
15
20
25
30
35
40
Total sample size (n)
d
Measured change in latitude
2
1
0
-1
-2
-3
-4
-5
5
10
15
20
25
30
35
40
Total sample size (n)

Figure 2

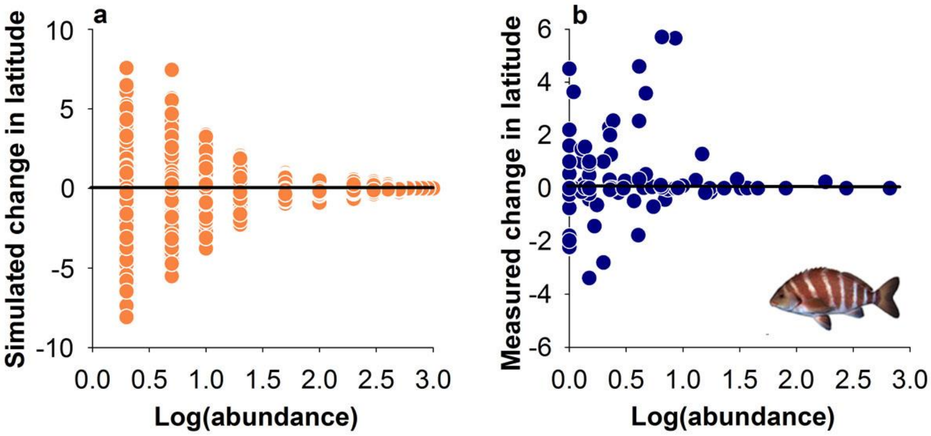
a
Simulated change in latitude
10
5
0
-5
-10
0.0 0.5 1.0 1.5 2.0 2.5 3.0
Log(abundance)
b
Measured change in latitude
6
4
2
0
-2
-4
-6
0.0 0.5 1.0 1.5 2.0 2.5 3.0
Log(abundance)

Figure 3

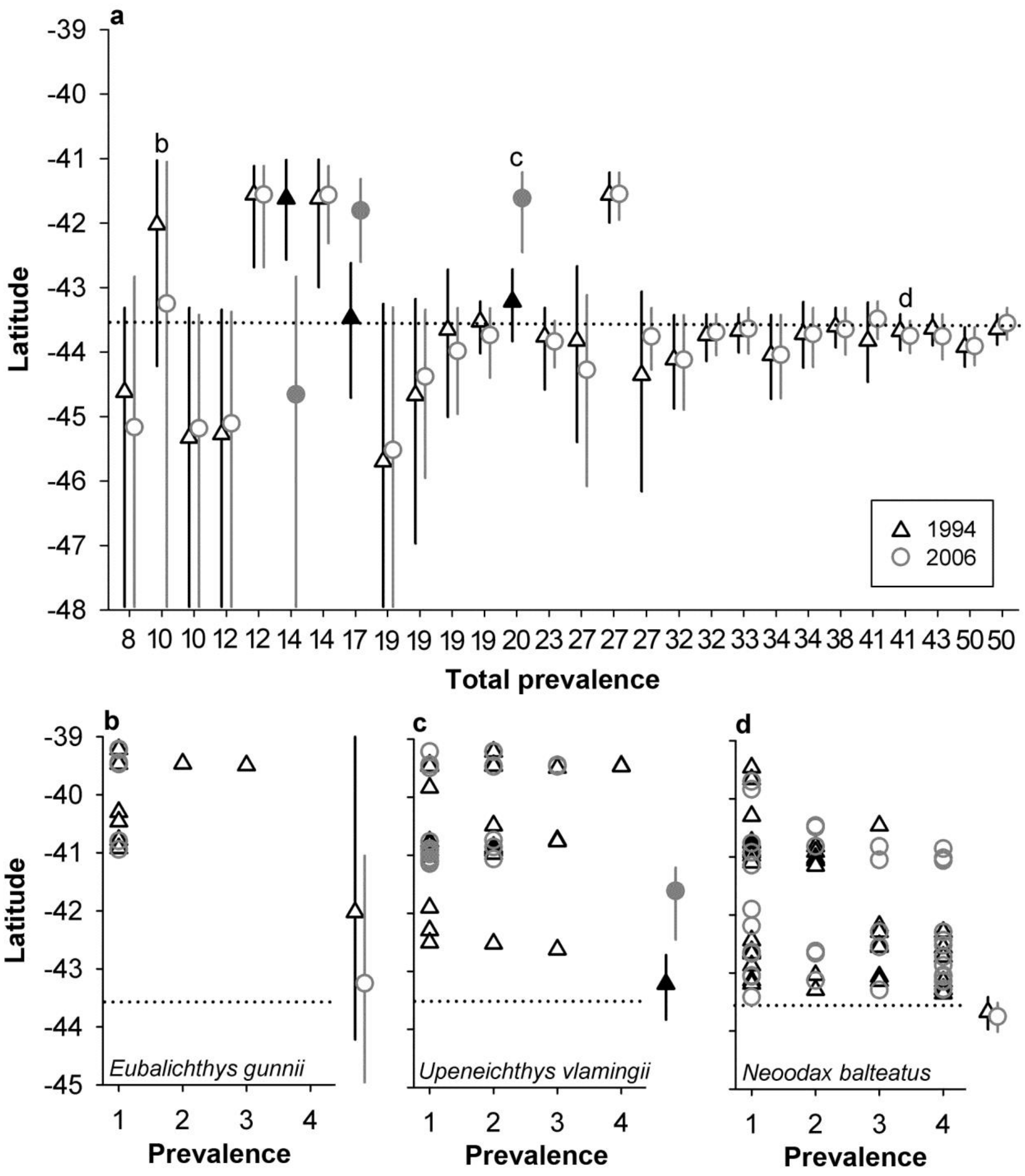
a
b
c
d
Latitude
-39
-40
-41
-42
-43
-44
-45
-46
-47
-48
8 10 10 12 12 14 14 17 19 19 19 19 20 23 27 27 27 32 32 33 34 34 38 41 41 43 50 50
Total prevalence
1994
2006
b
c
d
Latitude
Eubalichthys gunnii
Upeneichthys vlamingii
Neoodax balteatus
1 2 3 4
Prevalence

Figure 4

Supplementary Information

Table S1. Qualitative abundance of the macroalgal species estimated by experts[1,2,3] on a qualitative scale of 1 to 5 where 1 = rare, 2 = infrequent, 3 = common but low abundance, 4 = moderately abundant, 5 = highly abundant (the three experts scored algae within 2 units in all instances). Effort ratio is the number of museum records in1950 divided by the number of samples in 1990. Effort ratio, total sample size and change in latitude are reported in Wernberg *et al.* (2011): see main text methods.

Species	**Qualitative Abundance index**	**Effort ratio**	**Total sample size**	**Change in latitude**
Bornetia binderiana	3	0.9	21	-0.5
Callophycus oppositifolius	3	3.6	32	-0.6
Carpopeltis elata	3.7	2.3	20	-3.2
Carpopeltis phyllophora	3	0.3	14	-0.7
Caulerpa flexilis	4	3.2	25	-1.6
Caulerpa obscura	4	1.2	26	0.3
Caulerpa sedoides	3	2.2	16	-2.5
Caulerpa simpliciuscula	3.7	1.8	25	0.3
Caulocystis uvifera	2.5	1.9	29	0.7
Ceramium puberulum	2.5	1.4	12	0.9
Cladurus elatus	3	0.5	21	0.1
Claviclonium ovatum	1.7	2.5	28	0
Craspedocarpus blepharicarpus	3.5	0.6	18	-1
Cystophora brownii	3.3	1.7	16	-4.8
Dasyclonium incisum	2.3	2.1	28	-0.7
Dicranema revolutum	2	0.5	12	0.4
Dictyomenia sonderi	3.7	0.9	28	0.4
Dictyomenia tridens	2.5	1.1	15	-0.5
Dictyopteris muelleri	3.5	1.3	28	0.1
Dictyota fastigiata	2	0.7	12	-0.1
Erythroclonium muelleri	3.5	1.2	13	-1.8
Euptilota articulata	3	1.4	26	-1
Gigartina disticha	1.7	2.3	26	-1
Glossophora nigricans	2.7	1.3	16	0.9
Griffithsia teges	3	0.5	12	-3.1

Heterodoxia denticulata	3	2.1	37	0.3
Hypnea ramentacea	4.3	6.6	38	0.4
Kuetzingia canaliculata	3.5	1.6	26	-0.5
Laurencia elata	4	0.9	19	-1.3
Metagoniolithon chara	3.5	2	18	-0.7
Metagoniolithon stelliferum	4	1	18	0.4
Metamastophora flabellata	4	1.4	29	0.4
Myriodesma quercifolium	3.7	3.1	33	0
Nizymenia conferta	2.7	1.8	17	0.4
Osmundaria prolifera	2.5	3.7	33	0
Pachydictyon paniculatum	2.7	1.3	18	0.3
Platythalia angustifolia	2.3	1.1	17	0
Plocamium preissianum	3.7	1.6	18	-2.8
Pollexfenia lobata	3	3.4	22	-0.5
Pterocladia lucida	3.5	1.9	49	-1.2
Scaberia agardhii	3.5	3	24	0.4
Scytothalia doryocarpa	4.3	1.8	14	-1.6
Thuretia quercifolia	3	1.8	17	-1.4
Vidalia spiralis	3	1.9	20	0.1
Zonaria turneriana	3.5	0.3	27	1.6

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[3] Assoc. Prof. Thomas Wernberg, The University of Western Australia, Australia