Global Change Biology

celebrating 20 years

Global Change Biology (2014) **20**, 2383–2392, doi: 10.1111/gcb.12505

OPINION

Climate-change impacts on sandy-beach biota: crossing a line in the sand

DAVID S. SCHOEMAN[1], THOMAS A. SCHLACHER[1] and OMAR DEFEO[2]

[1]*School of Science and Engineering, University of the Sunshine Coast, Maroochydore DC, QLD 4558, Australia,* [2]*Faculty of Sciences, UNDECIMAR, Montevideo 11400, Uruguay*

Abstract

Sandy ocean beaches are iconic assets that provide irreplaceable ecosystem services to society. Despite their great socioeconomic importance, beaches as ecosystems are severely under-represented in the literature on climate-change ecology. Here, we redress this imbalance by examining whether beach biota have been observed to respond to recent climate change in ways that are consistent with expectations under climate change. We base our assessments on evidence coming from case studies on beach invertebrates in South America and on sea turtles globally. Surprisingly, we find that observational evidence for climate-change responses in beach biota is more convincing for invertebrates than for highly charismatic turtles. This asymmetry is paradoxical given the better theoretical understanding of the mechanisms by which turtles are likely to respond to changes in climate. Regardless of this disparity, knowledge of the unique attributes of beach systems can complement our detection of climate-change impacts on sandy-shore invertebrates to add rigor to studies of climate-change ecology for sandy beaches. To this end, we combine theory from beach ecology and climate-change ecology to put forward a suite of predictive hypotheses regarding climate impacts on beaches and to suggest ways that these can be tested. Addressing these hypotheses could significantly advance both beach and climate-change ecology, thereby progressing understanding of how future climate change will impact coastal ecosystems more generally.

Keywords: beach fauna, climate change, climate change detection, coastal ecology, marine ecology, mass mortality, range shift

Received 4 September 2013 and accepted 7 December 2013

Climate change and sandy beaches: what's so interesting?

For the past two decades, climate change has become an increasingly hot topic in ecology (Hoegh-Guldberg & Bruno, 2010), but our understanding of associated impacts has lagged in marine relative to terrestrial systems (Richardson & Poloczanska, 2008). Specifically, although ecological theory and mathematical modeling have been widely used to project (Box 1) potential ecological responses to future climate-change scenarios (e.g., Cheung *et al.*, 2009; Pike, 2013b), synthesis of observational evidence (Box 1) of such responses to contemporary climate change has until recently been neglected, especially for ocean systems (Poloczanska *et al.*, 2013).

Coastal systems supply disproportionate ecological services and benefits to human society (Barbier *et al.*, 2011), but coastal waters have warmed faster than those of the open oceans (Lima & Wethey, 2012). It is therefore unsurprising that more than half of the reported climate impacts synthesized by Poloczanska *et al.* (2013) came from coastal systems. However, the sandy beaches (Box 1) that comprise the world's longest land/sea interface have largely been overlooked in studies of the ecological and socioeconomic impacts of climate change (Dugan *et al.*, 2010; Barbier *et al.*, 2011).

Reviews of climate-change impacts to sandy beaches have hitherto been tentative and qualitative. The earliest work (Brown & McLachlan, 2002) emphasized the lack of robust parameterization of conceptual models of how beach species might respond to environmental change, and the resulting uncertainty of expected changes. Subsequent syntheses progressed slowly, relying largely on the general principles established by Intergovernmental Panel for Climate Change (IPCC) Assessment Reports: warming might result in poleward range shifts and altered phenology; sea-level rise and increased storminess might combine to increase rates of beach erosion; and ocean acidification might challenge species that incorporate calcified structures in their anatomy (Jones *et al.*, 2007; Schlacher *et al.*, 2008; Defeo *et al.*, 2009). None of these works include examples from the literature that document observational evidence of such responses by sandy beach biota or systems that are consistent with expectations (Box 1) under recent climate change. This is not to say that the authors overlooked evidence, but rather that such

Correspondence: David S. Schoeman, tel. +61 7 5456 5956, fax +61 7 5456 5010, e-mail: dschoema@usc.edu.au

Box 1 Explanations for terminology used in the text. Unless otherwise specified, we follow Intergovernmental Panel for Climate Change (IPCC) conventions (IPCC, 2007)

Observations, projections and predictions

We refer to direct measurements made in the field as *observations*, whereas we consider outputs from numerical models of ecological processes under alternative future climate scenarios that include assumptions to be *projections* (any description of the future described by a model) or *predictions* (the 'most likely' projection). Although theory, modeling, experiments and field observations all inform our understanding of climate-change responses, only long-term field observations can provide evidence that a species or system has responded to climate change (Brown *et al*., 2011).

Sandy beach

Sandy beaches are landforms at the marine/terrestrial interface formed by unconsolidated sands. Functionally, the land- and seaward boundaries of sandy beaches are conventionally defined as the limits of active sand transport and exchange, i.e., the limits of the littoral active zone (Schlacher *et al*., 2008). However, we refer in this paper primarily to the nonvegetated beach face between the base of the dunes and the low-water mark.

Expectations under climate change

The hypothetico-deductive method constructs explanatory hypotheses that, if properly formulated, lead to predictions open to testing and falsification. We refer to such theoretical *a priori* predictions as *'expectations'* to avoid confusion with predictions or projections made by numerical models. Our use of the term *expectation* – meaning a falsifiable statement derived from a hypothesis – is increasingly common in the literature on climate-change ecology (e.g., O'Connor *et al*., 2012; Parmesan *et al*., 2013).

Vulnerability to climate change, including exposure, sensitivity and adaptive capacity

Vulnerability to climate change incorporates three interacting elements: exposure, sensitivity and adaptive capacity (Dawson *et al*., 2011). *Exposure* is the degree to which the environment an ecological entity inhabits has or will experience climate change. *Sensitivity* is the degree to which the probability of persistence of an ecological entity is likely to alter if exposed to a change in climate. *Adaptive capacity* is the degree to which an ecological entity can respond to a changing climate by, for example, shifting its geographical range or altering its phenology, without incurring significant detrimental consequences.

Leading and trailing range edges

The geographical distribution of species is bounded by *range edges*. When climate changes, species have been demonstrated to respond by shifting these boundaries. Range edges that advance into previously unoccupied habitat (under global warming, habitat previously too cool to accommodate a given species) are known as *leading range edges*, whereas those that contract into habitat currently occupied (under global warming, occupied habitat that has come to exceed upper thermal limits of the species in question) are known as *trailing range edges*.

Detection and attribution of climate-change impacts

Detection of change is defined as the probabilistic demonstration that a statistical change has occurred in climate, or in a system that is affected by climate. As such, *detection* relies on observational measurements, rather than on model projections, and does not require an explanation of why the system changed. *Attribution* goes one step further than *detection* by quantifying statistically the relative contributions of alternative potential drivers of the observed change (Parmesan *et al*., 2013).

Tropicalization

A pattern of increasing representation of warm-water species within a biological community (e.g., Wernberg *et al*., 2012; Cheung *et al*., 2013).

evidence simply did not exist, and it continues to be sparse (Dugan *et al.*, 2010).

Neglect for sandy beaches in climate-change studies contrasts sharply with the important role that beaches play in modern society (Schlacher *et al.*, 2008): much of the world's most valuable residential real estate is located within a stone's throw of a beach; many countries boast strong cultural narratives associated with beach-based recreation; and commercial extraction of resources from beaches is common.

The fauna of beaches is diverse, comprising invertebrates from many phyla, and representatives from all vertebrate classes. Although most beach invertebrates are inconspicuous, they are numerous and functionally important, rapidly processing carbon (Coupland *et al.*, 2007) and linking oceanic productivity with high-order consumers (Bergamino *et al.*, 2011; Schlacher *et al.*, 2013). Similarly, numerous vertebrate species, many of conservation concern (e.g., turtles and seabirds), depend on beaches and dunes (Schlacher *et al.*, 2008). Beaches should therefore be of considerable conservation importance (Harris *et al.*, 2013).

Obligate beach species also provide unique opportunities to test hypotheses of climate-change ecology. First, beach invertebrate communities are structured mainly by habitat conditions (Defeo & McLachlan, 2005; Schlacher & Thompson, 2013) rather than by the competitive interactions that often structure other intertidal systems. This simplifies explanatory models of responses to changing environments. Second, because the beach matrix lacks the heterogeneity or stability characteristic of rocky shores (Meager *et al.*, 2011), and beach invertebrates are restricted to sediments within a few centimeters of the surface (Schlacher *et al.*, 2008), resident fauna have few opportunities to take advantage of microclimates. This means that beach invertebrates are likely to respond directly to broadscale changes in environmental variables. Finally, while the adults of most beach invertebrates are highly motile, they generally lack the ability to move significant distances alongshore, and many also lack dispersive larval stages (Schlacher *et al.*, 2008). This facilitates the development of simple hypotheses of differential responses to climate change, including range shifts, *in situ* adaptation, and extirpation.

In this Opinion, we summarize theory from the broader climate-change literature to formulate specific expectations for how sandy-beach species might respond to climate change. For turtles, such expectations are based on predictive models (e.g., Saba *et al.*, 2012; Pike, 2013b), but for beach invertebrates, no explicit models exist, so we are necessarily speculative within the constraints of associated theory. We then use long-term case studies to assess the degree to which field observations conform to these expectations. Finally, we argue that beaches offer exciting opportunities for ecological research in a changing world and ask the ecological research community to cross the metaphorical 'line in the sand' and accept the challenge of addressing the suite of emergent hypotheses that can be tested more easily on beaches than in most other ecological systems.

Building expectations for ecological responses to climate change

Population size or growth rate in the face of climate change is an integrated outcome of complex interactions among fundamental biological, ecological, and evolutionary traits and processes that together comprise adaptive capacity (Dawson *et al.*, 2011 – Box 1). These include (O'Connor *et al.*, 2012): (i) plasticity, the ability of individual organisms to accommodate a changing environment by altering their behavior or physiology; (ii) dispersal, the ability of individuals (or generations of individuals) within populations to colonize new locations (or to recolonize previously abandoned habitats), thereby minimizing the requirement for plasticity; and (iii) evolution (adaptation), changes in gene frequency within a population as individuals successful under certain environmental conditions outreproduce other members of the population.

Short-term studies of such phenomena contribute to our understanding of the variety and magnitude of effects that may be anticipated in an ecological system when the climate changes, as well as their underlying mechanisms (Hoegh-Guldberg & Bruno, 2010; Brown *et al.*, 2011; Parmesan *et al.*, 2013). This type of research tells us, however, little about how ecological communities have responded to recent climate change in the real world (Parmesan *et al.*, 2013). Such knowledge can be gleaned only from careful analysis of matched long-term observations of both ecological and environmental data (Brown *et al.*, 2011; Poloczanska *et al.*, 2013).

Extinction is the ultimate expression of vulnerability (Box 1) to climate change, so should be the most obvious ecological response. Yet few studies have identified proximate causes of putative climate-related extinctions (Cahill *et al.*, 2012). Instead, the scientific community rather observes the more subtle consequences of climate change, primarily shifts in species' ranges and phenologies (e.g., Parmesan & Yohe, 2003; Poloczanska *et al.*, 2013). Poloczanska *et al.* (2013) synthesized reported responses to climate change in the ocean and found that: (i) species' ranges expand poleward as climate warms, with leading range edges (Box 1) moving faster than the trailing range edges (Box 1); (ii) highly dispersive organisms are most responsive in terms of range shifts; (iii) marine organisms that are not functionally restricted to the ocean surface may seek thermal refuge at depth, although few studies have detected (Box 1) a depth-related response for marine biota; (iv) in terms of phenology, spring events, such as plankton blooms have shifted to occur earlier in the year, while fall events occur later; and (v) the largest shifts in phenology are by short-lived taxa.

Challenging expected responses to climate change with data from beaches

Although the literature contains explicit expectations for ecological responses to climate change (O'Connor *et al.*, 2012), as well as tests of some of these in the marine realm (Poloczanska *et al.*, 2013), these topics have yet to be addressed on sandy beaches. Some beach systems are nevertheless rich in data. Here, we synthesize long observational data series for beach-invertebrate communities of South America and for sea turtle nesting biology to explore the degree to which observations from beaches conform to expectations under climate change.

Case study 1: beach invertebrates of South America

Beach invertebrates are generally well studied, but they have not frequently been the subjects of climate-change research. Here, we examine observational studies of South American beach invertebrates to assess whether recent spatial and temporal trends, as synthesized at the continental scale, are consistent with expected responses to climate change.

The physical and ecological context

Mirroring global trends, an increase in sea surface temperature anomalies (SSTAs) has been observed over the past three decades along the Atlantic coast of South America; by contrast, the Pacific coast has cooled (Chavez *et al.*, 2011; Lima & Wethey, 2012). Despite cooling in the Pacific, a series of El Niño southern oscillation (ENSO) events caused short periods of particularly high sea-surface temperatures (Riascos *et al.*, 2011).

Suspension feeders dominate the biomass of invertebrate assemblages on South American beaches. On Pacific shores, this guild comprises the surf clam *Mesodesma donacium*, the wedge clam *Donax obesulus*, and the mole crab *Emerita analoga*. On beaches bordering the Atlantic, the yellow clam *Mesodesma mactroides*, the wedge clam *Donax hanleyanus*, and the mole crab *Emerita brasiliensis* fill equivalent niches. Because the genus *Mesodesma* is of Antarctic origin, these clams are distributed mainly in colder waters, and their northern range limit is constrained by warm-temperate waters. By contrast, the genera *Donax* and *Emerita* have stronger biogeographic affinities to the tropics, with their distributions extending equatorward into the Americas. All six species produce planktonic larvae. Only *Mesodesma* is commercially harvested.

> Hypothesis 1: Populations at their trailing range edges are susceptible to mass mortalities during periods of unusually high temperatures.

Both species of *Mesodesma* suffered mass mortalities caused by extreme SSTAs, particularly at the trailing edge of their ranges (Riascos *et al.*, 2011; Ortega *et al.*, 2012). In the Pacific, strong pulses of warming associated with the 1982/1983 and 1997/1998 ENSO events caused mass mortalities of *M. donacium* across the northern portion of its range, resulting in a significant poleward contraction of this species' trailing range edge (Riascos *et al.*, 2011). In the Atlantic, mass mortalities of *M. mactroides* occurred first in 1993 in southern Brazil and then followed isotherms southwards, reaching Argentina by 2002 (Fiori *et al.*, 2004). Mortalities were observed mostly in late spring and early summer, when high temperatures increased the susceptibility of these cool water clams to disease (Fiori *et al.*, 2004). None of the affected populations has yet recovered to premass-mortality levels (Herrmann *et al.*, 2011; Riascos *et al.*, 2011), with greatest mortality effects observed, as expected under climate change, at the trailing range edge.

> Hypothesis 2: Warming increases productivity at the leading range edge.

In contrast to the mortalities at their warm-water edge in the Pacific, commercial landings of *M. donacium* in colder waters of southern Chile were positively correlated with increased SSTAs associated with ENSO events. This suggests that short-term warming at the leading range edge enhanced productivity (Ortega *et al.*, 2012). Although this is a response to climate variability, rather than to climate change, it provides tentative evidence of the sensitivity (Box 1) of this species to aspects of climate change.

> Hypothesis 3: Individuals of populations at their trailing range edge are increasingly unable to acclimate to changing temperatures.

A 29-year population study of *M. mactroides* on Uruguayan beaches showed that several demographic and biological traits changed in ways consistent with expectations under climate change: (i) lower population densities; (ii) lower rates of fecundity, recruitment and adult survival; and (iii) increased signs of physiological stress, including incidences of morphological abnormalities and loads of epibionts and parasites [Ortega *et al.* (2012) and references therein].

> Hypothesis 4: Ecological communities exhibit 'tropicalization'(Box 1).

On both the Pacific and Atlantic shores, the composition of the suspension-feeder assemblages changed dramatically over recent decades, with species having stronger biogeographic affinities to the tropics increasing in prominence over those of cool water provenance. Specifically, clams of the genus *Mesodesma* that had dominated the biomass were virtually extirpated at their northern range edges, being at least partially replaced by the clam genus *Donax* and the mole crab *Emerita*, among other species (Arntz *et al.*, 1987; Defeo, 2003). While this seems to have been a response to climate change on the Atlantic coast, corresponding ecological changes on the Pacific coast were probably caused by severe ENSO events (i.e. climate variability).

> Hypothesis 5: Leading range edges expand rapidly with warming.

Ghost crabs of the genus *Ocypode* are widely distributed on tropical and temperate sandy shores. On beaches of the Western Atlantic, *Ocypode quadrata* is common, extending from near Rhode Island, USA, in the north to Brazil in the south. Historically, the southern range edge for adults of this species rarely extended to Uruguay, despite regular settlement of megalopae during summer, and occasional persistence of juvenile crabs into the fall (Defeo, personal observation). Cooler temperatures during the Uruguayan winter are believed to have cropped these southward range expansions back into Brazilian territory. Observations over the past decade (Martínez & Defeo, personal observation) hint, however, that young recruits might occur increasingly frequently on southern beaches and might maintain populations there for longer, tentatively suggesting a poleward shift in the leading range edge of the population.

Case study 2: beach-nesting activities of sea turtles

Sea turtles are among the best studied of vertebrates that depend on sandy beaches, being the subjects of several long time series of observational data. Theoretically, therefore, turtle nesting data from sandy beaches should be useful in assessing consistency with expectations under climate change.

The physical and ecological context

Sea turtles forage over much of the global ocean, but aggregate in coastal areas to mate, before females emerge onto tropical and subtropical sandy beaches, where they dig nests and lay their eggs (Poloczanska *et al.*, 2009). Turtles are therefore exposed to the full range of climate-change stressors in marine and coastal environments. Of interest here, however, are only expectations regarding climate-change effects on turtles while they are on beaches: that is, while adult females are nesting, while eggs are incubating, and while hatchlings are emerging and traversing the beach back to the ocean. Here, we assess whether long-term observational time series of turtle-nesting activity conform to expectations derived from several recent reviews of putative climate-change impacts on turtles (Hawkes *et al.*, 2009; Poloczanska *et al.*, 2009; Witt *et al.*, 2010).

> Hypothesis 1: Nesting ranges will expand poleward at their leading edge.

Turtles nest in a broad thermal band, roughly delimited by isotherms of annual mean air temperature: 20 °C in the north, and 25 °C in the south (Poloczanska *et al.*, 2009). As these isotherms shift poleward with global warming, nesting range is predicted to follow. Contradicting this trend is the regional nest-site fidelity exhibited by turtles (Hawkes *et al.*, 2009). Although many studies suggest poleward expansion of nesting range, explicit tests of this hypothesis, using long-term data, are rare. An exception is a 21-year investigation (1986–2006) that tentatively suggests a northward shift of loggerhead nesting activity over a 20-km study area in Florida, USA (Reece *et al.*, 2013). However, even in this case, links to climate change are tenuous, given the small spatial scale of the study and the lack of correlation between apparent range expansion and temperature.

> Hypothesis 2: Warming at rookeries will drive phenological responses, including earlier breeding and/or extended breeding seasons.

Some populations of turtles have been observed to nest earlier with warmer coastal air and/or sea temperatures (Mazaris *et al.*, 2008; Pike, 2009a), and this effect is strongest at high latitudes, close to their leading nesting-range edges (Mazaris *et al.*, 2012). It is also possible that the duration of the nesting season might increase when temperatures are warmer, but evidence is equivocal (Mazaris *et al.*, 2008, 2012). However, these phenological effects may not be related to processes on the beach: there are strong correlations between trends in air and sea temperatures over various spatial scales, and turtle nesting-activity patterns may have more to do with processes on their feeding grounds than with those at rookeries (Poloczanska *et al.*, 2009). Moreover, many studies detecting phenological change have failed to document corresponding upward trends in local air or water temperatures at rookeries (e.g., Weishampel *et al.*, 2004), indicating that any observed variation in nesting phenology is related either to climate variability rather than climate change, or to processes operating beyond the rookeries. Indeed, nesting trends are well predicted by large-scale metrics of ocean climate variability, including cycles such as the Pacific Decadal Oscillation and the Atlantic Multi-decadal Oscillation (Van Houtan & Halley, 2011; del Monte-Luna *et al.*, 2012), suggesting that a portion of the response may be attributed to trophic linkages, rather than to direct environmental forcing.

> Hypothesis 3: Warming will affect turtle demographics through changes in sex ratios, incubation periods, hatchling size and survival rates.

Short-term experimental and observational studies have shown that thermal conditions in turtle nests have a significant effect on the duration of incubation and on the survival rate of embryos, but most importantly on the sex ratio of hatchlings. Sex determination in turtles is thermal, with only females being produced when eggs are exposed to temperatures above a threshold at a critical time during incubation (Poloczanska *et al.*, 2009). There is much concern that warming may lead to female-biased or female-only populations. However, no long-term time series of direct observations of sex ratio are available with which to test this hypothesis (Witt *et al.*, 2010). This is justifiable because turtle hatchlings lack sexual dimorphism, and destructive histological studies are inappropriate due to the conservation status of most turtle populations (Hawkes *et al.*, 2009). Militating against this hypothesis is the likelihood that extant turtle species arose 50–100 million years ago (Poloczanska *et al.*, 2009) and have not been driven to extinction by previous global temperature cycles associated with glaciation processes. This may be because behavioral plasticity allows turtles to select nest characteristics delivering appropriate incubation temperatures (Hawkes *et al.*, 2009). The consequences of other putative effects of climate change on demographic parameters also remain untested for lack of published long observational time series.

> Hypothesis 4: The combined effects of sea-level rise, increased storminess and coastal squeeze will reduce turtle nesting habitat.

Turtles lay their eggs in the sand between the high-water mark and the base of the dunes; thus, any process that exacerbates erosion either in the short- (storms) or longer (sea-level rise) term will increase the chance that nests will be exhumed or washed away. Again, although shorter studies demonstrate a link between the rate of nest flooding and cyclone intensity (Van Houtan & Bass, 2007), long observational time series to test this rather straightforward expectation are lacking. Moreover, projections for sea-level rise are uncertain (Nicholls & Cazenave, 2010), and those for changes in mean significant wave height during summer (the turtles' incubation period) suggest a decrease rather than an increase for many rookeries (Hemer *et al.*, 2013). Of concern is that the effects of sea-level rise and storms will be greatest on nesting beaches where the dune edge cannot adapt to changing sea conditions by moving landwards because of coastal defenses that block beach migration (Pike, 2009b).

What climate-change ecology can learn from sandy-beach ecosystems

Our case studies highlight significant climate sensitivity in both invertebrate and vertebrate species typical of ocean beaches, providing strong indications for substantial vulnerability of sandy-beach biota to the effects of future climate change. More importantly, beach invertebrates, which have seldom been included in management, conservation or monitoring programs, for the first time yielded tentative evidence that they have been responding to recent temperature change in ways consistent with expectations under climate change. Our synthesis shows that temperature-related responses among South American beach invertebrates were initiated by mass mortalities of clams along both the Pacific and Atlantic coasts. Mirroring episodes of coral bleaching, mass mortalities on the Pacific coast were triggered by strong ENSO events, suggesting that the driver was climate variability rather than climate change. Nevertheless, mass mortalities on the Atlantic coast were more suggestive of climate-change impacts, with mortalities following isotherms southward over the period of a decade. In both instances, mass mortalities were followed by parallel sequences of ecological responses

Table 1 Emergent hypotheses for climate-change impacts on sandy beach biota and the ecosystems of ocean beaches

Theme	General expectation under climate change	Contextual information pertinent to beach ecosystems (‘unique characteristics’)	Hypotheses applicable to beach ecosystems	Possible tests
1. Sensitivity to climate change	Changed climate exposes organisms to significant alterations in their physical environment, which elicits measurable compensatory responses (Hoegh-Guldberg & Bruno, 2010; O’Connor *et al.*, 2012; Poloczanska *et al.*, 2013).	Marine species in general are more likely to be distributed according to their thermal limits than are terrestrial species (Sunday *et al.*, 2012). Beach-invertebrate species may be more sensitive still, because their assemblages are structured primarily by individuals reacting to physical and chemical variables (Schlacher & Thompson, 2013). This composite model of community organisation posits that beach species’ responses to climate change will be direct and immediate.	Beach invertebrates react readily and strongly to changes in habitat conditions, including those caused by climate change.	Assess the strength and shape of climate-change response curves in sandy-beach species.
2. Species extirpations	Climate change has been linked to widespread and substantial changes in the distribution, extent, and quality of habitats in several biomes, which increases the risk of extirpation or extinction (Barnosky *et al.*, 2012; Harnik *et al.*, 2012).	Populations of sandy-beach species prone to large variations in size following environmental change due to: (i) temporal instability of the beach habitat itself in response to physical forcing (e.g., sediment supply, storm-related erosion or accretion); (ii) the linear and narrow nature of the habitat, which is constrained by physical or anthropogenic limits at its landward boundary; and (iii) the absence of spatial refugia or compensatory habitats for obligate beach specialists. The general lack of competitive interactions in beach systems may, however, mean that extirpations are more likely than extinctions, because strong and direct biotic interactions have been implicated in all putative climate-related extinctions recently observed (Cahill *et al.*, 2012).	Beach species exhibit a high probability of local and regional extirpations as a result of climate change, but experience few extinctions.	Include obligate beach species in comparative analyses of species extirpation rates (or extreme range constrictions) across ecological systems, using historical vs. contemporary data.
3. Community structure	The composition and structure of ecological assemblages are undergoing unprecedented changes, including range extensions and the frequency of ‘invasive’ species records in many systems (Sorte *et al.*, 2010).	Sandy-beach assemblages are composed of a ‘core’ of unique beach species found in no other habitat, complemented by species with primarily terrestrial or marine affinities that use beaches as nesting or feeding sites. This tripartite provenance of species, together with the extreme ratio of boundary to core habitat should make beaches extremely vulnerable to the effects of invasive species. Moreover, because leading range edges might move faster than trailing range edges (Poloczanska *et al.*, 2013), and because beaches are often aligned orthogonal to ocean isotherms (especially in the Southern Hemisphere), species’ ranges will expand in real terms.	Beach assemblages undergo exceptional rates of compositional change in response to climate change.	Determine the temporal rates of assemblage change (species turnover) for beaches.
4. Food-web structure	Climate change effects primary productivity, and therefore the architecture of food webs, especially in terms of size	Intertidal beach food webs are underpinned almost exclusively by imports of carbon from the adjacent ocean in such forms as particulate organic matter, surf-zone diatoms, macrophyte wrack, and animal carcasses	Food webs of sandy beaches are sensitive to climate-driven changes in marine	Determine responses of whole beach food webs to changes in the quality, quantity, and

Table 1 (continued)

Theme	General expectation under climate change	Contextual information pertinent to beach ecosystems ('unique characteristics')	Hypotheses applicable to beach ecosystems	Possible tests
	spectra, and the biological processing of carbon (Chavez *et al.*, 2011; Hollowed *et al.*, 2013).	(Schlacher & Hartwig, 2013; Schlacher & Thompson, 2013; Schlacher *et al.*, 2013). Thus beach food webs are closely linked to – and functionally dependant on – processes in the abutting ocean (Bergamino *et al.*, 2011).	productivity and to the transport processes that link beach systems with the ocean.	import patterns of marine carbon.
5. Geochemistry	Widespread and substantial changes to ocean chemistry, especially declining pH and carbonate saturation, have been attributed to climate change at global scale (IPCC, 2007), with significant consequences for marine biota (Wittmann & Pörtner, 2013).	The high-energy, turbulent surf-zones of sandy beach systems are characterised by vigorous ocean-atmosphere mixing. This creates a water chemistry saturated with CO_2. However, sandy beaches themselves comprise large deposits of sediment that can contain a substantial biogenic carbonate fraction. These carbonates potentially represent a sizable buffer system for the massive volumes of coastal water that continually flush through the physical matrix of the beach. Such buffering should counteract any effects of ocean acidification on beach species.	Communities of resident beach invertebrates are more resilient to changes in the carbonate chemistry of the ocean than are those of adjacent coastal and ocean systems.	Compare the carbonate chemistry of interstitial waters of sandy beaches to that in adjacent surf-zone and coastal waters. Compare the degree of calcium limitation (e.g., shell thinning) for beach organisms relative to those in other coastal habitats.

that closely match the theoretical expectations under climate change. Specifically, increasing representation of the same two warm-water genera resulted in tropicalization of filter-feeding guilds on the Pacific and Atlantic coasts.

Turtles, by contrast, are conservation icons, and are hence the focus of numerous research initiatives and monitoring programs. Paradoxically, despite their relatively high research and public profiles, and frequent assertions in the literature that they are vulnerable to climate change, especially from threats acting on nesting beaches (e.g., Pike, 2013a), there is little direct observational evidence that trends in turtle nesting activities on beaches may be attributed (Box 1) to climate change. This situation for beach biota echoes the broader marine ecological literature, where studies of relatively low-profile groups like plankton have yielded more robust evidence for climate-change impacts than those of coral reefs, for example, despite a strong mechanistic understanding of how reefs may respond to climate change (Richardson *et al.*, 2012).

This paradox provides insights for climate-change ecology. Detecting climate-change impacts requires the collection of long time series of observations that are pertinent to addressing hypotheses regarding such impacts (Brown *et al.*, 2011). This should be self-evident, but because long time series are required to detect climate-change responses, few of the marine data sets that are currently available for the task were originally designed with this goal in mind. The data we examined for invertebrates proved more useful in assessing consistency with expectations under climate change than did the data for turtles largely because they considered multiple ecological attributes of the community, rather than a limited number of attributes of a single taxon. The utility of invertebrate data might, arguably, contain a measure of serendipity, but it nevertheless stresses the fact that research on basic population and community attributes of taxa that are rarely in the limelight can produce valuable outcomes. The fact that the fingerprints of climate-change impacts on beach invertebrates emerged only from a broadscale synthesis further reinforces the importance of coordinated collaborative research programs, ideally at large geographic scales and in multiple systems.

Also obvious from our case studies is that although sea-level rise and coastal squeeze are considered the prime threats to sandy-beach ecosystems globally (Defeo *et al.*, 2009), most impacts so far detected are tentatively attributed to warming. This suggests a fertile area for future research (Table 1). Another area is ocean acidification, which has been identified as the pre-eminent research field in ecology and environmental sciences (King & Pendlebury, 2013) at least in part due to our relatively poor understanding of how physiological and chemical responses of individual organisms extrapolate to whole ecosystems (Wittmann & Pörtner, 2013).

Finally, while our case studies demonstrate that relatively elementary hypotheses regarding climate-change impacts can be tested on beaches, beach systems themselves possess characteristics that in combination allow more sophisticated hypotheses to be addressed (Table 1) in ways that may be difficult or even impossible in other systems. Among these attributes, the most important are as follows: (i) the restriction of beach biota to a narrow fringe of sand between terrestrial and marine systems, which makes them accessible and easy to study; (ii) the frequent alignment of beaches orthogonally to temperature isoclines, which means that there are often strong thermal gradients along the shoreline; and (iii) the relatively minor role played by competitive interactions in structuring invertebrate assemblages, which means that ecological change can often be interpreted primarily in terms of environmental change.

Here, we have taken the first steps in building a framework comprising a series of explicit hypotheses that generate expectations for how climate change may affect beach biota. These hypotheses have a dual purpose: (i) they usefully extend broader expectations of climate-change ecology to sandy beaches by explicitly incorporating the unique biophysical properties of these systems; and (ii) they are intended to stimulate discussion about, and research into, climate-change effects on sandy-beach ecosystems. We now ask ecologists to design research programs to address these hypotheses. We also invite the broader ecological research community to criticize, improve and expand on our hypotheses, and – in the process – to develop a deeper understanding of the effects of climate change on ecological systems in general.

Acknowledgements

Funding for this work was provided by the Australian Research Council's Collaborative Research Network. OD acknowledges support by The Pew Fellows Program in Marine Conservation.

References

Arntz WE, Brey T, Tarazona J, Robles A (1987) Changes in the structure of a shallow sandy-beach community in Peru during an El Niño event. *South African Journal of Marine Science*, **5**, 645–658.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Sillman BR (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, **81**, 169–193.

Barnosky AD, Matzke N, Tomiya S *et al.* (2012) Has the earth's sixth mass extinction already arrived? *Nature*, **470**, 51–57.

Bergamino L, Lercari D, Defeo O (2011) Food web structure of sandy beaches: temporal and spatial variation using stable isotope analysis. *Estuarine, Coastal and Shelf Science*, **91**, 536–543.

Brown AC, McLachlan A (2002) Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. *Environmental Conservation*, **29**, 62–77.

Brown CJ, Schoeman DS, Sydeman WJ *et al.* (2011) Quantitative approaches in climate change ecology. *Global Change Biology*, **17**, 3697–3713.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC *et al.* (2012) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20121890.

Chavez FP, Messié M, Pennington JT (2011) Marine primary production in relation to climate variability and change. *Annual Review of Marine Science*, **3**, 227–260.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, **10**, 235–251.

Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. *Nature*, **497**, 365–368.

Coupland GT, Duarte CM, Walker DI (2007) High metabolic rates in beach cast communities. *Ecosystems*, **10**, 1341–1350.

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.

Defeo O (2003) Marine invertebrate fisheries in sandy beaches: an overview. *Journal of Coastal Research*, **35**, 56–65.

Defeo O, McLachlan A (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Marine Ecology Progress Series*, **295**, 1–20.

Defeo O, McLachlan A, Schoeman DS *et al.* (2009) Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science*, **81**, 1–12.

Dugan JE, Defeo O, Jaramillo E *et al.* (2010) Give beach ecosystems their day in the sun. *Science*, **329**, 1146.

Fiori S, Vidal-Martinez VM, Sima-Alvarez R, Rodriguez-Canul R, Aguirre-Macedo ML, Defeo O (2004) Field and laboratory observations of the mass mortality of the yellow clam, *Mesodesma mactroides*, in South America: the case of Isla del Jabalí, Argentina. *Journal of Sea Research*, **23**, 451–456.

Harnik PG, Lotze HK, Anderson SC *et al.* (2012) Extinctions in ancient and modern seas. *Trends in Ecology & Evolution*, **27**, 608–617.

Harris L, Nel R, Holness S, Sink K, Schoeman D (2013) Setting conservation targets for sandy beach ecosystems. *Estuarine, Coastal and Shelf Science*. doi: 10.1016/j.ecss.2013.05.016.

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. *Endangered Species Research*, **7**, 137–154.

Hemer MA, Fan Y, Mori N, Semedo A, Wang XL (2013) Projected changes in wave climate from a multi-model ensemble. *Nature Climate Change*, **3**, 1–6.

Herrmann M, Alfaya JEF, Lepore ML, Penchaszadeh PE, Arntz WE (2011) Population structure, growth and production of the yellow clam *Mesodesma mactroides* (Bivalvia: mesodesmatidae) from a high-energy, temperate beach in northern Argentina. *Helgoland Marine Research*, **65**, 285–297.

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science*, **328**, 1523–1528.

Hollowed AB, Barange M, Beamish RJ *et al.* (2013) Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, **70**, 1023–1037.

IPCC (2007) *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Quin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, HL M), Cambridge University Press, Cambridge, UK.

Jones AR, Gladstone W, Hacking NJ (2007) Australian sandy-beach ecosystems and climate change: ecology and management. *Australian Zoologist*, **34**, 190–202.

King C, Pendlebury DA (2013) Research Fronts 2013: 100 Top-Ranked Specialties in the Sciences and Social Sciences. Thompson Reuters (http://sciencewatch.com/sites/sw/files/sw-article/media/research-fronts-2013.pdf) (accessed 6 January 2014).

Lima FP, Wethey DS (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications*, **3**, 704.

Mazaris AD, Kallimanis AS, Sgardelis SP, Pantis JD (2008) Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology*, **367**, 219–226.

Mazaris AD, Kallimanis AS, Pantis JD, Hays GC (2012) Phenological response of sea turtles to environmental variation across a species' northern range. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122397–20122397.

Meager JJ, Schlacher TA, Green M (2011) Topographic complexity and landscape −temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Marine Ecology Progress Series*, **428**, 1–12.

del Monte-Luna P, Guzmán-Hernández V, Cuevas EA, Arreguín-Sánchez F, Lluch-Belda D (2012) Effect of North Atlantic climate variability on hawksbill turtles in the Southern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, **412**, 103–109.

Nicholls RJ, Cazenave A (2010) Sea-level rise and its impact on coastal zones. *Science*, **328**, 1517–1520.

O'Connor MI, Selig ER, Pinsky ML (2012) Toward a conceptual synthesis for climate change responses. *Global Ecology and Biogeography*, **21**, 693–703.

Ortega L, Castilla JC, Espino M, Yamashiro C, Defeo O (2012) Effects of fishing, market price, and climate on two South American clam species. *Marine Ecology Progress Series*, **469**, 71–85.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan C, Burrows MT, Duarte CM, Poloczanska ES, Richardson AJ, Schoeman DS, Singer MC (2013) Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, **16**, 58–71.

Pike DA (2009a) Do green turtles modify their nesting seasons in response to environmental temperatures? *Chelonian Conservation and Biology*, **8**, 43–47.

Pike DA (2009b) Natural beaches produce more hatchling marine turtles than developed beaches, despite regional differences in hatching success. *Biology Letters*, **5**, 268–269.

Pike DA (2013a) Climate influences the global distribution of sea turtle nesting. *Global Ecology and Biogeography*, **22**, 555–566.

Pike DA (2013b) Forecasting range expansion into ecological traps: climate-mediated shifts in sea turtle nesting beaches and human development. *Global Change Biology*, **19**, 3082–3092.

Poloczanska ES, Limpus CJ, Hays GC (2009) Vulnerability of marine turtles to climate change. *Advances in Marine Biology*, **56**, 151–211.

Poloczanska ES, Brown CJ, Sydeman WJ *et al*. (2013) Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 1–7.

Reece JS, Passeri D, Ehrhart L *et al*. (2013) Sea level rise, land use, and climate change influence the distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida). *Marine Ecology Progress Series*, **493**, 259–274.

Riascos JM, Heilmayer O, Oliva ME, Laudien J (2011) Environmental stress and parasitism as drivers of population dynamics of *Mesodesma donacium* at its northern biogeographic range. *ICES Journal of Marine Science*, **68**, 823–833.

Richardson AJ, Poloczanska ES (2008) Ocean science: under-resourced, under threat. *Science*, **320**, 1294–1295.

Richardson AJ, Brown CJ, Brander K *et al*. (2012) Climate change and marine life. *Biology Letters*, **8**, 907–909.

Saba VS, Stock CA, Spotila JR, Paladino FV, Tomillo PS (2012) Projected response of an endangered marine turtle population to climate change. *Nature Climate Change*, **2**, 814–820.

Schlacher TA, Hartwig J (2013) Bottom-up control in the benthos of ocean-exposed sandy beaches? *Austral Ecology*, **38**, 177–189.

Schlacher TA, Thompson L (2013) Environmental control of community organisation on ocean-exposed sandy beaches. *Marine and Freshwater Research*, **64**, 119–129.

Schlacher TA, Schoeman DS, Dugan J, Lastra M, Jones A, Scapini F, McLachlan A (2008) Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. *Marine Ecology*, **29**, 70–90.

Schlacher TA, Strydom S, Connolly RM, Schoeman D (2013) Donor-control of scavenging food webs at the land-ocean interface. *PLoS ONE*, **8**, e68221.

Sorte CJB, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. *Ecology*, **91**, 2198–2204.

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Van Houtan KS, Bass OL (2007) Stormy oceans are associated with declines in sea turtle hatching. *Current Biology*, **17**, R590–R591.

Van Houtan KS, Halley JM (2011) Long-term climate forcing in loggerhead sea turtle nesting. *PLoS ONE*, **6**, e19043.

Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology*, **10**, 1424–1427.

Wernberg T, Smale DA, Tuya F *et al*. (2012) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3**, 78–82.

Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology*, **213**, 901–911.

Wittmann AC, Pörtner H-O (2013) Sensitivities of extant animal taxa to ocean acidification. *Nature Climate Change*, **3**, 1–7.