

Quasi-deterministic responses of marine species to climate change

Grégory Beaugrand^{1,2,*}, Richard R. Kirby³

¹CNRS, Laboratoire d'Océanologie et de Géosciences UMR LOG CNRS 8187,
Université des Sciences et Technologies Lille 1 – BP 80, 62930 Wimereux, France

²Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

³Marine Biological Association, Citadel Hill, The Hoe, Plymouth PL1 2PB, UK

ABSTRACT: Perceived inconsistencies in the way a species may respond to temperature change across its thermal range can create confusion about the effects of climate change. Confusion can create doubt about the effects of temperature on a species, which can lead to controversy among scientists, ecosystem managers, and the general public. All this arises because empirical studies often take place at local scales, where responses to temperature can be quite different and where population dynamics can often appear to be random. At local scales, the long-term relationship between abundance and temperature can describe one of 3 scenarios: (1) a nil, (2) a negative, or (3) a positive relationship. Here, by showing that differential, regional biological responses to temperature are to be expected from ecological theory, we demonstrate that the 3 different responses to temperature depend upon the interaction between a species' thermal niche, the thermal local regime and its changes, and the magnitude of stochastic or uncontrolled processes. Using models mixing nonlinear, deterministic, and stochastic processes, we suggest that species' responses to climate change are quasi-deterministic at some spatial scales, enabling them to be theorised and anticipated, thereby removing future controversy.

KEY WORDS: Marine species · Climate change · Ecological theory · Temperature

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Climate has a strong effect on ecosystems and their associated biodiversity (Richardson & Schoeman 2004, Cloern et al. 2010). The potential influence of current climate change on ecological systems and biodiversity requires us to understand how life is arranged on Earth. Remarkably, and despite decades of research, there is still no consensus on either the processes or the mechanisms creating the current pattern of global biodiversity (Lomolino et al. 2006). Evidence already exists in the oceans for both deterministic (Darlington 1957, Allen et al. 2002, Rombouts et al. 2010) and stochastic influences acting upon the pattern of biodiversity (Hubbell 2001, Volkov et al. 2003); although in reality their effects are both likely to be entangled, with their respective

influences varying in scale, space, and time (Chase & Myers 2011). Understanding whether even a small component of marine biodiversity is deterministic (i.e. induced by the climatic regime) is critical however, as it will enable us to both theorise and anticipate the implications of climate change on the space and time distributions of marine ecosystems and their biodiversity, which is essential for humans.

We developed the MacroEcological Theory on the Arrangement of Life (METAL) — a model based upon the premise that there is a large deterministic component to the pattern of ocean biodiversity that can be explained by interactions between a species' ecological niche (Hutchinson 1957, 1978) and fluctuations in the environmental regime (Beaugrand et al. 2013c, Beaugrand 2015). The concept of the ecological niche is central to METAL, and allows for

*Corresponding author: gregory.beaugrand@univ-lille1.fr

consideration of underlying processes (genetic and physiological) that are difficult to identify and parametrise for a large number of species. At the species level, we assume that genetic background determines a species' physiology and therefore the species' niche, which in turn affects space and time alterations in species' abundances (Beaugrand et al. 2014). This does not prevent stochasticity from playing an important role locally, however (Beaugrand et al. 2013a, Planque 2016). METAL is particularly relevant at organisational levels ranging from species to biome, since it enables an understanding and prediction of both the individualistic responses of species to climate change (Beaugrand et al. 2013a) and their phenology and spatial distribution, including their phenologic and biogeographic shifts (Beaugrand et al. 2014). When METAL is applied at the species level, the prerequisite is to model the species' niche, and this can be accomplished through a variety of methods (Guisan & Thuiller 2005). We have often used the Non Parametric Probabilistic Ecological Niche Model (NPPEN), which has the advantage of modelling the niche from presence-only data (Beaugrand et al. 2011). The NPPEN model is particularly applicable in the context of METAL because it is an ecological niche model (ENM) rather than a species distribution model (SDM); SDMs cannot be used in the context of METAL because they primarily focus on habitat, not niche.

Interactions between niche, climatic, and environmental changes propagate from species to community levels, and are detectable from the smallest ecosystems to the whole ecosphere (Beaugrand et al. 2013c, 2015). Because we have demonstrated that a species' responses to environmental change are the results of interactions between its niche and fluctuations in the environment, we can create pseudo-communities comprising pseudo-species that each have a unique ecological niche (Beaugrand et al. 2013c, Beaugrand 2014). In this way, we can reconstruct spatial and temporal changes in communities to investigate spatial and temporal changes in biodiversity as well as key ecosystem properties (Beaugrand 2015, Beaugrand et al. 2015). At the community organisational level, METAL explains large-scale patterns in biodiversity (Beaugrand et al. 2013c) and long-term community shifts (Beaugrand 2014), including abrupt community shifts (also called regime shifts), and temporal (both past and contemporary) changes in biodiversity (Beaugrand et al. 2015). In addition, METAL has provided evidence for the lack of universality of Rapoport's rule (Stevens 1989), and has revealed that the mid-domain effect

(Colwell & Lees 2000) may occur in the Euclidean space of the niche, rather than in geographical space (Beaugrand et al. 2013c). METAL offers a way to make testable ecological and biogeographical predictions to understand how life is organised and how it responds to global environmental changes, including climate change (Beaugrand & Kirby 2010, Beaugrand et al. 2013a). Although changes in atmospheric circulation and the associated effects on the structure and chemistry of the water column are important for some planktonic groups (e.g. diatoms) (Margalef 1978, Cermeño et al. 2008, Alvarez-Fernandez et al. 2012, Alvain et al. 2013), our interests here lie in understanding how climate affects species through changes in the regional thermal regime (Aebischer et al. 1990, Planque & Fredou 1999, Petchey et al. 2010, Woodward et al. 2010).

In this study, we apply METAL with a stochastic component included for the first time in order to explain the apparent inconsistency in the individual responses of some species to climate-induced changes in temperature in both time and space. We test our theoretical predictions against data from the Continuous Plankton Recorder (CPR) survey for the well-known marine subarctic zooplankton species *Calanus finmarchicus*. *C. finmarchicus* has the advantage that it is only marginally influenced by human activities, and so its year-to-year response to temperature change is unperturbed by confounding factors such as fishing, pollution and habitat destruction. As a member of the plankton, *C. finmarchicus* is also likely to be in rapid equilibrium with the climatic regime, as its dispersal is unlimited by geographic barriers, in contrast to benthic species.

Our results indicate 3 different types of species response to regional temperature change (Planque & Fredou 1999, Beaugrand et al. 2014): (1) no response (i.e. random variability), (2) a negative response, and (3) a positive response. When all 3 responses are observed for the same species but in different locations or time periods, it may explain why scientists, policymakers, practitioners and stakeholders, or the general public may question the implications of climate-induced changes in temperature on species, or why they may misinterpret its effects. Consequently, our results show how apparent inconsistencies can be understood when the interaction between the species' ecological niche (here the thermal niche) and the climatic regime are considered together. We also show where, when, and how stochasticity influences the deterministic signal. The stochastic component may represent (1) a neutral process such as those considered in the unified neutral theory of biodiver-

sity and biogeography, UNTBB (Hubbell 2001) (e.g. random demographic and dispersal processes), (2) stochasticity related to our ignorance about species interactions or the lack of consideration of an ecological dimension of the niche, (3) stochasticity due to the noise associated with sampling, and (4) stochasticity related to the unpredictability of some events (Planque 2016).

2. MATERIALS AND METHODS

2.1. Environmental data

Monthly sea surface temperatures (SSTs) were obtained from the ERSST_V3 dataset (1958–2009). This dataset is derived from a reanalysis based on the most recently available International Comprehensive Ocean–Atmosphere Data Set (ICADS). Improved statistical methods have been applied to produce a stable monthly reconstruction on a $1 \times 1^\circ$ spatial grid, based on sparse data (Smith et al. 2008).

We used the photosynthetically active radiation (PAR; $E\ m^{-2}\ d^{-1}$), solar radiation spectrum in the wavelength range of 400–700 nm as a proxy for the level of energy that can be assimilated by photosynthetic organisms (Asrar et al. 1989). PAR regulates both the composition and the evolution of marine ecosystems, influencing the growth of phytoplankton and in turn, the development of zooplankton and fish. Data were provided by the GIOVANNI online data system, developed and maintained by the NASA GES DISC (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month). A monthly climatology of PAR at a spatial resolution of 9 km was carried out by compiling data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from September 1997 to December 2010.

Bathymetry data originated from the General Bathymetric Chart of the Oceans (GEBCO) database. All environmental data were interpolated on a global grid of 1° longitude \times 1° latitude using the inverse squared distance method (Beaugrand et al. 2000).

Monthly climatology data of upper ocean chlorophyll *a* (chl *a*) concentration were retrieved and calculated from the satellite SeaWiFS on a grid of 1° longitude \times 1° latitude.

2.2. Biological data

Data on *Calanus finmarchicus* originated from the CPR survey (Reid et al. 2003a). Abundance (*A*) data

were standardised between 0 and 1 using the following transformation:

$$A^* = A - \min(A) / [\max(A) - \min(A)] \quad (1)$$

2.3. Analyses

2.3.1. Theoretical abundance of *C. finmarchicus*

The deterministic model of *C. finmarchicus* was based on the NPPEN model (Beaugrand et al. 2011) applied on 4 environmental parameters at a monthly scale (Beaugrand et al. 2014). This technique is based on the generalised Mahalanobis distance and a simplified version of a non-parametric test called the multiple response permutation procedure (MRPP). This numerical tool is not correlative and tests the potential of a given spatial environment to accommodate a species by comparison to a niche-space reference matrix (i.e. *n*-dimensional environmental matrix within which the species is present). The NPPEN model has been used on benthic organisms, zooplankton, and fish (Beaugrand et al. 2011, Lenoir et al. 2011, Reygondeau & Beaugrand 2011, Rombouts et al. 2012, Chaalali et al. 2013, Raybaud et al. 2013, Fromentin et al. 2014) to characterise the state and variability of coastal systems (Goberville et al. 2011a,b), to identify biogeochemical provinces (Reygondeau et al. 2013), and in the terrestrial realm on trees (Goberville et al. 2015). This method is particularly well suited as part of METAL because the technique first models a species' niche, in contrast to SDMs where the focus is on the species' spatial distribution. In addition, the presence-only method is well adapted to the marine realm where it is difficult to know if the absence of a species is real or attributable to insufficient sampling.

The theoretical abundance of *C. finmarchicus* was assessed from 4 environmental parameters: monthly SSTs (1958–2009), bathymetry, and climatology of monthly chl *a* concentration and PAR. The niche was therefore 4-dimensional, but only annual SSTs varied on a year-to-year basis. Both chl *a* concentration and PAR were important to reconstruct the seasonal and spatial patterns of species distributions, and bathymetry was important for reducing the theoretical abundance of *C. finmarchicus* in shallow regions. More details on the model can be found in Beaugrand et al. (2014). Theoretical abundances were calculated for 15 areas that were chosen to cover a thermal niche from ~ 0 – 16°C (annual SSTs). In addition, a random noise was included, corresponding to 20% of the theoretical abundance, standardised between 0 and 1. This level of random noise was determined by

trial and error and was included to investigate the effect of sampling noise (e.g. error on abundance estimation, volume of seawater filtered by a sampler, uncontrolled processes and lack of an ecological dimension) on the theoretical biological responses to climate change. After the inclusion of the 20% noise (10% above and below theoretical values), theoretical abundances were standardised between 0 and 1 using Eq. (1). Prior to this transformation, abundances <0 or >1 were fixed to 0 or 1.

These calculations were first made in 4 areas of the North Atlantic Ocean to correspond to distinct thermal regimes located along 3 remarkable points along the species thermal niche. Those points (Fig. 1), defined in Beaugrand (2012), represent (1) the optimal temperature zone (T_{opt}), which is the region between the points (T_S) where both reproduction and growth are maximal and variability in species abundance as a function of temperature is low; (2) points of high variability (T_{HV} ; warm and cold sides), around which sensitivity to temperature is highest; and (3) the limit of temperature detection (T_D ; warm side), which is the threshold from where temperature effects are unlikely to be detected in the field because the species' thermal sensitivity becomes too small compared to stochasticity (Beaugrand 2012).

The first 4 areas we selected to examine the expected long-term patterns in abundance of *C. finmarchicus* were (1) East Atlantic Basin (47.5° N, 10.5° W), corresponding approximately to point T_D on the niche (Fig. 1), (2) East Labrador Sea (58.5° N, 46.5° W), corresponding to point T_{opt} , (3) West Labrador Sea (64.5° N, 60.5° W), corresponding to point T_{HV} on the left (cold) side of the niche, and (4) Reykjanes Ridge (60.5° N, 30.5° W), corresponding to point T_{HV} on the right (warm) side of the niche (see Fig. 2).

2.3.2. Annual relationship between predicted and observed abundance (1958–2009) in the niche space

To investigate the large-scale relationships between the predicted and observed abundance of *C. finmarchicus* along its thermal niche, 11 other areas were selected: (5) 56.5° N, 4.5° E, (6) 60.5° N, 2.5° E, (7) 56.5° N, 46.5° W, (8) 50.5° N, 10.5° W, (9) 55.5° N, 20.5° W, (10) 60.5° N, 40.5° W, (11) 60.5° N, 36.5° W, (12) 60.5° N, 60.5° W, (13) 60.5° N, 15.5° W, (14) 44.5° N, 2.5° W, and (15) 55.5° N, 20.5° W. Site selection was chosen to cover a thermal niche between ~ 0 – 16°C . Relationships were investigated using the deterministic and mixed deterministic/stochastic models (see Fig. 3).

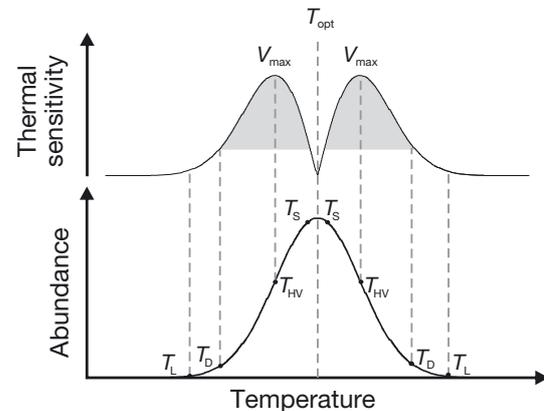


Fig. 1. Thermal niche (bottom curve) and the associated theoretical response (top curve) of a hypothetical species to climate-induced changes in temperature. The optimal part (T_{opt}) of the thermal niche corresponds to the centre of the species' distributional range and is associated with low year-to-year variability. The bimodal distribution of the year-to-year variability exhibits a maximal variability (V_{max}) corresponding to the greatest slopes (areas of high variability; T_{HV}) of the thermal niche. T_D : the threshold from where temperature effects are unlikely to be detected because the species' thermal sensitivity becomes too small; T_L : the temperatures below (towards the northern part of the distributional range) and above (towards the southern part of the distributional range) which temperatures become lethal. Grey areas: the region where the response of the species to climate-induced temperature changes is expected to be strong. Simplified from Beaugrand (2012)

2.3.3. Long-term changes in theoretical versus observed abundance (1958–2009)

Relationships between predicted (with no stochasticity) and observed abundance of *C. finmarchicus* were investigated in 3 regions of the North Atlantic (see Fig. 4). These regions corresponded only to the warm side of the copepod's thermal niche since no data were available for the left, cooler side. The 3 regions were (1) the North Sea (51.5–58.5° N, 3.5–8.5° E), with an average annual SST of 10.37°C ; ranging from 9.09 – 11.48°C ; (2) the Northeast Atlantic (47.5–55.5° N, 13.5–5.5° W) (average annual SST = 12.67°C ; 11.87 – 13.44°C); and (3) Subarctic Gyre (50.5–55.5° N, 45.5–30.5° W) (average annual SST = 8.99°C ; 8.03 – 10.17°C). These regions were characterised by a high density of CPR samples to minimise the number of missing years when observed annual abundance was calculated.

2.3.4. Correlation analyses

When a linear correlation was calculated on time series we also determined the autocorrelation func-

tion (ACF) to allow an adjustment of the actual degrees of freedom to assess the probability of significance of correlations more correctly (Pyper & Peterman 1998); this probability was termed p_{ACF} .

3. RESULTS

3.1. Theoretical examples

Expected year-to-year changes in the abundance of *Calanus finmarchicus* around T_D (i.e. the East

Atlantic Basin) exhibited a small reduction, mainly prominent after the end of the 1980s when major changes were reported in the Northeast Atlantic (Beaugrand & Reid 2003) (Fig. 2a). Here, the relationship with temperature was negative (Fig. 2a; $r = -0.90$; $p_{ACF} < 0.05$). When random noise was added to the model (Fig. 2a), both the long-term signal and the relationship with annual SSTs disappeared ($r = -0.28$; $p_{ACF} > 0.05$). This (expected) strong reduction in correlation when stochasticity was included in the model is explained by the low abundance level (low potential amplitude in the abundance; i.e.

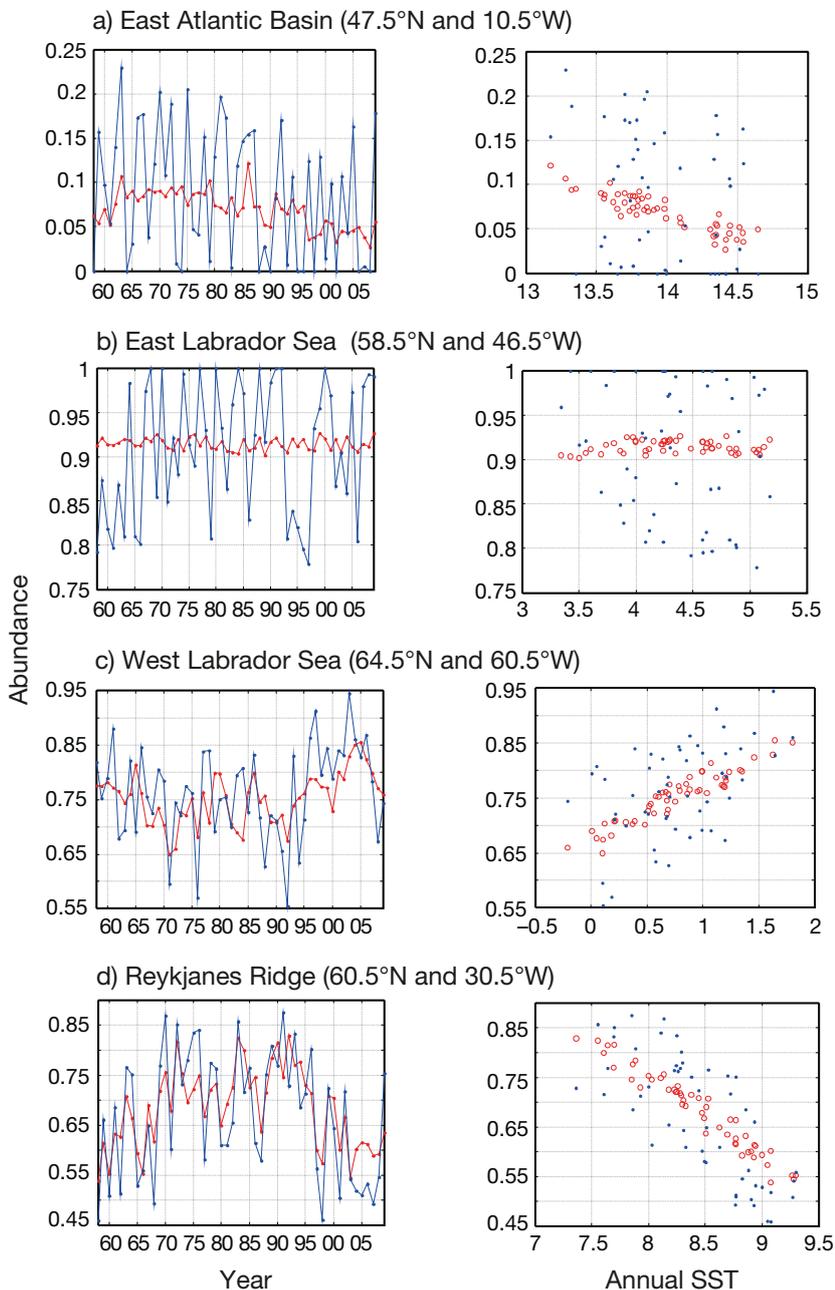


Fig. 2. Theoretical long-term (1958–2009) changes in the standardised abundance of *Calanus finmarchicus* (left) and relationships with annual sea surface temperatures (SSTs; right) in 4 areas of the North Atlantic: (a) East Atlantic Basin, (b,c) East and West Labrador Sea, and (d) Reykjanes Ridge, using a deterministic model (red dot) and a mixed deterministic/stochastic model (blue dot)

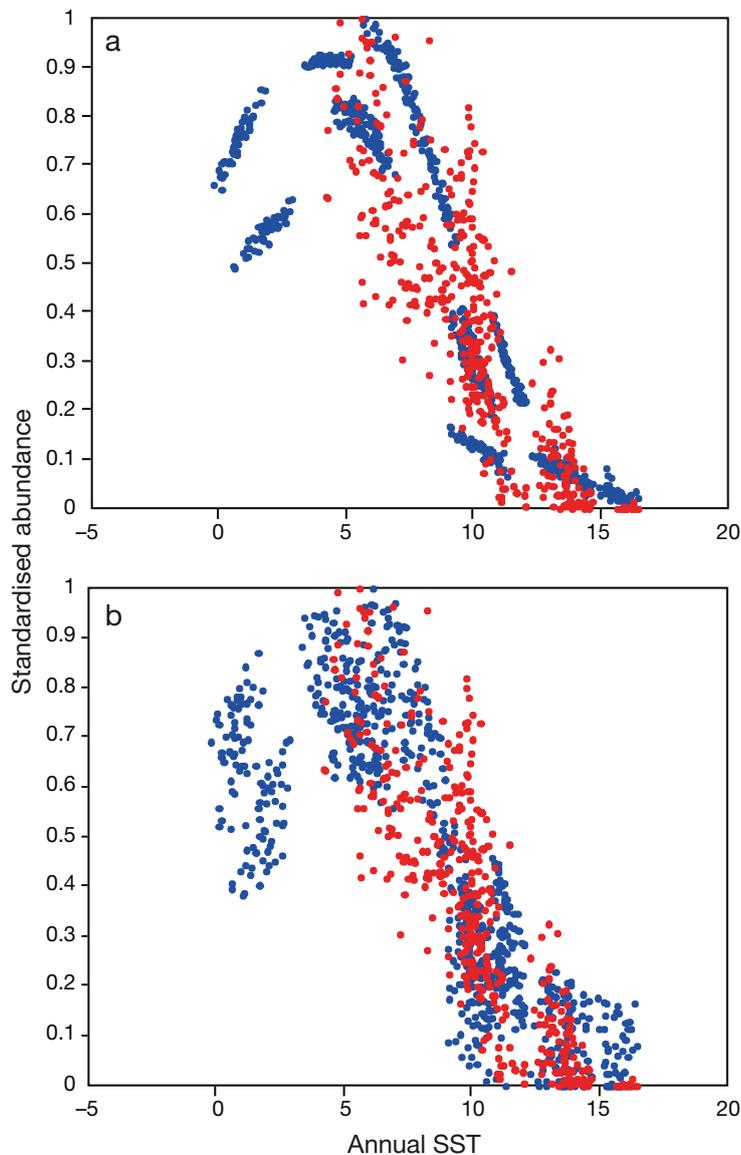


Fig. 3. Relationships between theoretical (blue) and observed (red) long-term (1958–2009) changes in the standardised abundance of *Calanus finmarchicus* as a function of annual sea surface temperatures (SSTs) for 14 areas of the North Atlantic Ocean determined using (a) deterministic model and (b) deterministic/stochastic model. Observed data originate from the continuous plankton recorder survey

between ~ 0 and ~ 0.2) that is readily influenced by stochasticity; here, the amplitude of stochastic variability equals the amplitude of deterministic fluctuations.

At the optimal part of the niche, between T_S points (i.e. the East Labrador Sea), there was no long-term change and no relationship with temperature either without ($r = 0.09$; $p_{ACF} > 0.05$) or with ($r = -0.18$; $p_{ACF} > 0.05$) stochasticity (Fig. 2b); here, the amplitude of stochastic variability is higher than the range of

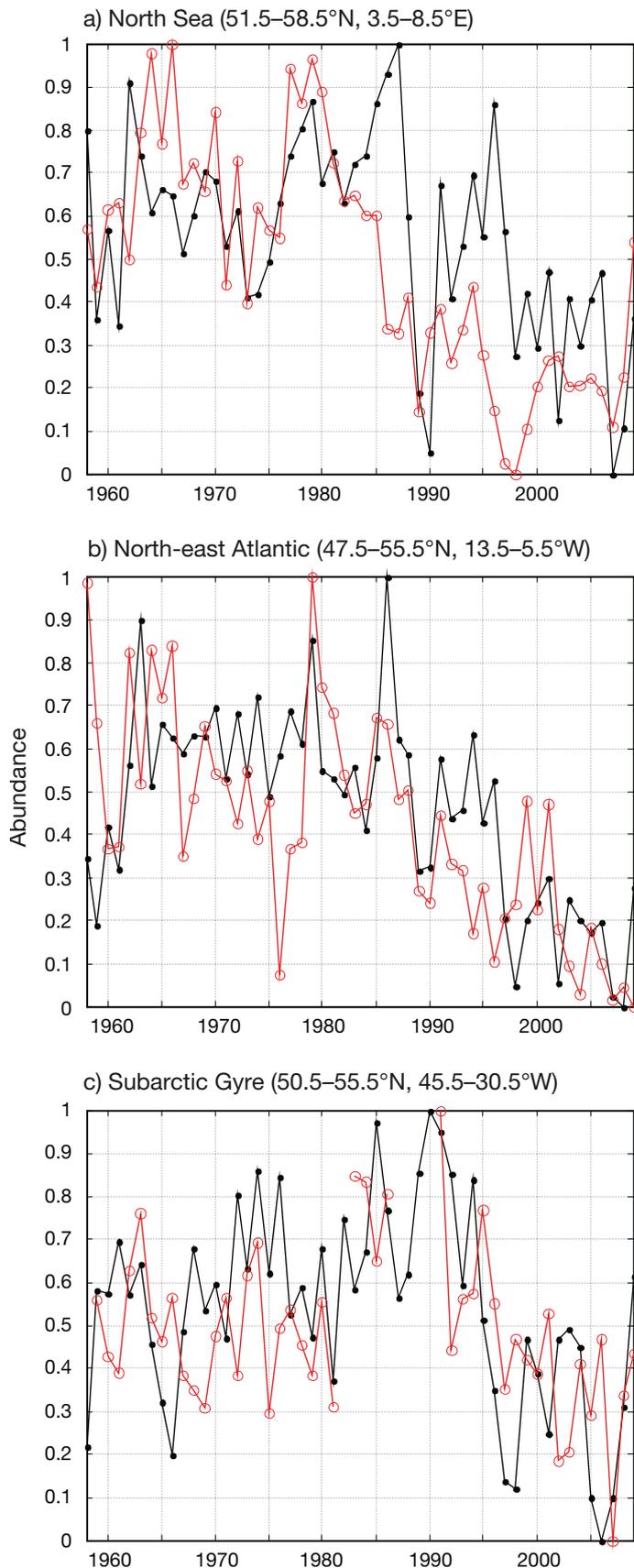
deterministic fluctuations. On the left (cold) side of the thermal niche (i.e. West Labrador Sea), year-to-year changes exhibit pseudo-cyclical variability, and a positive relationship with temperature is expected without ($r = 0.94$; $p_{ACF} < 0.05$; in red) or with ($r = 0.49$; $p_{ACF} < 0.05$; in blue) a 20% random noise. The opposite is anticipated on the right (warm) side of the niche (Reykjanes Ridge) and a negative relationship with temperature is expected without ($r = -0.97$; $p_{ACF} < 0.05$) or with ($r = -0.74$; $p_{ACF} < 0.05$) random noise. In the last 2 cases, the amplitude of stochastic variability is lower than the amplitude of deterministic fluctuations.

3.2. Theoretical versus observed abundance in the niche space

Year-to-year changes in the expected abundance of *C. finmarchicus* calculated for the 11 additional areas and the resulting year-to-year changes of the 15 areas (including the 4 previous ones) were represented as a function of annual SSTs without (Fig. 3a) and with (Fig. 3b) a 20% random noise. Observed abundances of *C. finmarchicus* from the CPR survey were also superimposed where estimations were available (see 'Materials and methods'). Expected and observed standardized abundances (between 0 and 1) were highly positively correlated without ($r = 0.73$; $p < 0.05$, $n = 420$) and with random noise ($r = 0.69$; $p < 0.05$, $n = 420$).

3.3. Theoretical versus observed long-term changes in abundance

As there was no biological data available corresponding to the thermal regime located on the left side of the copepod's thermal niche (see Fig. 3), the local relationships between the expected and observed abundance of *C. finmarchicus* were investigated in the North Sea, the Northeast Atlantic, and the Subarctic Gyre. All correlations were significant at $p_{ACF} \leq 0.05$ after accounting for temporal autocorrelation: $r = 0.51$ in the North Sea, $r = 0.55$ in the Northeast Atlantic and $r = 0.47$ in the Subarctic Gyre (Fig. 4).



4. DISCUSSION

Godfray & May (2014, p. 1) argued that ‘perhaps the key question in ecology today is the degree to which the dynamics of ecological communities are comprehensible’. Determinism should not be opposed to stochasticity, and in all biological and ecological systems, fluctuations in space and time have concurrent, deterministic, and stochastic components (Lande et al. 2003). Perhaps the unanswered question is when, where, and by how much is the deterministic signal more important than the stochastic signal, and vice versa. Our results suggest that regional species’ responses to climate-mediated changes in temperature are quasi-deterministic, conditioned by the interaction between the local thermal regime and the species’ thermal niche. Significant correlations between expected and observed changes in the abundance of *Calanus finmarchicus* varied between 0.47 for the Subarctic Gyre and 0.55 for the Northeast Atlantic. At a first glance, these values may seem low, despite being significant. However, the values are close to the range of correlation values calculated between theoretical abundance and observed annual SSTs (0.49–0.76) when a 20% random noise was included (see Fig. 2c,d; $|r| = 0.49$ for the west Labrador Sea and $|r| = 0.76$ for the Reykjanes Ridge). Empirical correlations generally observed for this species and for data collected from the CPR survey are rarely higher than 0.7 and are most often between 0.5 and 0.6 (Planque & Reid 1998, Beaugrand 2003, Reid et al. 2003b, Helaouët et al. 2011, 2016).

We found that long-term, local changes in the abundance of *C. finmarchicus* were well explained by the species’ 4-dimensional ecological niche and the thermal regime of each region. For example, a stepwise change was detected in both expected and observed abundance of *C. finmarchicus* in the Northeast Atlantic and the North Sea at the end of the 1980s, and in the Northeast Atlantic, the North Sea, and the Subarctic Gyre at the end of the

Fig. 4. Long-term expected (black) and observed (red) changes in the abundance of *Calanus finmarchicus* in 3 regions of the North Atlantic: (a) North Sea, (b) Northeast Atlantic, and (c) Subarctic Gyre

1990s (Fig. 4). The timing of all these shifts was similar to those already identified and attributed to climate effects in these 3 regions (Reid et al. 2001, Hatun et al. 2009, Alvarez-Fernandez et al. 2012, Beaugrand et al. 2013b). We have used the term ‘quasi-deterministic’ because while the deterministic signal is generally prominent in the present study (Figs. 3 & 4), it can partially (and temporarily) be obscured by a stochastic component at a local scale (Fig. 2). This is also the case at a higher organisational level, where biodiversity is determined largely by the interaction between the species’ niche and fluctuations in the environmental regime (Beaugrand et al. 2013c, 2015), even although locally, the influence of stochasticity may be pronounced. Our study provides an idea of the magnitude of stochasticity versus determinism for *C. finmarchicus* in the North Atlantic and from data sampled from the CPR survey. In our study, the noise was fixed at 20%, which tends to be close to our empirical expectations (Helaouët et al. 2013). However, we caution that more studies should be conducted to provide a better idea of the range of stochasticity versus determinism, and also that stochasticity is likely to vary among systems, spatial and temporal scales, species (depending on life history traits such as body size, dispersal capabilities and reproduction strategies) (Li 2002, Forster et al. 2012), and sampling programmes (Helaouët et al. 2016).

There are 4 different types of putative stochastic components in our study. (1) The first encompasses neutral processes such as those considered in the UNTBB (Hubbell 2001); i.e. random demographic and dispersal processes (e.g. chance colonisation) (Gaston & Chown 2005). Despite implicitly assuming that all species have the same ecological niche, the UNTBB can produce some macroecological patterns that are observed in the field (Volkov et al. 2003, Cottenie 2005). Nevertheless, if our stochastic component incorporates this effect it does not seem to explain much of the variance in our test using *C. finmarchicus*; this would agree with Cottenie (2005), who found that neutral processes fully structured natural communities in only 8% of cases. Although Cottenie (2005) found that the lack of consideration of neutral processes would result in missing important patterns in 37% of all studies, community structure was explained by environmental and spatial variables in 50% of the cases. (2) The second type of stochasticity is related to varied, small-scale (uncontrolled) processes such as species interactions that are difficult to estimate in time and space (we consider these to be a source of randomness), and failure

to consider the full ecological dimensions of the niche. The latter, while it does not seem to have a strong influence on *C. finmarchicus* (Figs. 3 & 4) — an animal that lives in an environment with few ecological dimensions and at a large spatial scale (Fig. 3) — it may, we caution, be more prominent in the benthic or terrestrial realms where the number of ecological dimensions typically increases (Lomolino et al. 2006). (3) The third type of stochasticity is that related to the noise associated with sampling (e.g. errors in abundance estimations of *C. finmarchicus* or in the volume of seawater filtered by the CPR) (Jonas et al. 2004). The fact that theoretical predictions fit well with field observations suggest that sampling noise had only a weak effect in our study, a result recently found for the same copepod species when using data from the CPR survey (Helaouët et al. 2016). (4) The fourth type of stochasticity is related to the unpredictability of some events and environmental perturbations (Planque 2016).

Overall, the importance of stochasticity will depend upon both the position of the local average thermal regime along the niche, and the strength of the deterministic signal (i.e. the magnitude of local temperature change or exposure to climate change; Beaugrand et al. 2015). As suggested by Schwartzman & Lineweaver (2005), determinism is likely to fade at smaller spatial scales because the ratio of stochasticity:determinism increases when the spatial scale decreases. For example, our results indicate that stochasticity affects the climatic signal less at a macro scale than at a local scale (Fig. 3 vs. Fig. 4), which explains the success of macroecology (Brown 1995, Gaston & Blackburn 2000). However, our study also shows that the degree to which determinism fades depends upon the position of the mean thermal regime (and its variability) along the niche (Figs. 1 & 3). For example, towards the outer limits of the niche (i.e. outside T_D) the deterministic signal is so highly sensitive to stochasticity that it is impossible to detect in practice; this is likely influenced by demographic stochasticity (the processes considered in the UNTBB), which tends to increase when populations are smaller (Lande et al. 2003). At the centre of the thermal niche, there should be no trend in abundance or any significant correlation between abundance and temperature (Fig. 1). This absence of trend or correlation here is more attributable to the deterministic signal than stochasticity because when populations are large the influence of demographic stochasticity is small (Lande et al. 2003). A positive or negative correlation between abundance and temperature is only likely to emerge in areas where the

thermal regime is close to either the cold or the warm edge of the niche around T_{HV} . Of course, the magnitude of all correlations between temperature and abundance depends on both the noise associated with sampling and any other processes operating at smaller spatial scales, lacking secondary ecological dimensions in the model or unpredictable environmental fluctuations. This means that the position of T_D along the thermal niche will vary according to the strength of all sources of stochasticity and so it may be neither symmetrical around T_{opt} nor constant along the niche space; this would particularly be the case if the niche was asymmetric (Ter Braak 1996).

Because all species have an ecological niche with different degrees of thermophily and eurythermy, their abundance should (except for extreme eurytherms) either demonstrate a nil, a negative, or a positive response to changes in the thermal regime across their distributional range, irrespective of whether the niche shape is Gaussian (Hutchinson 1978) or asymmetric (Ter Braak 1996). In addition, a nil, positive, or negative response may also be observed at the same location at a different time, depending on the time scale investigated and/or the magnitude of climate-induced changes in temperature. Our results therefore suggest that long-term observed stationarity in species abundance at any place does not guarantee that future climate-mediated changes in temperature will not affect their local abundance. The same applies to an absence of correlation between abundance and temperature; however, such a pattern does not mean that temperature is not a major factor determining a species' abundance. At some level of thermal warming, long-term stationarity in abundance may fade so that the abundance of a species may start to exhibit substantial changes (increasing or decreasing trend). For example, changes in temperature may become correlated with changes in abundance. Such changes may take place if the thermal regime located previously between the 2 T_S points moves to between T_S and T_{HV} (i.e. movement from the 'no change' to the 'negative change' zone of the niche), or similarly, if it moves from T_D to T_{HV} (from the 'no change' to the 'positive change' zone). Our theory therefore offers a way to predict such apparently surprising ecological outcomes. In the case of a key structural or an engineer species, such alterations may ramify subsequently, through the entire food web, to trigger cascading effects or trophic amplification (Cury et al. 2003, Kirby & Beaugrand 2009), which may then trigger an abrupt ecosystem or regime shift (Scheffer 2009). Such alterations may in turn affect trophodynamics,

and the balance of the entire ecosystem (Petchey et al. 2010, Woodward et al. 2010, Yvon-Durocher et al. 2010). Conversely, if the thermal regime moves either from T_{HV} (cold side) to T_S or from T_{HV} (warm side) to T_D , the strong past regional dependence of species abundance on temperature may diminish, and eventually disappear fully (Beaugrand 2012). This may already have happened for *C. finmarchicus* in the North Sea (Beaugrand 2012), where the abundance of the Subarctic copepod, which had been strongly negatively correlated with temperature changes, became unrelated to temperature (Kimmel & Hameed 2008, Beaugrand 2012). It is salient to note that this uncoupling occurred just before an abrupt community shift at the end of the 1980s that extended from the benthos to the pelagos and even to sea birds (Kirby et al. 2009, Luczak et al. 2012). Although this change in the type of relationships between temperature and the copepod appeared quite surprising at that time (Planque & Reid 1998, Beaugrand 2012), such non-linearities, so symptomatic of complex adaptive systems (Kump et al. 2004), are logically explained when the interaction between the thermal regime and the niche is considered.

Many researchers have argued that randomness may be the rule rather than the exception in ecological systems (Colwell & Lees 2000, Hubbell 2001), and as a result, others have questioned whether it is even possible to make ecological predictions (Boero et al. 2004, Planque 2016). Determinism seems perceptible in many fields of research, however. Einstein argued notably that 'the most incomprehensible thing about the universe is that it is comprehensible' (Godfray & May 2014, p. 1). Schwartzman & Lineweaver (2005) proposed that the Earth's ecosphere has evolved almost deterministically as a self-regulating system, arguing that temperature has constrained each major biological advance (such as the appearance of cyanobacteria; oxygenic photosynthesis), because organisms operate within thermal limits that are fixed by their physiology. Wächtershäuser (1998) also suggested that both biogenesis and microbial evolution advanced in a deterministic way from hyperthermophiles to mesophiles because the phylogenetic distance of some organisms (*Archaea*, *Bacteria* and *Eukarya*) from the last common ancestor (LCA) is correlated with maximum growth temperatures (Wächtershäuser 1998). The METAL concept we developed suggests that the arrangement of biodiversity on Earth in space and time is strongly determined by the interaction between the species' ecological niche and the local environmental regime

(Beaugrand 2015). The genetic background of species sets up their physiology, which determines their ecological niche (Helaouët & Beaugrand 2009). Tests of our theory have provided evidence that the thermal dimension of the niche is relevant in the marine pelagic domain (Beaugrand et al. 2013c, 2014, 2015, Beaugrand 2014). Other theories, such as the metabolic theory of ecology (MTE; Brown et al. 2004), also suggest that biological processes and ecological phenomena are controlled by temperature. However, despite being debated (Rombouts et al. 2011), the MTE is rarely challenged on the importance it attaches to the role of temperature for biological and ecological processes.

Our study shows that the responses of species to climate change are intelligible, i.e. they have a strong deterministic component. This result is important because it suggests that the effects of temperature, and climate-induced changes in temperature in particular, can be theorised and understood, and this is important since it may allow us to anticipate the potential implications of global climate change on ecosystems and their biodiversity (Beaugrand et al. 2015). By showing that determinism and stochasticity are intertwined, we reveal how they may act in concert at both regional and local spatial scales. Local departures from long-term equilibria of a species resulting from deterministic (expected) changes may therefore provide a quantification of the stochasticity component throughout the entire distributional range of a species. We think it is fair to suggest that such findings may be generalized to all marine and terrestrial species, although it may be more difficult to establish a link between theory and observations in other systems, where additional confounding factors such as life-history strategies (longevity, dispersal), habitat heterogeneity, and the effects of human activities are likely to obscure the relationships.

LITERATURE CITED

- Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753–755
- Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–1548
- Alvain S, Le Quéré C, Bopp L, Racault MF, Beaugrand G, Dessailly D, Buitenhuis ET (2013) Rapid climatic driven shifts of diatoms at high latitudes. *Remote Sens Environ* 132:195–201
- Alvarez-Fernandez S, Lindeboom H, Meesters E (2012) Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Mar Ecol Prog Ser* 462:21–38
- Asrar G, Myneni R, Kanemasu ET (1989) Estimation of plant canopy attributes from spectral reflectance measurements. In: Asrar G (ed) *Theory and application of optical remote sensing*. Wiley, New York, NY
- Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fish Oceanogr* 12:270–283
- Beaugrand G (2012) Unanticipated biological changes and global warming. *Mar Ecol Prog Ser* 445:293–301
- Beaugrand G (2014) Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Philos Trans R Soc Lond B Biol Sci* 370:20130264, doi:10.1098/rstb.2013.0264
- Beaugrand G (2015) *Marine biodiversity, climatic variability and global change*. Routledge, London
- Beaugrand G, Kirby RR (2010) Spatial changes in the sensitivity of Atlantic cod to climate-driven effects in the plankton. *Clim Res* 41:15–19
- Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Glob Change Biol* 9:801–817
- Beaugrand G, Reid PC, Ibañez F, Planque P (2000) Biodiversity of North Atlantic and North Sea calanoid copepods. *Mar Ecol Prog Ser* 204:299–303
- Beaugrand G, Lenoir S, Ibañez F, Manté C (2011) A new model to assess the probability of occurrence of a species based on presence-only data. *Mar Ecol Prog Ser* 424:175–190
- Beaugrand G, Mackas D, Goberville E (2013a) Applying the concept of the ecological niche and a macroecological approach to understand how climate influences zooplankton: advantages, assumptions, limitations and requirements. *Prog Oceanogr* 111:75–90
- Beaugrand G, McQuatters-Gollop A, Edwards M, Goberville E (2013b) Long-term responses of North Atlantic calcifying plankton to climate change. *Nat Clim Change* 3:263–267
- Beaugrand G, Rombouts I, Kirby RR (2013c) Towards an understanding of the pattern of biodiversity in the oceans. *Glob Ecol Biogeogr* 22:440–449
- Beaugrand G, Goberville E, Luczak C, Kirby RR (2014) Marine biological shifts and climate. *Proc R Soc B* 281:20133350, doi:10.1098/rspb.2013.3350
- Beaugrand G, Edwards M, Raybaud V, Goberville E, Kirby RR (2015) Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat Clim Change* 5:695–701
- Boero F, Belmonte G, Bussotti S, Fanelli G and others (2004) From biodiversity and ecosystem functioning to the roots of ecological complexity. *Ecol Complex* 1:101–109
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, IL
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Cermeño P, Dutkiewicz S, Harris RP, Follows M, Schofield O, Falkowski PG (2008) The role of the nutricline depth in regulating the ocean carbon cycle. *Proc Natl Acad Sci USA* 105:20344–20349
- Chaalali A, Beaugrand G, Raybaud V, Goberville E, David V, Boët P, Sautour B (2013) Climatic facilitation of the colonisation of an estuary by *Acartia tonsa*. *PLoS One* 8:e74531
- Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales.

- Philos Trans R Soc Lond B Biol Sci 366:2351–2363
- Cloern JE, Hieb KA, Jacobson T, Sanso B and others (2010) Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. *Geophys Res Lett* 37:L21602, doi:10.1029/2010GL044774
- Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol Evol* 15:70–76
- Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett* 8: 1175–1182
- Cury P, Shannon L, Shin YJ (2003) The functioning of marine ecosystems: a fisheries perspective. In: Sinclair M, Valdimarsson G (eds) *Responsible fisheries in the marine ecosystem*. FAO and CAB International, Rome
- Darlington PJ (1957) *Zoogeography: the geographical distribution of animals*. Wiley, New York, NY
- Forster J, Hirst AG, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc Natl Acad Sci USA* 109: 19310–19314
- Fromentin JM, Reygondeau G, Bonhommeau S, Beaugrand G (2014) Oceanographic changes and exploitation drive the spatio-temporal dynamics of Atlantic bluefin tuna (*Thunnus thynnus*). *Fish Oceanogr* 23:147–156
- Gaston KJ, Blackburn TM (2000) *Pattern and process in macroecology*. Blackwell Publishing, Padstow
- Gaston KJ, Chown SL (2005) Neutrality and the niche. *Funct Ecol* 19:1–6
- Goberville E, Beaugrand G, Sautour B, Treguer P (2011a) Early evaluation of coastal nutrient over-enrichment: new procedures and indicators. *Mar Pollut Bull* 62: 1751–1761
- Goberville E, Beaugrand G, Sautour B, Tréguer P (2011b) Evaluation of coastal perturbations: a new mathematical procedure to detect changes in the reference state of coastal systems. *Ecol Indic* 11:1290–1300
- Goberville E, Beaugrand G, Hautekeete NC, Piquot Y, Luczak C (2015) Uncertainties in species distribution projections and general circulation models. *Ecol Evol* 5: 1100–1116
- Godfray HCJ, May RM (2014) Open questions: Are the dynamics of ecological communities predictable? *BMC Biol* 12:22, doi:10.1186/1741-7007-12-22
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8: 993–1009
- Hatun H, Payne MR, Beaugrand G, Reid PC and others (2009) Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. *Prog Oceanogr* 80: 149–162
- Helaouët P, Beaugrand G (2009) Physiology, ecological niches and species distribution. *Ecosystems* 12:1235–1245
- Helaouët P, Beaugrand G, Reid PC (2011) Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Prog Oceanogr* 91:217–228
- Helaouët P, Beaugrand G, Edwards M (2013) Understanding long-term changes in species abundance using a niche-based approach. *PLoS One* 8:e79186
- Helaouët P, Beaugrand G, Reygondeau G (2016) Reliability of spatial and temporal patterns of *C. finmarchicus* inferred from the CPR survey. *J Mar Syst* 153:18–24
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427
- Hutchinson GE (1978) *An introduction to population ecology*. Yale University Press, New Haven, CT
- Jonas TD, Walne A, Beaugrand G, Gregory L, Hays GC (2004) The volume of water filtered by a CPR: the effect of ship speed. *J Plankton Res* 26:1499–1506
- Kimmel DG, Hameed S (2008) Update on the relationship between the North Atlantic Oscillation and *Calanus finmarchicus*. *Mar Ecol Prog Ser* 366:111–117
- Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. *Proc R Soc B* 276:4095–4103
- Kirby RR, Beaugrand G, Lindley JA (2009) Synergistic effects of climate and fishing in a marine ecosystem. *Ecosystems* 12:548–561
- Kump LR, Kasting JF, Crane RG (2004) *The Earth system*. Pearson Prentice Hall, Upper Saddle River, NJ
- Lande R, Engen S, Saether BE (2003) *Stochastic population dynamics in ecology and conservation*. Oxford University Press, New York, NY
- Lenoir S, Beaugrand G, Lecuyer E (2011) Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Glob Change Biol* 17:115–129
- Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419: 154–157
- Lomolino MV, Riddle BR, Brown JH (2006) *Biogeography*. Sinauer Associates, Sunderland, MA
- Luczak C, Beaugrand G, Lindley JA, Dewarumez JM, Dubois PJ, Kirby RR (2012) North Sea ecosystem changes from swimming crabs to seagulls. *Biol Lett* 8:821–824
- Margalef R (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol Acta* 1: 493–509
- Petchey OL, Brose U, Rall BC (2010) Predicting the effects of temperature on food web connectance. *Philos Trans R Soc Lond B Biol Sci* 365:2081–2091
- Planque B (2016) Projecting the future state of marine ecosystems, 'la grande illusion'? *ICES J Mar Sci* 73:204–208
- Planque B, Fredou T (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 56:2069–2077
- Planque B, Reid PC (1998) Predicting *Calanus finmarchicus* abundance from a climatic signal. *J Mar Biol Assoc UK* 78:1015–1018
- Pyper BJ, Peterman RM (1998) Comparison of methods to account for autocorrelation analyses of fish data. *Can J Fish Aquat Sci* 55:2127–2140
- Raybaud V, Beaugrand G, Goberville E, Delebecq G and others (2013) Decline in kelp in west Europe and climate. *PLoS One* 8:e66044
- Reid PC, Borges M, Svenden E (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish Res* 50:163–171
- Reid PC, Colebrook JM, Matthews JBL, Aiken J and others (2003a) The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–173
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003b) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fish Oceanogr* 12:260–269
- Reygondeau G, Beaugrand G (2011) Future climate-driven

- shifts in distribution of *Calanus finmarchicus*. *Glob Change Biol* 17:756–766
- Reygondeau G, Longhurst A, Beaugrand G, Martinez E, Antoine D, Maury O (2013) Toward dynamic biogeochemical provinces. *Global Biogeochem Cycles* 27:1046–1058
 - Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the northeast Atlantic. *Science* 305:1609–1612
 - Rombouts I, Beaugrand G, Ibañez F, Gasparini S, Chiba S, Legendre L (2010) A multivariate approach to large-scale variation in marine planktonic copepod diversity and its environmental correlates. *Limnol Oceanogr* 55:2219–2229
 - Rombouts I, Beaugrand G, Ibañez F, Gasparini S, Chiba S, Legendre L (2011) Marine copepod diversity patterns and the metabolic theory of ecology. *Oecologia* 166:349–355
 - Rombouts I, Beaugrand G, Dauvin JC (2012) Potential changes in benthic macrofaunal distributions from the English Channel simulated under climate change scenarios. *Estuar Coast Shelf Sci* 99:153–161
- Scheffer M (2009) *Critical transitions in nature and society*. Princeton University Press, Princeton, NJ
- Schwartzman D, Lineweaver CH (2005) Temperature, biogenesis and biospheric self-organization. In: Kleidon A, Lorenz R (eds) *Non-equilibrium thermodynamics and the production of entropy: life, earth and beyond*. Springer, Berlin
- Smith TM, Reynolds RW, Peterson TC, Lawrimore J (2008) Improvements to NOAA's historical merged land-ocean surface temperature analysis (1880–2006). *J Clim* 21: 2283–2296
 - Stevens GS (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. *Am Nat* 133:240–256
- Ter Braak CJF (1996) *Unimodal models to relate species to environment*. DLO-Agricultural Mathematics Group, Wageningen
- Volkov I, Banavar JR, Hubbell SP, Maritan A (2003) Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037
- Wächtershäuser G (1998) The case for a hyperthermophilic, chemolithoautotrophic origin of life in an iron-sulfur world. In: Wiegel J, Adams M (eds) *Thermophiles: the keys to molecular evolution and the origin of life?* Taylor & Francis, London
- Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organisation. *Philos Trans R Soc Lond B Biol Sci* 365:2093–2106
 - Yvon-Durocher G, Jones JI, Trimmer M, Woodward G, Montoya JM (2010) Warming alters the metabolic balance of ecosystems. *Philos Trans R Soc Lond B Biol Sci* 365: 2117–2126

Editorial responsibility: Mauricio Lima, Santiago, Chile

*Submitted: November 26, 2015; Accepted: April 14, 2016
Proofs received from author(s): June 13, 2016*